EFFECTS OF LATE ROTATION FERTILIZATION AND NUTRIENT CYCLING ON PINE PLANTATION PRODUCTIVITY IN THE MPUMALANGA PROVINCE OF SOUTH AFRICA

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DECLARATION

I declare that this thesis, submitted for the degree of Doctor of Philosophy of Science at the University of the Witwatersrand, Johannesburg, contains the results of my own investigation. It has not been submitted for any degree or examination at any other University.

Anthony Ifechukwude Odiwe

14th day of October 2009

ABSTRACT

The southern African forestry and forest products industry is an important part of the southern African economy and there is the need to increase and improve plantation productivity to meet both domestic and external needs. Fertilizer applications have been widely used to increase productivity and there has been increasing interest in late rotation fertilization applications. This study evaluated the impact of late rotation fertilization on soil properties and biologically based processes in *Pinus patula* and *Pinus elliottii* species in order to increase the understanding of nutrient cycling and impact on tree growth. The 3-PG and Nitrogen (N) mineralization model were used to improve the predictive understanding of the system.

The late rotation fertilization trial established in 11-year-old *P. patula* plantations in 2001 and a new late rotation fertilization trial in a 17-year-old *P. elliottii* plantation established in 2006 in the Mpumalanga province, South Africa were sampled. Six existing fertilizer treatments in four *P. patula* sites, with two, replicates were used, whereas four treatments with four replicates were sampled at the *P. elliottii* site. The treatments in *P. patula* were 100 kg ha^{-1} N fertilizer applied in various combinations of limestone ammonium nitrate (LAN) and urea in 2001 and 2003; while in *P. elliottii*, 200 kg ha^{-1} N as LAN and 100 kg ha^{-1} phosphorus (P) as Super Phosphate was applied in 2006. Soil properties were analyzed in 2006 and 2007; litter fall, litter decomposition, litter accumulation and N mineralization rates were determined from May 2006 to May 2007; foliar sampling and litter accumulation and nutrient concentrations were also determined. The outputs of the 3-PG model, quadratic mean diameter at breast height, basal area and stand volume, were compared with the field measurements.

Late rotation fertilization generally had no significant effects on the measured tree growth parameters, soil properties and other biological process for either of the two species. These findings indicate that the sites are not nutrient limited. Tree growth, litter fall, litter accumulation and nitrogen mineralization rates differed significantly across the *P. patula* sites. Large amounts of N and P were found in the forest floor litter with *P. patula* having

293-614 kg ha^{-1} and 14-36 kg P ha^{-1} and *P. elliottii* 94-150 kg N ha^{-1} and 5-11 kg P ha^{-1}. High foliar Calcium:Nitrogen (17-42) and Potassium:Nitrogen (29-48) ratios can be used as indicators of nutrient availability at the sites and possibly as indicators of response to fertilization. Climatic factors, especially the limited rainfall amount and its variable distribution, played a confounding role in understanding the response to the late rotation fertilizer applications.

Tree growth parameters were well predicted with the 3-PG model, high correlations for quadratic mean DBH (r = 0.99), stand volume (r = 0.95-0.99) and basal area (r = 0.080-0.98) were found for all of the *P. patula* sites, except at the Elandshoogte site, where basal area was poorly predicted. The tree growth parameters at the *P. elliottii* site were well predicted, with 2-10% deviation, for 2006 and 2007. Deviations in the longer term (2017) were much larger (23%).

The systems based approach to nutrient cycling and the two models used in this study were valuable in understanding the response to late rotation fertilization. These approaches pointed to key processes e.g. forest floor litter accumulation, nutrient concentrations and decomposition rates; foliar nutrient ratios, which need careful monitoring and management to facilitate high nutrient turnover. Late rotation fertilization should only be used as a management practice in areas with soil nutrient limitation and where rainfall is high with a reliable distribution. Sustainable plantation productivity continues to be a challenge especially in South Africa and will become worse as the global financial crisis deepens and the climate variability increases.

DEDICATION

To my loving wife, Ajibola; my kids, Ifeayin and Emeka for
their understanding, perseverance and sacrifices
for a better tomorrow

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LIST OF ABBREVIATIONS

Symbol	Description
Al	Aluminium
BD	Bulk density
Ca	Calcium
CBD	Citrate-bicarbonate dithionite
cmol	Centimole
D	Depth
DBH	Diameter at breast height (1.3 m above soil surface)
df	Degree of freedom
ECEC	Effective cation exchange capacity
Fe	Iron
FH	Fermentation-Humus
FR	Fertility rating
GLM	General linear model
ICFR	Institute for Commercial Forestry Research
K	Potassium
KCl	Potassium chloride
LSD	Least significant difference
M	Molar
MAP	Mean annual precipitation
MAT	Mean annual temperature
Mg	Magnesium
Mn	Manganese
N	Nitrogen
P	Phosphorus
P_i	Inorganic phosphorus
P_o	Organic phosphorus
Sappi	South Africa Pulp and Paper Industry

VPD	Vapour pressure deficit
3-PG	**P**hysiological **P**rinciples in **P**redicting **G**rowth **M**odel

CHAPTER 1

INTRODUCTION

1.1 The Southern African Forestry Industry

The southern African (South Africa and Swaziland) forestry and forest products industry is an important part of the southern African economy and is one of the most globalised industrial sectors (Pallet and Sale, 2004). The forest industry makes a significant contribution to the national economy; benefits gained from this sector include employment, contribution to the national gross domestic product, provision of household livelihoods, especially in rural areas, and acquisition of foreign exchange due to export earnings (DWAF, 1997 cited by Campion, 2005). Industrial forestry in southern Africa faces several challenges to remain viable in the long term. Three of the important challenges that are shared with other global enterprises include: (1) achievement and/or maintenance of high levels of production and quality to remain economically competitive; (2) timber production on a basis that is demonstrably sustainable from an ecological perspective; and (3) socio-political equity and stability (du Toit and Scholes, 2002).

The ability to predict tree growth and the impact of management practices are dependent upon the depth of knowledge we have of ecosystem processes controlling forest productivity. Growth modelling plays a central role in forest management planning in the prediction of future yields, standing volumes, yield optimization and sustainable utilization of wood resources in forest plantations (Institute for Commercial Forestry Research (ICFR) Annual Research Review, 2004). Therefore, there is the need to better the understanding of the cause and effect of yields obtained in plantations.

Forestry in southern Africa is conducted in areas where the soils are clayey, highly weathered, leached (dystrophic), very acidic, and weakly structured. Forestry occurs in the high rainfall areas along the eastern seaboard: in the provinces of Kwazulu-Natal, Mpumalanga and Limpopo in South Africa and in Swaziland. Temperature and rainfall in the areas where the tree species are planted are conducive to support plant growth, though the rainfall is highly variable. The plantations are located in areas where the occurrence of frost and fires is dominant. South Africa generally is a country of low mean rainfall. Most of the natural vegetation is non-woody grassland. The indigenous vegetation is characterized by natural forests consisting of a narrow broken belt of closed canopy forest along the southern and eastern seaboard and open canopy savanna woodlands in the north and eastern interior of the country (Owen and van der Zel, 2000).

The indigenous landscape over the years has been transformed from non-woody grasslands, especially those at high altitudes, to plantations of exotic species like *Pinus*, *Eucalyptus* and in some cases *Acacia* species. This transformation took place from 1875 (Owen and van der Zel, 2000) and plantations cover approximately 12,661.96 km^2 (Godsmark, 2008). The growing human population and improved living standards require more land for food, fiber, timber and fuel wood. Unfortunately, land availability is a challenge in the forestry industry which is why there is a need for proper land use planning, this is to ensure that the natural resources of the soils can be sustained to ultimately improve site productivity and increase yield. Fertilizer application has been one of the major ways of improving and sustaining site productivity and increases in yield, evidence of responses to fertilization by plantation species and improvement of yield has been recorded in southern African and the rest of the world (Carlson *et al*., 2000; Fisher and Garbett, 1980; Haines and Haines, 1979; Pritchett and Smith, 1972; Turner *et al*., 1996; Xu *et al*., 1995). Rotation length is defined as the average number of years that individual tree species or genera at a regional, country level, globally level. The rotation length is influenced by silvicultural, marketing and financial considerations, with the length being shorter in southern Africa than in many other countries and dictated by whether the timber is destined for pulp or sawtimber (Marsh, 1978).

1.2 Studies Conducted Globally and in Southern Africa on Plantation Tree Growth and Nutrient Cycling in Response to Fertilization

Fertilizer application is an intensive management practice that has received tremendous attention in research programmes in southern Africa and in the rest of the world. The successful use of fertilizer to improve and maintain productivity in pine plantations abounds in southern Africa (Carlson *et al*., 2000; Donald *et al*., 1987; Morris, 1986, 2003; Noble and Ramsden, 1992) and in the rest of the world: in New Zealand (Hunter and Smith, 1996); in Australia (Turner *et al*., 1996; Xu *et al*., 1995); and in the south eastern United States of America (U.S.A.) (Fisher and Garbett, 1980; Haines and Haines, 1979; Pritchett and Smith, 1972). Site (parent material), stand age (crop development) and climate (temperature and rainfall) have been reported to play major roles in influencing tree growth responses to fertilizer application. Thinning at the time of fertilizer application, season and stand age at the time of fertilizer application have also been found to affect tree growth responses positively (Allen, 1987; Carlson, 2000; Carlson and Soko, 2000; Carlyle, 1995a; Donald, 1987; Morris, 1992a, b, 2003; Sheriff, 1996; Turner *et al*., 1992). Results have shown positive responses to nitrogen (N) and phosphorus (P) fertilizer applied individually or in combination (Carlson and Soko, 2000; Fisher and Garbett, 1980; Turner *et al*., 1992; Xu *et al*., 1995).

Plantation establishment in southern African forestry is sometimes associated with fertilizer application at planting. Fertilizers are not usually applied during the rotation. However, there has been increasing interest in post-establishment fertilization in pine plantations especially at mid rotation (Carlson *et al*., 2000; Donald *et al*., 1987; Morris, 1986, 1993b and 2003). Carlson *et al*., (2000) have listed some of the advantages of post-establishment fertilizer application which include: a shorter compound interest period; improved wood quality compared to fertilizer applications made at planting; easier and more cost effective application; less root scorch and subsequent mortality as is often the case when fertilizer is applied to seedlings. Application of fertilizer has also been reported to increase the rate of litter fall which has intensified the problem of litter accumulation and hence nutrient availability in southern African plantations (Dames *et al*., 1998; Morris, 1995; Schutz, 1990; Wienand and Stock, 1995). Studies at Usutu, in Swaziland, have shown that as a result of forest floor accumulation a substantial amount of nutrients, especially N, were immobilized in the forest floor litter. However, increased timber volumes and higher economic returns were reported in response to N fertilizer applied to *Pinus patula* (Schlecht. et. Cham.) at 12 and 14 years after planting (Morris, 1994 cited by Crous, 2007).

The Institute for Commercial Forestry Research in South Africa has identified and shown interest in late rotation fertilization. Late rotation fertilization is defined in this study as taking place in the last third of the rotation age. There is evidence in the South African literature that productivity has declined with rotation age and the number of rotations. It is suggested that the decline can be offset by additional application of fertilizer towards the end of the rotation. There are on-going trials in South Africa to address fertilization effects, but only one such trial is a late N fertilization study established in Mpumalanga in 2001 by the forestry industry. This trial is located across four different sites, at high altitude, in a *P. patula* compartment in the Mpumalanga region. The trial aims to measure tree volume responses to different N fertilizer treatments. Results from that on-going trial have been variable, with the tree growth data being difficult to explain in response to the fertilizer applications. There is no clear trend in the pattern of tree growth responses in relation to the fertilizer treatments across the sites even though all occur on the same geology (shale).

1.3 Rationale and Experimental Approach for this PhD Study

The *P. patula* trial established in 2001 was a classical forestry trial in which only a limited number of measurements, focused on timber volume, were taken. Understanding the factors controlling plant productivity is not simple. Tree growth is the net and integrated product of a large number of biotic and abiotic processes. Detailed measurements of a very limited subset of these processes will be unlikely to lead to an in-depth understanding of the controlling factors. A systems approach, in which, nutrient cycling integrated with tree growth and climatic conditions is needed in order to fully understand the drivers. The variability in the data collected from the late rotation trail, along with limited initial soil property and tree measurements prompted the initiation of this PhD study. There was some hesitation shown by the forestry industry to study only one species therefore, a new trial was established in 2006 with the assistance of the ICFR in Graskop, in the Mpumalanga province to establish the cause and effect of late rotation fertilizer application on the growth of *Pinus elliottii* (var. elliottii Englem).

This project focused on the measurements of biologically based processes using different N and P fertilizer treatments across the sites and tree growth parameters (stem density, tree height, stand volume and basal area). This project had three components: firstly, the existing *P. patula* trial site, established in 2001, was sampled; secondly, a new *P. elliottii* trial site established in 2006 also in Mpumalanga, was sampled; and thirdly, the **P**hysiological **P**rinciples in **P**redicting **G**rowth **M**odel (3-PG model) was used to predict the tree growth parameters measured in this study in both the *P. patula* and *P. elliottii* plantations and to predict future tree growth until the end of the rotation (28 years) in *P. elliottii*. *Pinus patula* in this study was grown for pulpwood with a rotation age of 19 years, fertilizer were applied in 2001 and 2003 when the trees were 11 and 13 years old, whilst *P. elliottii* was grown for saw timber with a rotation age of 28 years and the fertilizers were applied in 2006 when the plantation was 17 years old.

Although the university works in collaboration with the forestry industry, its involvement in matters of decision making is limited in the area of the establishment of new trial sites, their location and choice of species. This is because it falls exclusively within the brief of the forestry industry to make these decisions, which are based on industry priorities at each given time. It was the decision of the industry to establish the trial at the chosen sites. The two species, *P. patula* and *P. elliottii* are very important pulp and saw log species planted in South Africa, and this is why these species were planted.

1.4 Contribution to Science

Fertilizer is applied to reach the potential yield of a site by economically correcting growth limiting nutrient deficiencies. Nitrogen, P, Potassium (K^{+}) and sometimes Calcium (Ca^{2+}) fertilizers are usually applied. It is generally reported that N and P are the most limiting nutrients in forest ecosystems (Binkley *et al*., 2000; O'Connell and Rance, 1999; Van Miegroet *et al*., 1990; Vitousek and Farrington, 1997). Fertilizers are usually applied at plantation establishment in southern African and seldom thereafter except perhaps to correct a rare deficiency. The practice of post-establishment fertilization in pine plantations is gradually becoming more regular in a bid to sustain productivity and improve yield.

However, little research work has been done on mid or late rotation fertilization in pine plantations (Carlson *et al*., 2000; Donald *et al*., 1987; Morris, 1993b and 2003).

Post-establishment fertilization has been reported to lead to increases in log wood size and better quality of the additional wood. This is due to there being less juvenile wood and a lower financial risk because of the short time period between the application of the fertilizer and the return of the investment (Carlson *et al*., 2000; Donald, 1987; Schutz, 1976). The increase is expected because additional nutrients will be available for plant uptake from the soil to increase leaf area, photosynthesis, net primary production, shifts in allocation of photosynthate from root to stem production, tree height, basal area and log production. Nutrient cycling processes involve an understanding of the quantity of materials present in the system, which may include chemical elements in various vegetation components such as foliage, wood, bark, roots, in the litter and humus layers of the forest floor, in soil organic matter, in the soil solution and the soil pools. The pathways by which the chemical elements are recycled are the fluxes, while the vegetation, litter and soil components are the pools that make up the system. The importance of each of these pools varies greatly between elements and the elemental availability varies between the different nutrient pools. Plant biomass can be either a flux or pool depending on the size and rate of nutrient turnover. Various pathways such as litter fall, nutrient uptake, mineralization, immobilization, cation exchange and anion retention play a big role in the way nutrients are cycled within and between the plantation system, and they link the different components within the plantation system.

There is the need to understand how the nutrients are transferred between, and among the pools of a plantation system and the ways by which the nutrients are added or removed from the various pools. Previous studies at this study site focused only on measuring yield without an understanding of the components that make up the yield (Crous, 2007). This study therefore focused on measuring the nutrient cycling pools, with the intention of increasing the understanding of the nutrient fluxes of a plantation system. Some of the key findings of this PhD included: the sites chosen for these trials were not nutrient limited therefore there were no overall responses to the fertilizer applications but there were significantly different site responses; the climatic factors, especially rainfall, played a significant role in determining the pattern of tree growth across the sites; the concentration and amount of nutrients in the forest floor litter, as well as the tight coupling of nutrient availability and decomposition, provide evidence that the management of the litter is key in maintaining the productivity of the sites; foliar nutrient concentration ratios, especially Ca:N and K:N, can be used as indicators of nutrient availability at the sites and possibly as indicators of response to fertilization; and the predictive understanding of the system can also be improved through the use of 3-PG model and the N mineralization model.

1.5 Hypotheses and Key Questions

The following hypotheses and key questions were addressed in this study:

1.5.1 Hypothesis I

Late rotation fertilization of *P. patula* and *P. elliottii* with inorganic fertilizers, will result in increased tree height, basal area and stand volume, across the sites, if other environmental growth conditions are favourable.

Key Questions:

1. What are the main environmental factors that influence the tree height, basal area and stand volume of *P. patula and P. elliottii* species across the sites?

2. How do different late rotation fertilization treatments affect tree height, basal area and stand volume of *P. patula* and *P. elliottii* across the sites?

1.5.2 Hypothesis II

The growth response in tree height, basal area and stand volume in *P. patula* and *P. elliottii* with late rotation fertilization is positively correlated with soil exchangeable bases (Ca^{2+}, Mg^{2+} and K^{+}) and negatively correlated with exchangeable acidity and pH across the sites.

Key Questions:

1. How do the different late rotation fertilizer treatments alter the concentrations of soil exchangeable bases (Ca^{2+}, Mg^{2+} and K^{+}) and tree height, basal area and stand volume across the sites?

2. What is the relationship between soil exchangeable acidity and pH on tree height, basal area and stand volume across the sites?

1.5.3 Hypothesis III

Late rotation fertilization of *P. patula* and *P. elliottii* will lead to short term enhanced soil N mineralization rates due to decreased C:N ratios in the litter and soil.

Key Questions:

1. How do soil exchangeable bases (Ca^{2+}, Mg^{2+} and K^{+}) and exchangeable acidity influence soil N mineralization rates and the concentration of N in the litter across the sites?

2. What is the relationship between tree height, basal area and stand volume and the rate of soil N mineralization and the concentration of N in the litter across the sites?

1.5.4 Hypothesis IV

The concentration of N, P, P:N ratios and concentration of cations (Ca^{2+}, Mg^{2+} and K^{+}) in the foliage of *P. patula* and *P. elliottii* with late rotation fertilization is positively correlated with tree height, basal area and stand volume in *P. patula,* as well as in *P. elliottii* across the sites.

Key Questions:

1. How well can foliar nutrient concentrations be used as indicators for predicting tree height, basal area and stand volume in *P. patula* and *P. elliottii* across the sites?

2. How do the levels of N, P and their ratios affect the growth response of *P. patula* and *P. elliottii* across the sites?

3. What is the effect of late rotation fertilizer applications on the nutrient concentrations in the foliage and the litter?

1.5.5 Hypothesis V

Tree height, basal area and stand volume are positively correlated with the rate of litter fall, accumulation, decomposition and nutrient concentrations in *P. patula* and *P. elliottii* litter across the sites following late rotation fertilization.

Key Questions:

1. How does late rotation fertilization influence the amounts of litter fall, forest floor litter accumulation and litter decomposition and the effect on tree growth in *P. patula* and *P. elliottii*?

1.5.6 Hypothesis VI

The predictive capacity of the growth of *P. patula* and *P. elliottii* with late rotation fertilization using the climatic factors and other input parameters across the sites was improved using the 3-PG model.

Key Questions:

1. How well can the tree growth parameters (stand volume, basal area and quadratic mean diameter at breast height) for *P. patula* and *P. elliottii* be predicted using the 3-PG model across the study sites?

2. How well can the 3-PG model be used to predict tree growth parameters for *P. elliottii* at the end of the rotation in 2017 (at 28 years old)?

1.6 Structure of the Thesis

The study is presented in seven chapters. This first chapter serves as an introduction, while chapter two is a general literature review and chapter three describes the site, the experimental approach and the methods used. Results from this study are presented in chapter four. An overall discussion and the conclusions of this study are presented in chapters five and six respectively, while the references are presented in chapter seven.

CHAPTER 2

LITERATURE REVIEW

This study deals with the impact of late rotation fertilization on biologically based processes, for example, tree growth, litter fall, litter decomposition, litter accumulation, N mineralization and the evaluation of a growth yield model. The information from this study was used to improve the predictive understanding of the growth responses of *P. patula* and P. *elliottii* to late rotation fertilization, which is vital to forestry development, yield sustainability and management.

2.1 Nutrient Fluxes in Plantation and Forest Ecosystems

Forest ecosystem function and productivity are determined by a complex array of interactive processes related to the soil, the vegetation, the environment, and these processes can be described quantitatively (Kimmins, 1994; Landsberg and Gower, 1997). Nutrient cycling processes include the quantity of materials present in the system (pool size) as well as the rate of movement between the various pools also referred to as the flux (Likens *et al*., 1977). The primary factors controlling forest productivity are energy, water and nutrient supply; the nutrient requirements for growth and maintenance are met through nutrient cycling (O'Connell and Sankaran, 1997).

Switzer and Nelson (1972) reviewed by O'Connell and Sankaran (1997) identified three scales of nutrient cycling, namely (i) geochemical cycling through inputs from weathering and atmospheric deposition or through outputs from leaching and volatile emissions (ii) biochemical cycling where nutrients are redistributed within the plant to meet demands for growth and (iii) biogeochemical cycling in which, for example, nutrients released from plant residues or through canopy leaching or stem flow enter the soil and are then taken up by the plant roots and ultimately returned to the atmosphere or the soil. Nutrient distribution in trees is reported to be affected by a number of abiotic and biotic factors including site, tree age and species. Generally the foliage and branches contain a major portion of the nutrients, especially when compared to the total biomass (Fölster and Khanna, 1997; Goncalves *et al*., 1997 cited by Tiarks *et al*., 1998).

The dynamics of nutrient supply in forest ecosystems are primarily driven by the fluxes. A forest ecosystem can be visualized as consisting of compartments, which may include chemical elements in the atmosphere, the various vegetation components such as foliage, wood, bark, and roots, in the litter and humus layers of the forest floor, in soil organic matter, in the soil solution and on the surfaces of the soil minerals. Various processes such as deposition, mineralization, immobilization, cation-exchange, anion retention, nutrient uptake and litter fall, link the different compartments within the forest ecosystem. Inputs of chemical elements via precipitation (wet and dry deposition), fertilizer additions and mineral weathering, and outputs via harvesting, volatilization (fire) and leaching connect the different compartments with the environment (Fölster and Khanna, 1997).

Likens *et al*., (1977) have reported that the major pathways through which nutrient inputs are returned to the terrestrial ecosystems include atmospheric deposition, mineral weathering, biological N-fixation and anthropogenic inputs. Lateral fluxes (such as colluvial movement and lateral drainage), as well as the fluxes attributable to the movement of fauna, are of secondary importance in most ecosystems (Ranger and Turpault, 1999). Atmospheric deposition of nutrients occurs through four major processes, dry particulate fallout, rainfall, mist interception and gaseous uptake by foliage (Likens *et al*., 1977). Binkley (1986) and Ranger and Turpault (1999) have reported that significant amounts of P, Ca^{2+}, Mg^{2+} and K^{+} may also be added through deposition.

Ranger and Turpault (1999) have pointed out that soil mineral weathering and its dynamics characterize the geochemical function of soil and its resilience. A flux of cations released by weathering replaces the nutrients taken up by the vegetation and buffer the acidity generated internally or brought about by pollution (Ranger and Turpault, 1999). In extensively managed plantations, weathering controls the productivity of the ecosystem in the long-term (Clayton, 1979). Mineral weathering has been reported not to be an important short-term nutrient source because very small amounts of P, K^{+}, Ca^{2+} and Mg^{2+} become available to the trees (Jorgenson *et al*., 1975), this has been confirmed by du Toit and Scholes (2002), cited in

Dovey and du Toit (2006) in South African plantations growing on soils that are highly weathered.

Nitrogen fixation has been reported to play a major role in making nutrients available to plants. Some plants are able to convert N_2 into ammonia (NH_3) by means of free living and symbiotic organisms (Vitousek, 2004; Vitousek and Howarth, 1991). These plants are referred to as N_2-fixers because they are able to break the strong bond between the two gaseous atoms ultimately forming NH_3 (Blackstock, 1989). Soil chemical, physical and biological characteristics (Dixon and Wheeler, 1983; Israel, 1987; Marschner, 1986; Naidu *et al*., 1990) have been reported to influence N fixation rates. Nitrogen fixation will only become an important process in plantation systems in South Africa if the under storey is dominated by N fixing forbs.

Anthropogenic inputs e.g. fertilization, is the most common method of increasing site productivity. The growth of forest stands is closely related to the supply and uptake of N and P (e.g. Albaugh *et al*., 2004; Binkley and Reid, 1984; Fisher and Garbett, 1980; Martin and Jokela, 2004; Schulze *et al*., 1995; Sword Sayer *et al*., 2004). Fertilization increases nutrient availability, uptake, tissue nutrient concentrations, tree growth, and forest floor mass (Meason *et al*., 2004; Shan *et al*., 2001; Will *et al*., 2002). The successful use of fertilizers to increase commercial productivity in tropical and sub-tropical regions is well documented all over the world (Barros *et al*., 1990; Cromer *et al*., 1993; Goncalves, 1995; Gurlevik *et al*., 2004; Herbert and Schönau, 1989; Linder, 1995; Morris, 1986, 2003; Nambiar *et al*., 1990; Prescott *et al*., 2000; Sheriff, 1996; Turner *et al*., 1992).

The major pathways by which nutrients are lost from forest ecosystems are biomass removal (harvesting), which results in a substantial loss of nutrients from a forest plantation, burning of plantation biomass, erosion and nutrient leaching beyond the rooting zone (Binkley, 1986; du Toit and Scholes 2002; Grossmann and David, 2007; Likens *et al*., 1977; Ranger and Tarpault, 1999). Birk (1993) showed that highly productive sites produce more biomass and hence create a higher potential for larger nutrient losses with harvesting and burning. Even on fertilized soils the productivity of plantations has been shown to be adversely affected by the removal of N and P due to harvesting (Harrison *et al*., 2000). This has serious implications for the sustainable productivity of forests (Fisher and Binkley, 2000).

Burning of plantation biomass and residue burning may also result in significant losses of nutrients from a site. The effect of fire on the quantity of nutrients lost from the fuel complex has been reported to depend on the quantity of fuel present on the site, fuel composition, moisture content of the fuel, climatic conditions, the amount of fuel burnt, and existing nutrient budgets (Attiwill, and Leper, 1987; Bird, 2001; Fahey *et al*., 1991; Geldenhuys *et al*., 2004). Fire intensity and fire residence time impacts the amount of nutrients present and the site fertility (Bird, 2001; Bird and Scholes, 2005; de Ronde, 1990; Geldenhuys *et al*., 2004 cited in Ross *et al*., 2005).

Soil erosion and leaching of nutrients, N, K^{+}, Ca^{2+} and Mg^{2+} out of the rooting zone has been shown to be a significant nutrient loss mechanism (Marques *et al*., 1997). However, very little is known about leaching of nutrients out of the tree rooting zone in South African commercial forestry, with most estimates being derived from catchment studies. The rate of nutrient leaching loss varies from one site to another as leaching is dependent on factors such as, precipitation intensity and distribution, soil texture and structure, soil chemistry, slope and root distribution (Dovey and du Toit, 2006).

2.2 Nitrogen and Phosphorus Cycling in Plantations

Nutrients in soil exist either organically or inorganically and in different states. Nutrients are usually taken up by roots from the soil solution as inorganic ions either by mass flow or diffusion processes. Organically bound nutrients are mineralized or immobilized primarily via microbial processes, whereas the inorganically bound nutrients undergo cation exchange, dissolution and fixation processes, and reduction and oxidation reactions (Fölster and Khanna, 1997 cited in Nambiar and Brown, 1997).

2.2.1 Nitrogen

Nitrogen traditionally has been considered as one of the most important nutrients for plant growth. It regulates the development of foliage, which controls the amount of plant production, and therefore, the extent of wood increment (Schönau and Herbert, 1989 cited by Campion and Scholes, 2003). Nitrogen is an essential component of nucleic acids, amino acids, and chlorophyll**.** The availability of soil N is controlled by a host of soil biological, physical and chemical processes, with litter fall and the rate of decomposition supplying the largest amounts of nutrients for plant growth (Scholes, 2002; Singh *et al*., 1999; Weltzin *et al*., 2005).

Nitrogen cycle

Nitrogen exists in many forms, the chemical transformations of N, such as nitrification, denitrification, mineralization, and N-fixation are performed by a variety of soil organisms (Fig 2.1). Nitrogen gases can move freely between the soil and the atmosphere depending on gradients. Although the N cycle is complex, it is probably the most important nutrient cycle to understand because N is usually the most limiting factor for plant growth in terrestrial ecosystems.

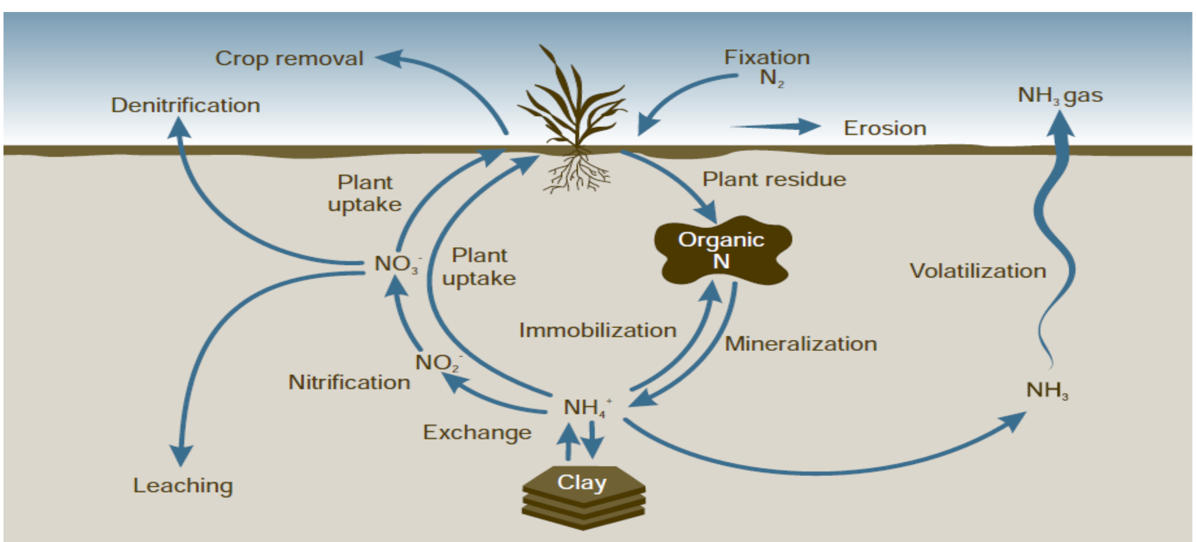

Figure 2.1 Nitrogen cycle showing different components and pathways (http://www1.agric.gov.ab.ca/$department/deptdocs.nsf/all/epw11920/$FILE/2-1.pdf)

Nitrogen-fixation is carried out to a lesser extent through lightning and other electrical discharges in the atmosphere and biological-fixation. Atmospheric fixation by lightning involves the N molecule being transformed, enabling the atoms to combine with oxygen forming N oxides (Epstein, 1972). These dissolve in rain, forming nitrates (NO_3^-) that are carried to the earth. There is also biological-fixation which requires a complex set of enzymes and a large expenditure of Adenosine triphosphate (ATP). The first stable product of the process is NH_3, but this is quickly incorporated into protein and other organic N compounds. The biological-fixation of N is brought about by the activities of micro organisms which include bacteria that are either free living or live in symbiotic association with plants (Epstein, 1972; Vitousek, 2004). There are a number of ways that fixation can occur:

- Symbiotic relationship with higher plants especially the legume family (e.g. soybeans, alfalfa).
- Symbiotic relationships with plants other than legumes (e.g. alders).
- Symbiotic relationships with animals, e.g. termites and "shipworms" (wood-eating bivalves).
- Free-living N fixing bacteria.
- Nitrogen-fixing cyanobacteria (Miller and Donahue, 1990; Singer and Munns, 1987; Sprent and Sprent, 1990; Vitousek, 2004).

The process of decomposition involves the break down of organic compounds into inorganic compounds using both fungi and bacteria. The processes are mostly aerobic and result in ammonium (NH_4) being released into the soil solution together with a number of other compounds. Carbon dioxide in released to the atmosphere.

Ammonia and NH_4 can be taken up directly by plant roots. However, in many systems the NH_3 produced by decomposition is converted into NO_3^- in a two-step process. The first being carried out by bacteria of the genus *Nitrosomonas* which oxidizes NH_3 to nitrites (NO_2^-), and then the bacteria of the genus *Nitrobacter* oxidizes the NO_2^- to NO_3^- which are available to plant roots. These two groups of autotrophic bacteria are called nitrifying bacteria.

The three processes, N-fixation, decomposition and nitrification transforms N and in this way cycles N through the ecosystem; while denitrification processes reduce NO_3^- to N gas, again cycling N through the system. Micro organisms are essential for all of the above processes, including aerobic and anaerobic groups.

The application of N fertilizers to plantation soils is a common management practice (Smaill, *et al.,* 2008). Nitrogen fertilization has been reported to increase the C and N content of both the forest floor organic matter (Prescott *et al*., 2000; Sjöberg *et al*., 2004; Smith *et al*., 2000) and mineral soil (Gurlevik *et al*., 2004; Jandl *et al*., 2003). Nitrogen applications have the potential to influence other aspects of soil chemistry, as fertilization has been found to induce long-term decreases in mineral soil pH across a range of forests (Ballard, 2000; Nohrstedt, 2001), and has been associated with increased rates of N and trace element leaching (Ring, 2004). In managed forest systems, the knowledge of N supply rates in relation to tree requirements for N is critical for the optimum maintenance of economic tree growth through appropriate fertilizer regimes (O′Connell and Rance, 1999).

Growth of many natural and plantation forests is limited by N supply (Binkley *et al*., 1997; Galloway and Cowling, 2002; Miller and Donahue, 1990). The majority of N available for plant growth is derived from mineralization of organic residues through biochemical reactions mediated by the soil microbial community (O'Connell and Rance, 1999). Most soil N occurs in an organically bound form which should be mineralized into NH_4^+ or NO_3^- before uptake by plants (Fölster and Khanna, 1997). The processes of N mineralization in forest ecosystems, can supply up to 90% of the N available for plant uptake on an annual basis and this process varies significantly between sites (Scholes, 2002). Different factors have been reported to affect the process, Cabrera *et al*., (1994) reported that soil depth affects N mineralization rates with the upper layer contributing larger proportion than the lower layer. Heterotrophic micro organisms play a major role in the process of decomposition of organic materials into NH_4^+. Barnes *et al*., (1997) and Nambiar and Booth (1991) have described several cases where above ground productivity of forest ecosystems correlates well with the rate at which soil micro organisms release N from soil organic matter. The rate of mineralization of organically bound N depends on soil environmental factors, principally soil moisture and temperature (Sierra, 1997) and soil chemical and physical factors that determine the potential supply rate of mineralizable N (O'Connell and Rance, 1999).

Reich *et al.,* (1997) compiling data from several forest types found a linear relationship between the rates of N mineralization and stand growth. In climates, where there are clear wet and dry seasons, moisture availability has also been pointed out to be a factor. Louw and Scholes (2002) in their study on the influence of site factors on N mineralization in plantation soils of the Mpumalanga region of South Africa found a significantly positive correlation between NH_4 mineralization during summer and the growth of *P. patula*. Several studies have shown that fertilization affects the rate of N mineralization. Gurlevik *et al*., (2004) in their study on N mineralization following vegetation control and fertilization in a 14-year-old *Pinus taeda* (Linn) stand in North Carolina, U.S.A. reported that both vegetation control and fertilization increased field net N mineralization, with there being a strong positive interaction between the fertilizer treatments. They however, pointed out that seasonal patterns in net mineralization were poorly correlated with soil temperature and moisture, both in the field and laboratory, thereby suggesting that other factors (e.g. labile C inputs) may also be important in controlling net N mineralization rate.

There are a number of published studies on the effects of N fertilization on N mineralization rates (Aarnio and Martikainen, 1992; Carlyle, 1995b; Fox, 2004; Hart and Stark, 1997). The results from these studies are often conflicting. Fox's (2004) study on N mineralization following fertilization of Douglas-fir forests with Urea in Western Washington, U.S.A. showed increased N mineralization potential in the soils following N fertilization. He, however, pointed out that soil N mineralization rate followed a quadratic relationship with the total amount of N applied in fertilizer over the 6 year treatment period, increasing up to total application rate of 450 kg N ha^{-1} and then declining at higher rates. The decrease in N mineralization rates at the high N fertilization rates were attributed to changes in the quality of soil organic matter, which reduced the effectiveness of extra cellular enzymes and thereby, decreased the rate of decomposition and mineralization. Decreases in extractable Ca^{2+} and Mg^{2+} levels in the soil, accompanying the decline in soil pH, was also noted. These results suggest that high rates of nitrification occurred and that NO_3^- leaching was stripping Ca^{2+} and

Mg^{2+} from the cation exchange complex in these soils. He pointed out that repeated applications of Urea fertilizer at low to intermediate rates might increase long-term N availability and thus improve soil quality. However, annual applications of high rates of Urea were reported to decrease soil quality, because under these circumstances N mineralization did not increase and there was a loss of cations from the soil.

In contrast, Aarnio and Martikainen (1992) in Finland have shown that repeated fertilization with Urea over a 16-year period increased N mineralization in the forest floor more than a single application in a mixed *Pinus sylvestris* (Linn) and *Picea abies (*Linn) stand. They attributed this to changes in soil microbial populations, including autotrophic NH_4 and NO_3^- oxidizers, caused by the initial fertilization. Likewise, Prescott *et al.,* (1995) found higher levels of mineralizable N in stands that were fertilized six times receiving a total of 672 kg N ha^{-1}. Chappell *et al*., (1999), however, found that N fertilization did not increase N mineralization in the forest floor of nine Douglas-fir stands in coastal Washington and Oregon that received between 898 and 1120 kg N ha^{-1} from 1969 to 1985. Other factors that affect N mineralization rates include: temperature (Rice and Havling, 1994), soil water content and aeration (Goncalves and Carlyle, 1994; Tisdale *et al*., 1985), C:N ratio of organic material (Barnes *et al*., 1997; Gunderson *et al*., 1988; Tisdale *et al*., 1985; Van Miegroet *et al*., 1990), soil pH (Harris ,1988; Tisdale *et al*., 1985) and soil P (Carlyle *et al*., 1990).

2.2.2 Phosphorus

Phosphorus is an important nutrient element for plant growth and is sometimes called 'the key to life' because it is directly involved in most life processes. It is a component of every living cell and tends to be concentrated in seeds and in the young parts of plants (Thompson and Troeh, 1978). It is involved in controlling key enzyme reactions and in the regulation of metabolic pathways (Theodore and Plaxton, 1993). It is also an important plant macronutrient making up about 0.2% of plant dry weight and it is the second most frequently limiting macronutrient for plant growth (Schtachtman *et al*., 1998). Phosphorus occurs in different forms in the soil mostly as inorganic P of varying solubility, and of organic P. Organic P can form 10% to greater than 90 % of total P in forest soils, with greater than 50% being a common value for surface soils (Fölster and Khanna, 1997; Richardson, 1994). Soil humus holds organic P in labile, resistant and aggregated forms (Coleman *et al*., 1983). Litter fall, root decay and death of organisms return biologically held forms into forms available for plant uptake (Gressel and McColl, 1997). Phosphorus has low solubility and low mobility in soils and therefore losses through leaching, run-off and erosion are generally low (Gressel and McColl, 1997; Tainton, 1984; Walker and Syers, 1976).

Phosphorus cycle

Phosphorus is present mostly in mineral and organic forms that are not immediately available to plants. Phosphorus distribution in soil can be classified into the following major pools, non-labile P which includes the P in primary (apatite) and secondary minerals, inorganic P (P_i) and organic P (P_o) sorbed to Fe and Al on clay minerals, insoluble Ca salts; labile (inorganic P), and solution P (Figure 2.2) (Crews *et al.*, 1995; Walker and Syers, 1976). The processes involved in P transformations are precipitation-dissolution and adsorption-desorption which control the abiotic transfer of P between the solid phase and soil solution, and biological immobilization-mineralization process that control the transformation of P between inorganic and organic forms (Frossard *et al*., 2000) (Figure 2.2).

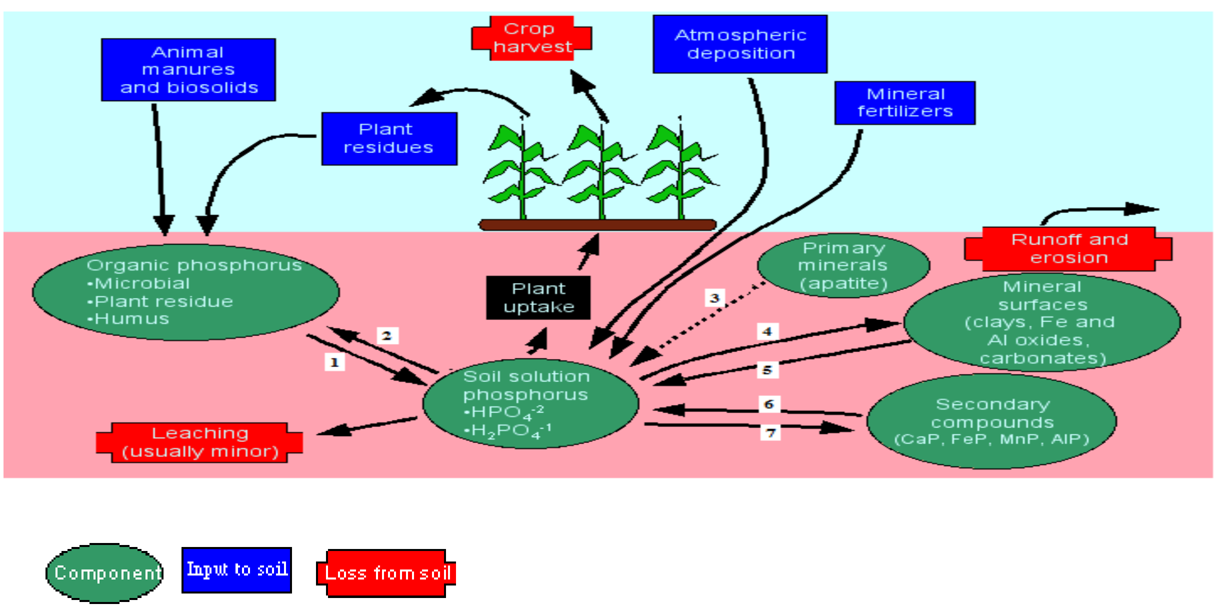

Figure 2.2 Phosphorus cycle showing component, input and loss from soil. 1 stands for immobilization, 2 = mineralization, 3 = weathering, 4 = adsorption, 5 = desorption, 6 = dissolution and 7 = precipitation. (msucares.com/crops/soils/phosphorus.html)

The complete transformation of P from primary mineral forms to sparingly soluble Al and Fe phosphates (occluded P) occurs through the formation of a number of intermediate forms, over a geological timescale (Tate and Salcedo, 1988). The longer-term evolution of P forms in the soil ecosystems has been reported to be controlled by the less dynamic pedological pathways and this leads to the accumulation of P in mainly occluded forms, while in the short-term, the pathway by which P becomes more or less available to plants and soil micro organisms can be summarised by the following equilibria:

$$\text{Soil solution} \quad \underset{\text{fast}}{\rightleftarrows} \quad \text{labile } P_i \quad \underset{\text{low}}{\rightleftarrows} \quad \text{non-labile}$$

Mineral weathering releases P into solution, where P can be taken up by plants and micro organisms, sorbed onto solid surfaces, form secondary minerals or be lost through erosion or leaching (Gressel and McColl, 1997; Walker and Syers, 1976). Phosphorus losses from soils occur by leaching at very low rates in undisturbed ecosystems (Frossard *et al*., 1989; Letkeman *et al*., 1996; St.Arnaud *et al*., 1988; Walker and Syers, 1976).

Labile P_1 (orthophosphate ions, $H_2PO_4^-$ and HPO_4^{2-} adsorbed to mineral surfaces) is the readily available fraction of the total P that exhibits a high dissociation rate and rapidly replenishes decreases in solution P due to plant uptake. The remaining portion of adsorbed P that does not readily desorb is called non labile, and is not available to plants. The labile Pi (inorganic P) per unit soil volume, soil solution P concentration, the ability of the soil to replenish solution P, and the rate of replenishment, all interact to control the overall P supply (Tate and Salcedo, 1988).

When the primary P mineral (apatite) is exposed to water and acidity, it weathers and releases P as biologically available P (PO_4). Orthophosphate is the simplest phosphate (PO_4^{3}), some of which is taken up by plants, and utilized by animals that consume plants, and ultimately is recycled back into the soil (Figure 2.2). Some (PO_4^{3-}) is precipitated or adsorbed by secondary minerals within the soils (Vitousek, 2004). The release of inorganic phosphate from organic phosphates is called mineralization and is facilitated by micro organisms, breaking down organic compounds. The activity of micro organisms is highly influenced by soil temperature and soil moisture. The process is most rapid when soils are warm and moist but well drained (Sharpley, 2000).

Symbiotic associations can be formed with mycorrhizal fungi and these associations play an important role in the acquisition of P for the plant (Bolan, 1991; Smith and Read, 1997). Mycorrhizae associations can be divided into three main groups based on their morphological characteristics: ectomycorrhizae, endomycorrhizae and ectendomycorrhizae (Harley and Harley, 1987). Ectomycorrhizae, are the most widely spread in the plant kingdom including the pines species where fungi are symbiotically involved with the plants and play a role in the absorption and transfer of P for plant use (Vogt *et al*., 1997).

Most ectomycorrhizal is made up of considerable network of hyphae or hyphal strands which penetrate the outer layers of roots and increase the extent of root exploration, thereby aiding plants with direct P absorption from roots**.** Plant root geometry and morphology are important for P uptake because the larger the ratios of root surfaces, the higher the effectiveness and the ability of the roots to penetrate and absorb P for plant use. Therefore, the formation of the fungal sheath around the roots contributes significantly to the amount of fungal tissue involved in mycorrhizal symbiosis and also helps in increasing the diameter of the root (Harley, 1989; Smith and Read, 1997). In some other plants, root clusters are formed in response to P limitations, these specialized roots exudes high amounts of organic acids, which acidify the soil and chelate metal ions around the roots, resulting in the mobilization of P and some micronutrients (Marschner, 1995).

In neutral and calcareous soils, inorganic P in soil solution becomes adsorbed to the surfaces of clay and lime minerals. In acid soils, the soluble ion $H_2PO_4^-$, rapidly reacts in soil solution to form insoluble phosphate (Miller and Donahue, 1990), the phosphates ions adsorb to insoluble Fe and Al hydrous oxides surfaces, thereby fixing soluble P into an unavailable form, thereby reducing the amount of P that is available for plant use (Sanchez, 1976).

The mineralization of organic P has been reported to occur through biochemical reactions that are mediated by the plant roots and soil microbial activities (Fölster and Khanna, 1997).

The mineralization of the available pool of P occurs predominantly in the rhizosphere (López-Gutiérrez *et al*., 2004). Micro organisms play an important role in the short-term cycling and availability of P by mechanisms such as uptake-storage-release, mineralization and solubilisation (Lee *et al*., 1990; McLaughlin *et al*., 1988; Parfitt *et al*., 1989; Singh *et al*., 1989). Soil pH governs transformation of soluble P into insoluble hydroxyl phosphates (Jordan, 1985). In mineral soils, P is most available at pH 6.5, increased Al^{3+} activity occurs at low pH, which increases P fixation and reduces P availability. Organic matter has an indirect influence on P availability, in addition, increased Al^{3+} and Fe^{2+} can be complexed by organic matter (Thompson and Troeh, 1978).

In the study on *Pinus radiata* (D. Don.) stands in Australian, Falkiner *et al*., (1993) reported that the addition of superphosphate increased soil N mineralization. They reported that the application of 200 kg P ha^{-1} as super phosphate to trenched plots in a *P. radiata* stand increased soil mineral-N by 122% and 82% above the control, on two occasions. Applications of 500 kg P ha^{-1} as super phosphate either alone or in combination with lime (10 Mg ha^{-1}) was also shown to increase *in situ* soil net N mineralization in a dry sclerophyllous eucalypt forest from 20.7 (control) to 28.3 (+P) and 30.2 (+P + lime) kg N ha^{-1} yr^{-1} $20cm^{-1}$. The response of N mineralization following the application of fertilizer was attributed to the combined effect of lower soil pH (acidic) and organic C present in the soil. They however pointed out that mechanisms underlying the response are still poorly understood and also limit the ability to predict N mineralization significance for tree nutrition on specific forest sites.

Aggangan *et al*., (1998) showed that P application either reduced or had no effect on N mineralization potential and cumulative N mineralization in a laboratory incubation study of soils from eucalyptus plantations in Australia. Phosphorus fertilization of planted forest stands is a common practice on the highly weathered soils in the U.S.A., New Zealand, Australia and Brazil. A one-time P application can transform a low productivity stand into a highly productive forest (Ballard, 1978). The effect of one P application when applied at an early stage of the rotation has been reported to last for the entire rotation in *P. elliottii*, (Pritchett and Comerford, 1982); *P. taeda*, (Allen *et al*., 1990) and *P. radiata*, (Ballard, 1978).

The existence of P deficiencies in pine plantation soils as well as the effectiveness of a single P fertilizer application in plantations have been well documented (Allen, 1987; Allen, *et al*., 1990; Ballard, 1978; Harding and Jokela, 1994; Humphreys and Pritchett 1971; Pritchett and Lewellyn, 1966). However, fewer studies that document either the quantity of residual P remaining in the soil years after fertilization, the effect that a large growth response to fertilization has on soil P and forest floor status, or the effect that a single fertilization has on the tree growth of the subsequent rotation, are available (Comerford *et al*., 2002; Crous *et al*., 2008). Foliar P may be an important regulator of photosynthesis in some species (e.g. *P. radiata*, (Attiwill and Cromer, 1982; Reid *et al*., 1983); and *Pinus contorta* (var. murrayana), (Kirschbaum *et al*., 1992). These authors have reported that P fertilization has been used to correct leaf nutrient deficiency resulting in increased photosynthetic capacity. Graciano *et al*., (2006) in their study in Argentina concluded that N and P fertilization affects growth to different extents depending on the soil characteristics. They reported that P fertilization increased growth more than N fertilization in the three soils used, in spite of the low natural N concentration of the red sands and the loamy sands.

Studies on the impacts of P fertilizer applications on tree growth are available in southern Africa. Carlson (2000) reported a positive growth response to the application of P fertilizer in 8-year-old *P. patula* compartments in the Mpumalanga region. The sites at high altitude on granitic parent material tended to respond to the applications of P and K, while lower altitude granite-derived soils and those derived from quartzitic parent material did not respond at all to the nutrient additions. The trials on shale-derived parent materials responded immediately to N, but the response was short lived, with responses to P and K applications becoming significant three years after fertilization applications. The response to P on shales also disappeared five years after fertilizer application (Carlson, 2000). In addition, Morris (2003) showed that significant volume increments were observed with P fertilizer applied to 6- and 11- year-old stands but not when applied to the 3-year-old stand of *P. patula* at Usutu, Swaziland. The mean response to 100 kg ha^{-1} P applied to the 6- and 11- year-old stands was 25 m^3 ha^{-1} over five years.

2.3 The Effects of Fertilization on Plantation Productivity

Nitrogen and P are very important and are often limiting nutrients in plantation ecosystems (Fisher and Binkley, 2000). The application of N and P fertilizers are regularly used to correct site nutrient deficiencies, replace the lost nutrients and boost plant growth. The application is usually done at the beginning of plantation establishment in southern Africa. However, evidence of post-establishment fertilization, to boost productivity and improve yield, exists for pine plantations in southern Africa especially, at the mid rotation stage (Carlson *et al*., 2000; Donald *et al*., 1987; Morris, 1986, 1993a and 2003). Campion (2008) in her review on the effects of mid and late rotation fertilizer application on tree growth and wood quality in softwood saw timber stands highlighted the economic advantages of mid and late rotation fertilizer application to include:

- An increased log size and therefore value per unit volume (Carlyle, 1995a; Yang, 1998);
- A lower risk associated with the shorter time period between nutrient addition and return on investment (harvesting) when hail or insect pests can damage the trees (Carlson *et al*., 2000);
- The high value of the additional wood produced, which is denser than juvenile wood, being clear (knot free), high quality, mature wood (Donald, 1987; Schutz, 1976; Turner *et al*., 1992);
- A reduction in the length of the compound interest period (Donald, 1987; Pritchett and Comerford, 1983; Schutz, 1976);
- Fertilizer application is easier (Schutz, 1976) (broadcast application as opposed to fertilizing on a per tree basis, which is common practice at planting in South Africa), thus preventing root scorch and mortality (Carlson *et al*., 2000).

Tree growth response of a plantation following fertilization has been reported to be affected by a number of factors (Allen, 1987; Williams and Farrish, 1995). These factors were reported by Crane (1984) to interact with soil nutrients to determine the success and profitability of plantation fertilization, and have been reviewed by Campion (2008) to include: timing of fertilizer application in relation to season, fertilizer rates, forms and methods of application, ratios of elements (nutrient balance, soil types and stand factors, which include age and stage of development (Crane, 1984; Morris 2003), as well as initial basal area and site index (Duzan *et al*., 1982). In addition, soil water availability (Fisher and Binkley, 2000; Jokela *et al*., 1988; Pritchett and Comerford, 1983; Sherriff, *et al*., 1986), stand condition (tree size, stocking and vigour) (Fisher and Binkley, 2000), species (Allen *et al*., 2005), inherent site nutrient availability, stand nutrient requirements, sivicultural techniques (Jokela *et al*., 1988), and incidence of disease or insect pests, can influence the response to fertilization (Jokela *et al*., 1988; Pritchett and Comerford, 1982).

Several other studies on fertilization responses in plantations have been reported in southern Africa. Herbert and Schönau (1989) found that the major response when fertilizing Eucalyptus, at planting, in the summer rainfall region, is to P. The response to N is mainly additive and depends on the organic matter in the topsoil and on the rate of soil mineralization, which in turn is affected by the intensity of soil preparation at the site. Carlson *et al*., (2001) in their study on response in Eucalyptus species reported highly significant positive responses to N and P, each having been applied individually, which occurred immediately after planting. They pointed out that the response to N appeared to be more sustained than the response to P. The response was attributed to P and N being limiting based on the very low foliar concentrations of P, and lower N and K^+ concentrations compared with the optimal conditions given by Herbert (1992).

Morris (2003) in his study on *P. patula* plantations in Swaziland reported that meaningful responses to fertilizer can be obtained when applied to established pulpwood stands without thinning. He reported significant responses with P fertilizer applied to 6- and 11- year-old stands but not when applied to 3-year-old stands. Positive responses to N fertilizer when applied to 11-year-old stands and significant volume increments with K when applied to 3-

and 6-year-old stands were obtained, but the growth was significantly reduced when applied to11-year-old stands. The response to fertilizer was attributed to both to stand age at application and soil parent material. Noble and Ramsdem (1992) in their study to ascertain the effects of N, P and K applications on the growth and yield of an 8-year-old stand of *P. patula* also reported that a significant response to mid rotation fertilization can be obtained without thinning being a prerequisite, though this is in contrast with the findings of Donald (1987); Carlson (2000) and Carlson and Soko (2000) reported that tree growth was influenced by nutrient addition when thinning was carried out and the explanation given was linked to the removal of non-productive trees and the return of nutrients to the soil from the thinnings.

The study by Crous *et al*., (2008) on *P. patula* in Usutu, Swaziland showed that in plots where K or P fertilizer was applied for the first time, the application of 50 kg K ha^{-1} increased the foliar N, P and K concentrations whereas the application of 50 kg P ha^{-1} increased only the foliar P and K concentrations. Volume increment over a 2-year period was increased by 7 or 8 m^3 ha^{-1} when either foliar P was above 0.14% or K was above 0.50%. The maximum volume increment was reported to be achieved when both nutrients were at levels above their respective critical values. In the senesced needles, P fertilizer increased the P concentration, while K fertilizer increased the K concentration, which showed that the application of fertilizer reduced these nutrient deficiencies. There was evidence that the foliar nutrient response to residual P fertilizer was greater than the response to residual K fertilizer (Crous *et al*., 2008).

Significant responses to N and P fertilization are well documented from the rest of the world. Sheriffs' (1996) study on *P. radiata* in Australia showed that there are strong interactions between fertilizer and water in water limited environments. Thinning takes places in order to reduce the competition between trees which otherwise would have led to a slowing of growth, the remaining trees show an increase in growth rate due to an increase in the availability of water per tree. It was pointed out that on sites where mineral nutrient supply is limiting, growth responses to fertilizer application depended on an adequate supply of other resources (light and water), and it involved non-linear interactions among mineral nutrients and between nutrients and other growth limiting environmental factors. Results reported by Lindgren *et al*., (2007) on the 10-year growth response of young *P. contorta* to thinning and repeated fertilization treatments in Canada showed that at the tree level, fertilization treatments significantly increased diameter at breast height (DBH), basal area and volume growth. They pointed out that pruning may mitigate some of the negative stem forms and wood quality attributes associated with fast-growing trees without adversely affecting stem growth.

Results have been reported by Hynynen *et al*., (1998) on 11- to 14-year-old *P. taeda* in southeastern U.S.A. that responses to N additions are immediate, if N is limiting. Similarly Ballard (1981) reported an immediate increase in growth following N fertilization, peaking during the first four years after fertilization, followed by a rapid decline. Albaugh *et al*., (2004) working in an 8-year-old *P. taeda* stand growing on a droughty, nutrient-poor, sandy site in Scotland County, North Carolina reported that there were increases with fertilization, throughout the 9-year study period, in tree growth because the site is primarily nutrient limited. Standing stem mass was increased 100% by fertilization and the annual increment of stem biomass production was increased 119% by fertilization. However it was shown that stem density (stems ha^{-1}) was not significantly affected by treatment in any year of the study.

Leggett and Kelting (2006) in their study on fertilization effects on carbon pools in *P. taeda* plantations on two upland sites in U.S.A. have reported that, average DBH, total height, volume, and basal area differed significantly between sites at age 11. Fertilization had a significant effect on yield at age 11, with fertilization increasing volume yield by 44% on average across both clayey and sandy sites. They showed that there was no statistically significant site by fertilization interactions, indicating that the growth response to fertilization was similar on both sites. However, the fertilization effect on yield was shown to be only statistically significant on the clayey site, where fertilization was reported to increase volume yield by 65 m^3 ha^{-1}, representing 49% gain over no fertilization.

Nilsen and Abrahamsen, (2003) in their study in Norway also reported that both *P. sylvestris* and *Picea Abies* (Linn) stands responded strongly to N additions of 30 and 90 kg N ha^{-1} yr^{-1}, which resulted in a relative volume increment of 150 and 250%, respectively, compared to the control. They reported that the increment effect in the pine experiment ceased after 4 years, but that the difference between the two N doses was still significant after 9 years. They pointed out that the application of 16.4 kg ha^{-1} P had a slightly significant positive effect on volume increment in two of the 9 years in the pine experiment, with no effect of 5.3 kg P ha^{-1} yr^{-1} on volume increment. Other workers have reported significant responses to N and P fertilization in *P*. *taeda* and *P*. *elliottii* in the south eastern U.S.A. (Fisher and Garbett, 1980; Haines and Haines, 1979; Pritchett and Smith, 1972); in *P. elliottii* and *P. radiata* plantations in Australia (Turner *et al*., 1992; Xu *et al*., 1995)

In all of above studies, on nutrient limited sites, there was an increase in growth in response to fertilization, however the extent and the duration of the response is variable and probably associated with other limiting resources e.g. water. Management practices e.g. thinning and pruning have a major impact on the response to fertilization. Predicting the impact of the response is difficult and frequently limited by the measurements taken during the trial where only the components of yield are measured and not the rates of the range of abiotic and biotic factors that are known to control plant growth. This PhD study hopes to contribute to the understanding of multiple element interactions as well as interactions with abiotic factors, thereby enhancing the understanding of the variable tree plant growth observed at the sites described in this study.

2.4 Role of Litter fall and Litter Decomposition in Nutrient Cycling

Litter production, standing crop of litter (litter accumulation) and litter decomposition have received considerable attention as major pathways of nutrient cycling for sustaining and increasing soil fertility (Barlow *et al*., 2007; Moretto *et al*., 2001; Pandey *et al*., 2007; Xuluc-Tolosa *et al*., 2003; Zhang *et al*., 2008). They are fundamental ecosystem processes in tropical forests and plantations, representing some of the major pathways of nutrient cycling (Aber and Melillo, 1991; Berg and Meentemeyer, 2002; Finér, 1996; Heal *et al*., 1997 cited in Cadisch and Giller, 1997; Vitousek, 1984). The rates at which forest litter falls and subsequently decays regulate energy flow, primary productivity and nutrient cycling in forest ecosystems (Bray and Gorham 1964; Olson, 1963). The litter layer plays an important role including:

- acting as an insulating layer,
- protecting the soils from extreme changes in moisture and temperature, and
- protecting the soil from erosion and frost thereby improving water infiltration (Hering, 1982, Schutz, 1990, Veneklaas, 1995).

Generally, the course of nutrient dynamics during decomposition follows three phases:

- initial nutrient release through leaching,
- net immobilization when decomposer micro organisms retain or import nutrients, followed by,
- nutrient release when nutrients are released from the litter at a rate paralleling mass loss (Prescott *et al*., 1993, Sanchez, 2001).

The rate of litter decomposition has been shown to be affected by many factors in an ecosystem. In sub-tropical environments, the climate especially, seasonality characterized by alternating wet and dry periods, plays a vital role in regulating the rates of litter decomposition (Bunnel *et al*,. 1977; Meentemeyer, 1978; Sanchez, 2001; Tripatthi and Singh, 1992). The initial concentrations of cellulose, hemicellulose, lignin, and N, P and K have been shown to play a vital role in litter decomposition in different ecosystems (Osono and Takeda, 2001, 2004; Tripatthi and Singh, 1992). Substrate quality (Fogel and Cromak, 1977; Heal *et al*., 1978; Melillo *et al*., 1982; Swift *et al*., 1979) and the succession of microbial communities on the decomposing organic matter have been reported to be other factors that play a significant role in litter decomposition and nutrient dynamics.

Nitrogen fertilization has been reported to influence the rates of litter fall, forest litter layer and nutrient concentrations in the litter. The study by Vitousek (1982) showed an increase in litter fall with N addition, resulting in increased accumulation of plant organic matter on the forest floor. Smaills' (2008) research in *P. radiata* plantations in New Zealand showed that N fertilization significantly increased the N content and decreased the C:N ratio of the litter fall. The mass of the fermentation-humus (FH) layer, N concentration and carbon pool in the FH layer were increased as a result of the N fertilization. The mineral soil N concentration was also increased while the C:N ratio and pH decreased. The significant effects of fertilization were attributed to the variations in the fertilization regime and site characteristics. Litter accumulation on the forest floor has been reported to be a threat to site productivity (Morris, 1995). Substantial quantities of essential nutrients can be immobilized in the accumulated litter. In addition, organic acids are released and moisture penetration altered. This could lead to reduced nutrient turnover and availability and ultimately threaten long-term productivity (Dames *et al*., 1998; Morris, 1995; Wienand and Stock, 1995).

2.5 Impact of Geology on Tree Growth

In South Africa, the geology or parent material was shown to be an important factor determining forest productivity and the nature of the tree growth response obtained at different sites under fertilization (Louw, 1997; Louw and Scholes, 2006; Morris, 2003). The site conditions, especially the geology, on which plantations have been established in South Africa varies enormously, and responses in tree growth following nutrient applications vary accordingly (Carlson and Soko, 2000, Louw and Scholes, 2002). Numerous site-factors have been shown to have strong correlations between underlying geology and indices of forest productivity such as site index (Smith *et al*., 2005). Geology has been reported to play an important role in forest productivity and this has been used as a classification criterion in a number of forestry site classification systems in South Africa (Dotkin, 1993; Kunz and Pallet, 2000; Louw, 1995; Pallet and Morris, 1990). However, some of these studies did not show which of the soil properties related to geology were key to plant growth or which classification criteria were used to separate different geological groupings (Smith *et al*., 2005).

The impact of site in influencing tree growth response in other parts of the world has also been reported. Turner *et al*., (1992) working on *P. radiata* growing on two sites with different geologies in New South Wales, Australia showed that N and P fertilizer when applied together after the 2nd or 3rd thinning resulted in the most significant growth responses. The largest response occurred 4 years after application and no additional absolute response for either of the two sites 7 years after application. The site underlain by siltstone showed the largest fertilizer response of 70 m^3 ha^{-1} than the other granitic site with a response of 36 m^3 ha^{-1} site over the 7 years.

In New Zealand, Hunter and Smith (1996) reported that most forest soils are identified as been responsive to only one nutrient, while on many other sites there are nutrient interactions. The upland heaths of Britain and the claylands of northern New Zealand were shown to respond to P while the welded-pumice soils of southern Kaingaroa responded only to Mg^{2+} (Hunter *et al*., 1986). Sites in New Zealand differ in their natural fertility for both P and N, some sand dune forest sites were reported to be grossly deficient in N (Hunter and Smith, 1996).

2.6 Impact of Climate on Tree Growth Response

A clear understanding of the way environmental factors act on, and interact with, plant growth is essential. Climate is one of the most important factors that influence, among others factors (physiographic, edaphic, biotic) vegetation growth and distribution (Critchfield, 1983; Kutiel *et al.*, 2000; Padopoulos *et al*.,, 2008). Rainfall affects various soil biological activities because of its influence on soil moisture and temperature (Salamanca *et al*., 2003). The soil water availability determines both the response to nutrient additions and also the magnitude of the observed response, in water limited environments, fertilizer responses are likely to be modest (Allen, 1987; Sands and Mulligan, 1990). Nambiar *et al*., (1984, 1990) reported that competition adversely affects nutrition and water relations of young *P. radiata* in Australia plantations grown in soils low in available water and nutrients. They suggested that there is the need to understand how scarce resources can be managed in order to support productive forests. Several studies have pointed out the importance of water on tree growth response following fertilization in southern African (Carlson and Soko, 2000). Sheriff’s (1996) study on *P. radiata* stands showed that reducing the competition for water through thinning enhanced the fertilizer response. Morris (1993b) also showed the importance of rainfall on tree growth response following fertilizer applications on 12-year-old *P. patula* in Swaziland. He observed that the greatest responses to N occurred when application was made in mid-summer (December-January).

Climatic effects can have a marked impact on decomposition rates and the patterns of mineralization resulting from biogeochemical nutrient cycling (Swift *et al*., 1979). The onset of the wet season has been reported to accelerate decomposition and release available nutrients (Swift *et al*., 1981). Furthermore, wetting and drying cycles can accelerate the mineralization of labile nutrients such as those stored in the microbial biomass, and also increase the rate of turnover of more recalcitrant and protected organic pools of litter and surface soil (Cabrera, 1993 and Van Veen *et al*., 1984).

Other factors like temperature and photosynthetically active radiation (PAR) have been reported to affect tree growth response. Landsberg (1997) showed that plant growth is driven by the amount of photosynthetically active radiation absorbed by the foliage and the efficiency of use.. Louw and Scholes (2006) in *P. patula* plantations in South Africa showed that tree growth is positively correlated with mean annual temperature, and this was explained in terms of the stimulating effect that higher temperatures have on nutrient cycling and plant physiological processes. Research by Pérez *et al*., (2005) on *P. sylvestr*is in Brandenburg, Germany showed that the trees were adapted to the seasonal cycle, having a dormancy period during winter, triggered mainly by seasonal variation in temperature.

2.7 Foliar and Soil Analyses as Diagnostic Tools to Determine Nutrient Availability

Foliar analysis and interpretation has been reported to be a powerful diagnostic tool in evaluating forest and plantation nutrient status (Carlson and Soko, 2001; Chetty and du Toit, 1999; Linder, 1995; Louw and Scholes, 2003). Different diagnostic techniques have been commonly used to assess plant nutrient status and these include: the critical nutrient approach (Melsted *et al*., 1969; Ulrich, 1952; Ulrich and Hills, 1967), the diagnosis and recommendation integrated system (DRIS) (Beaufils, 1971, 1973; Campion and Scholes, 2007), vector analysis (Timmer and Stone, 1978), and optimum nutrient ratios (Campion and Scholes, 2007; Crous *et al*., 2008; Erricsson, 1994; Erricsson *et al*., 1992; Ingested, 1979; Linder, 1995).

Soil tests and foliar analysis have been used to identify sites where marginal deficiencies of nutrients or where other growth limiting factors, such as soil moisture, may limit the response to improved nutrition (Allen, 1987; Jokela *et al*., 1988). In general, foliar analyses have been shown to be more reliable than soil analyses for identifying nutrient deficiencies. Foliar analyses provide an integrated assessment of all the factors that influence nutrition (Crane, 1984 and Needham *et al*., 1990 reported by Campion, 2008; Ulrich and Hills, 1967), while soil analyses only show a measure of soil nutrient status and not a measure of nutrient demand of trees (Allen, 1987).

Louw and Scholes 2003 have reported that the current most widely used technique of foliar diagnosis is that based on the concept of critical levels. The critical levels concept has been explained as the tissue concentration of a particular element below which a significant yield response to the application of that nutrient is expected (Colbert and Allen, 1996). This concept has been remarkably successful in forestry e.g.

- Foliar nutrient concentrations were often reported to correlate significantly with forest site index values (Louw, 1997; Schutz, 1990; Turvey and Smethurst, 1994; Wang, 1995).
- It has also been useful in monitoring fertilizer response and changes in foliar nutrient concentration following fertilization (Carlson and Soko, 2001; Schonau, 1981).

Foliar analysis has been widely used to identify nutrient deficient stands in both South Africa (Campion and Scholes, 2007; Carlson and Soko, 2001; Crous *et al*., 2008; Louw and Scholes, 2003) and the rest of the world (Mead and Gadgil, 1978; Snowdon and Waring, 1990; Wells and Allen, 1985). However, foliar analyses must be viewed with caution as there are many other factors which can result in incorrect interpretations (Louw and Scholes, 2003). The factors include climate (Louw and Scholes, 2003), stand age, sampling position in the crown and season (Lambert, 1984; Linder, 1995; Payn and Clough, 1987). Linder (1995) pointed out that dilution effects on needle concentrations, associated with the increase in dry weight due to storage of carbohydrates, can also lead to substantial variation in foliar nutrient concentration.

Other studies have used leaf nutrient status of healthy and unhealthy trees, or using optimum nutrient ratios (Linder, 1995) or the diagnosis and recommendation integrated system (DRIS) (Beaufils, 1971, 1973; Campion and Scholes, 2007) norm to assess nutrient balance. Linder (1995) also used the method of nutrient ratios to identify, detect, correct nutrient imbalances, and maintain optimal nutrient status in *P. abies* trees. Target values were set for the foliar nutrient concentrations of each element, based on results obtained from laboratory studies and long-term forest nutrition experiments, in which plant nutrient requirements were established (Linder, 1995). The quantities of nutrients to be applied were estimated in relation to the target value (Linder, 1995). Some of the assumptions of the optimal nutrient ratio technique as reported by Linder, (1995) are as follow:

- Over a wide concentration range, the proportions of elements relative to N are at least, if not more important than the absolute nutrient concentration;
- Optimal growing conditions can only occur if all essential nutrients are presented in the correct proportions, and
- Optimal nutrient element proportions are similar for all higher plants and can be defined relative to N.

The DRIS approach was reported to be a multifactorial approach to identifying optimal tree nutrition (Beaufils, 1973). Beaufils (1973) reported that factors that potentially influence yield e.g. soil properties, climatic conditions, management practices and plant composition must be identified, and the relationships existing between these factors and yield must be defined. The established relationships are expressed as diagnostic indices which form calibrated norms, used for diagnosis and recommendation purposes (Beaufils, 1973). The approach was reportedly based on several assumptions, which include:

- Ratios of nutrient elements are often superior indicators of nutrient status than single element concentrations;
- Some nutrient ratios are more important than others; and
- Maximum yields can only be attained when ratios approach an optimal value, deviations from this value result in lower growth (Jones, 1981).

The "norms" are identified by the foliar nutrient concentrations and ratios of foliar nutrients for high-productivity stands. Stands with nutrient concentrations lower than optimum or ratios values are expected to respond well to fertilization. This approach has been reported to be more inclusive than the approach based solely on critical levels, but its reliability has been reported to be affected by the problem of weak definition, calibration and validation. The potential application of this technique has been documented for *P. radiata* (Romanyà Vallejo, 1996; Svenson and Kimberley, 1988), *P. Patula* (Schutz, 1990), and *P. taeda* (Hockman and Allen, 1990; Needham *et al*., 1990).

2.8 Forest Productivity Models

Forest resource managers face a number of important challenges, one of which is the need to provide forest products for an increasing world population in the face of a declining natural resource base, challenged by global change, desertification, and environmental pollution (Peng, 2000). There is the need to manage the available information about the present and future resource conditions in order to maximize and/or sustain productivity. Growth modelling plays a central role in forest management planning in the prediction of future yields, standing volume, harvesting schedules, yield optimization and sustainable utilization of wood resources in plantations (ICFR Annual Research Report, 2004).

A number of forest simulation models such as FOREST BGC (Running and Coughlan, 1988), BIOMASS (McMurtrie *et al*., 1990), PnET (Aber and Federer, 1992), G'DAY (Comins and McMurtrie, 1993) and CENTURY (Parton *et al*., 1988) have been developed for many reasons and for different users including resource managers, ecologists, economists, financial advisers, and students. These models have been used for the following purposes:

- Predicting tree volume (Battaglia and Sands, 1998);
- Optimizing appropriate silvicultural input for maximizing yield (Bossel,1991);
- Understanding forest succession (Bossel, 1996);
- Assessing effects of environmental stress such as air pollution, acid rainfall, and climate change (Botkin e*t al*., 1992);
- Evaluating sustainability of forest ecosystems (Botkin, 1993), and
- Testing various hypotheses about tree structure and function (Bugmann and Solomon, 1995).

The importance of forest simulations and applications in forest management are well documented in southern African (Campion *et al*., 2005; Dye, 2001; Dye *et al.*, 2004; Gush, 1999), and in the rest of the world (Almeida *et al.*, 2004a; Battaglia and Sands; 1998; Coops and Waring, 2001; Coops *et al.*, 1998; Landsberg, 2003a; Landsberg and Gower, 1997; Landsberg and Waring, 1997; Landsberg *et al.*, 2001; Nightingale *et al*., 2008; Paul *et al.*, 2007; Rodríguez *et al.*, 2002; Sands and Landsberg, 2002; Stape *et al.*, 2004). The origin of modern forest simulation systems lies in the development of a yield table by mensurationists in Germany in the late 18th century, published approximately 200 years ago (Vuokila,1995 cited by Peng, 2000). Extensive collection of forest biomass data and estimates of existing timber volumes led to the development of growth and yield models as powerful predictive tools for forest management since last century. Most of these growth and yield models used a site index to determine the potential or maximum growth rate (Clutter et *al*., 1983; Vanclay, 1995). The models are broadly divided into three categories as shown in Table 2.1 (Peng, 2000). (1) Forest growth yield models (empirical approach), (2) Forest succession models (hybrid approach), and (3) Forest process models (mechanistic approach).

Table 2.1: Comparison of three types of forest simulation models

Description	Growth and Yield models	Succession Models	Process Models
Purpose	management of timber production	ecological studies of forest dynamics and education tools	ecological studies of forest structure and function, and education tools
Forest types	mainly managed forest or plantations	mainly mature forests	natural or managed forests
Model complexity	low	intermediate to high	intermediate to high
Simulation time	short (10-20 years)	intermediate to long (50-1000 years)	intermediate to long (50-1000 years)
Attributes	Description	Explanation	Explanation
History	About 200 years	About 25 years	About 15-20 years
Data requirement	site-specific tree and environmental data	site-specific tree and environmental data and species-specific tree data	climate data, soil data, specific species tree data
Measure of environmental factors	site index	multiplication of effects of single factors	temperature, light, water, nutrients and disturbance
Simulation area	large (hundred or more hectares)	small (a gap size usually 0.01-0.1 ha)	small to large (few to many hectares)
Number of species Simulated	one to several commercial (timber) species	a few (or even more than 100) ecologically important species	single species or mixed stands
Modelling spatial relations among trees	vertical: function of tree size; distance dependent or independent	vertical: light extinction function; horizontal: generally distance independent	vertical: function of tree process; horizontal: distance independent
Model testing	calibration and validation	Calibration	calibration and validation
Examples	DMD[a]	FORSAK 2.0[b]	CENTURY4.0[c]

[a]DMD: Density Management Diagram (Smith and Woods, 1997)
[b]FORSKA 2.0: a forest succession (Leemans and Prentice,1989; Price and Apps, 1996)
[c]CENTURY 4.0: a process-based plant soil model (Metherell, 1992; Parton *et al*., 1987)
Note: The table was extracted from Peng (2000).

The emphasis of this research project was on process-based models and therefore more information will be presented for these models. Process-based or mechanistic models simulate stand growth in terms of the underlying physiological processes or mechanisms that govern growth, and the way stands are affected by the physical conditions, which trees are subjected to, and with which they interact (Landsberg and Gower, 1997; Landsberg *et al.*, 2001). Process-based models were originally developed for research purposes and other applications including:

- Prediction of growth and yield from existing plantations;
- Site-species matching;
- Exploration of the effects of different silvicultural practices on the utilization of site resources;
- Assessment of risks associated with plantation locations or management decisions;
- Evaluation of the effects of events such as fertilization and thinning;
- Improved understanding of production constraints and growth potential of a site, and
- Questions for which 'real time' experiments are not feasible, such as long-term impacts of practices on sustainability (Battaglia and Sands, 1998; Landsberg, 2003a; McMurtrie *et al.*, 1990).

However, few process based productivity models are adopted for forest management systems as they are either too complex, poorly validated, require large amounts of input data, of fundamental processes, such as carbon allocation, which are not readily available or economically obtainable (Battaglia and Sands, 1998; Landsberg, 2003a; Landsberg *et al.*, 2001).

Generalized models and a simplified process model, specifically the Physiological Principles Predicting Growth (3-PG) Model (Landsberg and Warring, 1997) have been developed to bridge the gap between conventional empirical, mensuration-based growth and yield models, and process-based, carbon balance models (Johnsen *et al.*, 2001; Landsberg, 2003a, b; Sands and Landsberg, 2002). The 3-PG model is a simple process-based, stand level model of forest growth that requires only readily available site, climatic and species data as inputs, and predicts the time-course of stand development in a form familiar to the forest manager, as well as biomass pools, stand water use, and soil available water. This model has received considerable attention and is widely used because it was developed with the end user in mind (user friendly), is robust with a simple and transparent structure, is extensively documented, the data inputs are readily obtained, outputs are of interest to the forest manager, and the model and source-code are freely available (Sands, 2004). Model validation has been reported to be very important in testing the performance of the model in predicting growth and productivity. Various aspects of the 3-PG model have been tested, e.g. stem diameter and volume growth (Almeida *et al.*, 2004a; Landsberg *et al.*, 2001; Rodríguez *et al.*, 2002; Stape *et al.*, 2004), leaf area index and above- and below-ground biomass (Landsberg *et al.*, 2003), stem number and available soil water (Coops and Waring, 2001; Dye, 2001), and sap-flow rates (Dye *et al.*, 2004).

There are five sub-models in the 3-PG model which include: the assimilation of carbohydrates, the distribution of biomass between foliage, roots and stems, the determination of stem number, soil water balance, and conversion of biomass into variables of interest to forest managers (Landsberg and Waring, 1997; Sands and Landsberg (2002). The mandatory inputs that are required by the model are monthly weather data (average values of daily solar radiation and temperature, atmospheric vapour pressure deficit (VPD), total rainfall and frost days per month), site specific factors, initial stand conditions and species specific parameter values. The model can be run for any number of years, using either monthly weather data or long-term monthly averages. Other inputs are factors describing the physical properties of the site: latitude, site fertility rating, maximum available soil water, and a general descriptor of soil texture. Long term climatic averages are normally used except when addressing a specific event such as fertilization, and droughts (Landsberg *et al*., 2001). The flow diagram (Figure 2.3) of the 3-PG model shows the sequence of calculations (Landsberg and Waring, 1997).

Flow diagram: 3-PG

INPUTS

Weather data (for representative year or year considered)
monthly average values: radiation, frost days per month, humidity
total precipitation
Initial biomass values
foliage (w_f), stems(w_s), roots (w_r)
Variables
max. available soil water
initial stem number
stand age maximum stand age
Parameter values
canopy quantum efficiency (α_c)
ratio $P_N/P_G = C_{pp}$
max. stomatal conductance (g_{cmax}), max. canopy conductance (g_{cmax}) parameters of the allometric equations
soil type parameters
max. litter fall rate
root turnover rate

↓

CALCULATE

Monthly time step

L* from foliage mass, $\varphi_{p.a}$
vapour pressure modifier to g_s max. g_c max
monthly transpiration from the **P**enman-**M**onteith equation
soil water balance, moisture ratio, soil water modifier
stem mass/tree = w_s/stem number
stem diameter from stem mass/tree
Utilizable φp.a ($\varphi_{p.a..u}$) from $\varphi_{p.a}$ and modifiers
$P_G = \alpha c \text{ X } \varphi_{p.a..u}$
$P_{N} = P_{G} \times C_{pp}$
carbon allocation coefficient (η_r, η_s, η_f)
component mass increment: $\Delta w_f = \eta f\ P_N$……etc.
update component mass: $w_f(t) = w_f(t-1) + \Delta w_f$…..etc.

↓

Annual time step

Figure 2.3 Flow diagram of 3-PG model showing the sequence of calculations (Landsberg and Waring, 1997)

The applications of the 3-PG model are well documented in the literature. Dye *et al.*, (2004) in South Africa reported that the 3-PG model can realistically simulate growth and water use over a wide range of rotation age and growth conditions. Esprey and Sands (2004) have also pointed out that the model is an ideal tool to determine site constraints on growth and potential productivity over a range of sites. This model has yielded credible predictions for a wide range of species across several countries, e.g. Australia and New Zealand (Landsberg and Waring, 1997; Nightingale *et al*., 2004, 2008; Paul *et al*., 2007; Sands and Landsberg, 2002), Brazil (Almeida *et al.*, 2004a; Stape *et al.*, 2004), Chile (Rodríguez *et al.*, 2002), USA (Coops and Waring, 2001; Landsberg *et al.*, 2001), South Africa (Campion *et al*., 2005; Dye, 2001; Dye *et al.*, 2004; Esprey *et al*., 2004), and Sweden (Landsberg *et al.*, 2003b).

The 3-PG and 3-PGS models were used to predict regeneration of old-growth rainforest and forest regeneration from seedlings in response to human-induced and natural disturbances in tropical rainforests in Australia (Nightingale *et al*., 2008). They reported statistically significant relationships between predicted and field measured estimates of stand structural attributes including, basal area, DBH and above-ground biomass. Nicholas *et al*., (2005) used the 3-PG model to predict the dominance and distribution of *Pinus ponderosa* (Doug. ex Loud.) in the Pacific Northwest of North America over the past 100 years, using climatic data provided by the Oregon Climate Service over the period from 1900 to 2000 produced by the Hadley Climate Center, UK.

Zhao *et al*., (2009) in China used the 3-PG model successfully to parameterize and validate the predictions of differently aged Chinese fir plantations using recent and long-term field measurements acquired at the Huitong National Forest Ecosystem Research Station. The model was used to simulate leaf area index, net primary productivity, biomass of stems, foliage and roots, litter fall, and shifts in allocation over a period of time and also to estimate changes in root C storage and decomposition rates in the litter fall pool as well as in total soil respiration. They reported that the predicted averaged above and belowground net primary productivity (13.81 t ha^{-1} a^{-1}) of the Chinese fir plantations was much higher than that of Chinese forests (4.8 - 6.22 t ha^{-1} a^{-1}), indicating that Chinese fir is a suitable tree species to grow for timber and also acting as a potential C sequestration sink.

CHAPTER 3

MATERIALS AND METHODS

3.1 Study Area

The study was conducted in *P. patula* and *P. elliottii* plantations at two separate sites, one located in Ngodwana and the other in Graskop in the escarpment area of the Mpumalanga province (Figure 3.1). The province of Mpumalanga is situated in the eastern part of South Africa; it is a summer rainfall region with precipitation occurring mainly in the form of thunderstorms. The mean annual rainfall varies from 350 mm in the north east to 1600 mm on the escarpment. Cold winters with heavy frost and occasional snowfalls are experienced on the escarpment, which is often cloaked in mist (Schulze, 1972).

Figure 3.1 Map of Mpumalanga Province in South Africa showing (by arrow) Graskop and Ngodwana, where the *Pinus elliottii* and *Pinus patula* sites are located

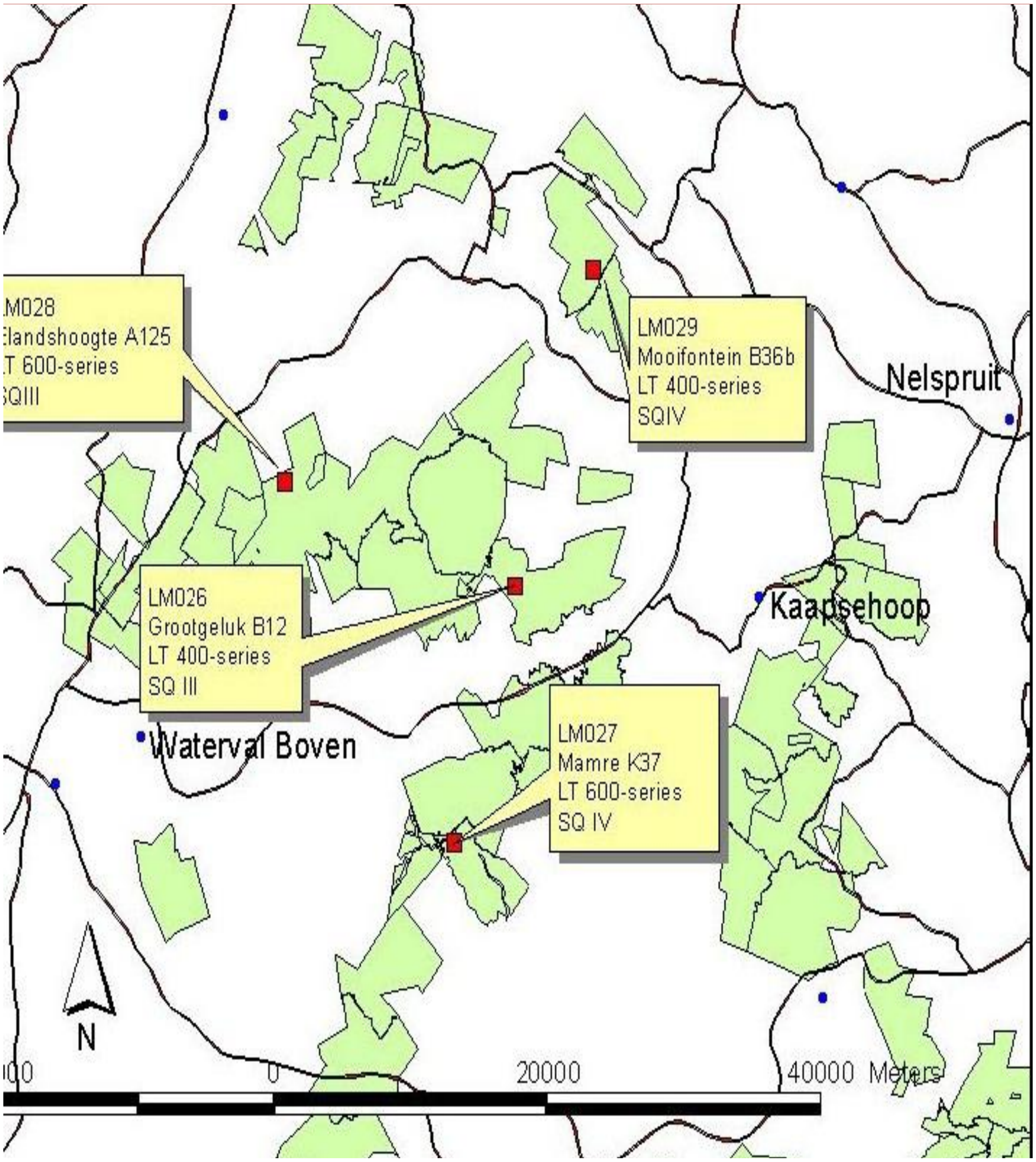

Figure 3.2 Map showing the *Pinus patula* study sites in Ngodwana, Mpumalanga Province of South Africa

3.2 Study Sites

3.2.1 *Pinus patula* plantations

Four existing trial sites of *P. patula* that were established in 2001 were used for this study, the sites are all in their second rotation and the rotation age is 19 years (Figure 3.2). The study sites are located on latitudes that range from 25° 23' 39" S to 25° 41' 43" S and longitudes 30° 26' 11.34" E to 30° 39' 38" E. The plot sizes are 26.4 x 26.4 m, 11 × 11 trees with 2.4 × 2.4 m spacing, with the inner measured plots being 21.6 x 21.6 m (9 × 9 trees were measured). There are four existing trial sites which are replicated twice with six treatments giving a total of 48 plots (4 × 2 × 6).

The details of the study sites with respect to trial number, plantation name, compartment, dominant geology, soil textural class, site quality, altitude, mean annual precipitation (MAP), mean annual temperature (MAT), land type according to the South Africa Pulp and Paper Industry (Sappi) general land type classification (Pallet, 1991), and other descriptions are given in Table 3.1. Severe drought mortality was observed at the Elandshoogte site in 2005 and 2006; and tree damage was caused by strong winds at the Grootgeluk site and, to a lesser extent, at the Mooifontein site during August of 2006. The annual rainfall at the Elandshoogte and Mooifontein sites and temperature for the study period are presented in Figure 3.3. These rainfall data were also used for the Mamre and Grootgeluk sites as they were the closest data set available in terms of altitude and location, since there was no complete data set available for the Mamre and Grootgeluk sites. The forest contractors responsible for the experimental sites were not required to collect these data. The temperature data were not available for the *P. patula* study sites, therefore, mean monthly and annual temperatures of Lydenburg at an altitude of 1436 m above seal level, and latitude 25° 11" S and longitude 30° 48" E, were used.

Table 3.1: Description and Classification of the *Pinus patula* Study Sites located in Ngodwana, Mpumalanga Province of South Africa

Site description	Study Sites			
	Elandshoogte	**Grootgeluk**	**Mamre**	**Mooifontein**
Trial number	LM 028	LM 026	LM 027	LM 029
Compartment	A125	B12	K37	B36
Number of Plots	12	12	12	12
Fertilization date	24th Jan. 2001	23rd Jan. 2001	25th Jan. 2001	25th Jan. 2001
	8th Jan. 2003	7th Jan. 2003	9th Jan. 2003	7th Jan. 2003
Age (year) of fertilization application	11(2001) and 13 (2003)	11(2001) and 13 (2003)	11(2001) and 13 (2003)	11(2001) and 13 (2003)
Initial stock stem density (#stems ha^{-1})	1420	1409	1414	1693
Planting date	Sep. 1989	Dec. 1989	Dec. 1989	Nov. 1989
Trial starting age	11 years (2001)	11 years (2001)	11 years (2001)	11 years (2001)
Trial end age	18 years (2007)	18 years (2007)	18 years (2007)	18 years (2007)
Geology	Andesite	Shale	Andesite/Shale	Shale
Pruning (2m)	31st Aug. 1994	30th Nov. 1993	30th Nov. 1993	1st Jan. 1994
Site Index$_{15}$	19.6	19	18.6	18.1
Site quality	3	3	4	4
Soil Textural class	Clay	Clay loam	Clay loam	Clay loam
Latitude	25° 30' 14" S	25° 33' 37" S	25° 41' 43" S	25° 23' 39" S
Altitude (m) above sea level	1740	1520	1700	1500
MAP (mm year $^{-1}$)	912	1174	1140	1174
MAT (°C)	14.6	15.7	14.7	15.7

The plantations were never thinned and fertilizer was not applied at planting
Particle-size distribution described by Pallet, 1991
Site Index$_{15}$ = the height of dominant trees at the reference age 15
Site quality is according to Sappi land type classification, where 3 is of better soil fertility than 4
MAP = Mean annual precipitation, and MAT = Mean annual temperature.

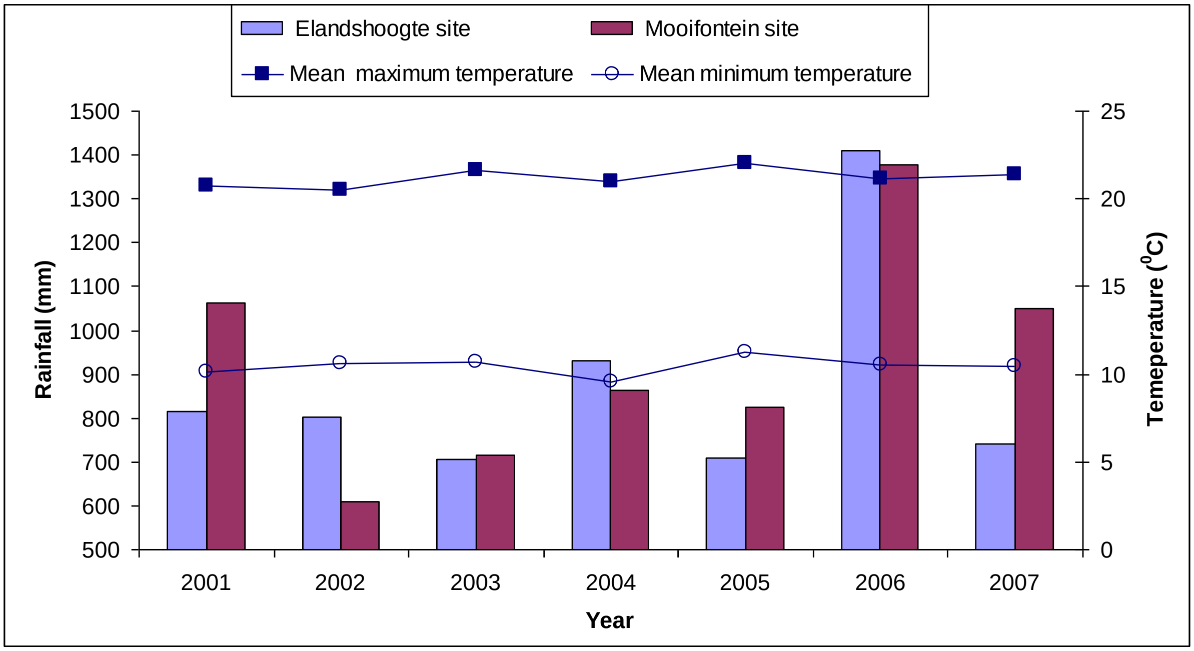

Figure 3.3 Annual rainfall (mm) and temperature (ºC) (maximum and minimum) for *Pinus patula* at the Elandshoogte and Mooifontein sites. The rainfall data from the Elandshoogte and Mooifontein sites were also used for Mamre and Grootgeluk sites

3.2.2 *Pinus elliottii* plantations

A new trial site of *P. elliottii* was established in 2006, in Graskop. The trees were planted in 1989 making them 17 years old in 2006. The study site is located on latitude 24° 36' 34" S and longitude 30° 30' 6" E. The plot sizes are 56.7 x 35.1 m, 21 × 13 trees with 2.7 × 2.7 m spacing; with the inner measured plot being 40.5 x 18.9 m (18 to 21 trees were measured). The trial was replicated four times with four treatments creating 16 plots (4 × 4). Effective soil depth of the site is greater than 150 cm, with the depth limiting material being saprolite. The details of the study site with respect to trial number, compartment, fertilization date, initial stock (stem density), and other descriptions are given in Table 3.2. The monthly climatic data, rainfall (mm) and temperature ºC for the area during the study period are presented in Figure 3.4.

Table 3.2: Description and Classification of the *Pinus elliottii* site located in Graskop, Mpumalanga Province of South Africa

Site description	**Study site**
Name of Plantation	Graskop
Trial number	N15a
Compartment	Tweefontein , Graskop KLF
Initial stock, stem density (#stems ha^{-1})	1372
Planting date	November, 1989
Fertilization application date	1st February, 2006 (17 years)
First tree measurements	27th February, 2006 (17 years
Second tree measurements	31st May, 2007 (18 years)
Fire incident at the site	End of July, 2007 (18 years)
Geology	Dolomite
Thinning	1-8 years, 2-12 years, and 3-17 years (January 30th 2006, before fertilizer application)
First pruning at 3 m **second at 5 m** **third at 6 m** **fourth at 7 m** **fifth at 9 m**	Done at 6 years (1995) at 7 years (1996) at 8 years (1997) at 10 years (1999) at 11 years (2000)
Site Index$_{15}$	22.1
Site quality	1
Soil Textural Class	Clay loam
Latitude	24° 36' 34" S
Altitude (m) above sea level	1360
MAP (mm year^{-1})	1300
MAT (°C)	17

Site Index$_{15}$ = is the height of the dominant trees measured at the reference age 15

MAP = Mean annual precipitation, and MAT = Mean annual temperature.

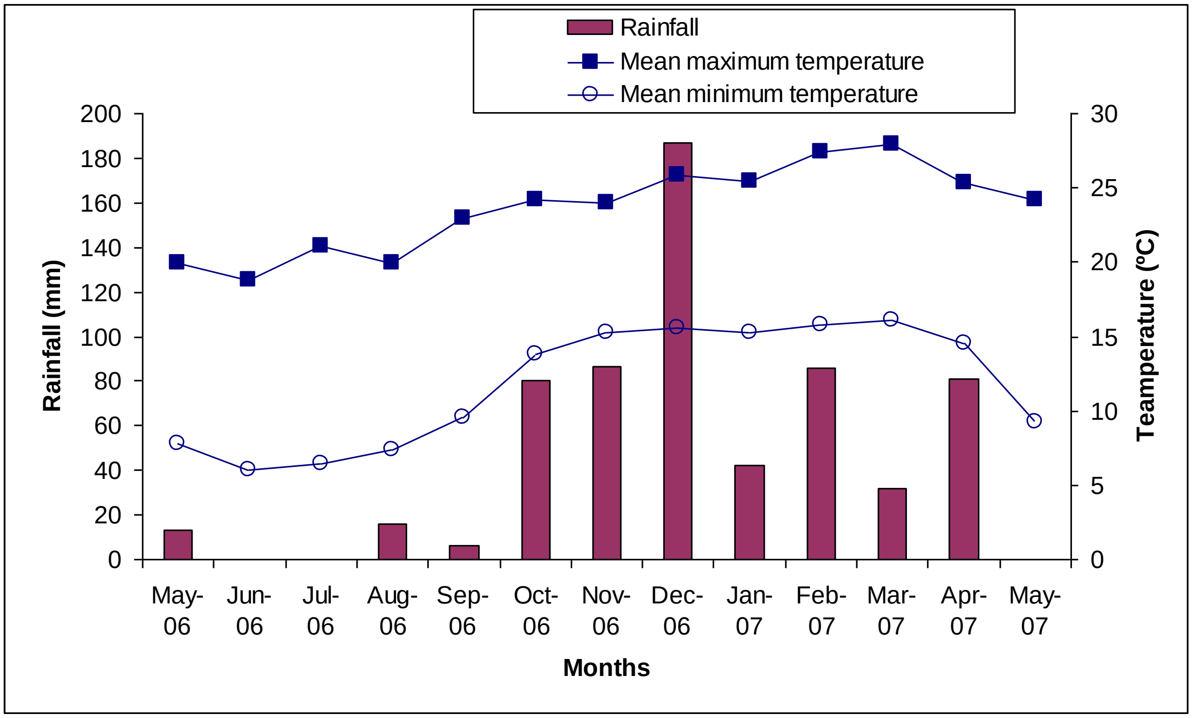

Figure 3.4 Monthly rainfall (mm) and temperature (ºC) (maximum and minimum) for *Pinus elliottii*, Graskop area during the study period (2006-2007)

3.3 Experimental Design and Treatments

3.3.1 *Pinus patula* plantations

There are four existing trial sites which are replicated twice giving a total of 48 plots (6 × 4 × 2). Each plot size is 699.96 m^2, 11 × 11 trees with 2.4 × 2.4 m spacing. Six existing fertilizer treatments on four different sites of *P. patula* were used for this study.

The treatments were as follow:

1. Control: No fertilizer was applied (no LAN and no Urea)

2. 100 kg ha^{-1} N as LAN (28%) at 11 years old

3. 100 kg ha^{-1} N as Urea (46%) at 11 years old

4. 100 kg ha^{-1} N as LAN (28%) at 13 years old

5. 100 kg ha^{-1} N as LAN (28%) at 11 and 13 years old (Total 200 kg ha^{-1} N)

6. 100k kg ha^{-1} N as Urea (46%) at 11 and 13 years old (Total 200 kg ha^{-1} N)

Where LAN = Limestone ammonium nitrate
Note: 217 kg Urea (46%) = 357 kg LAN (28%) = 100 kg N.

3.3.2 *Pinus elliottii* plantations

The design is a 2 × 2 factorial, with four replicates and four fertilizer treatments giving a total number of 16 plots (4 × 4). All fertilizers were broadcasted. The study was planned to last for two years (2006-2008), but lasted for one year because of a fire which occurred in July, 2007 and burnt the entire site.

The treatments were as follow:

1. Control: No fertilizer was applied (no LAN, no Super phosphate)

2. 100 kg ha^{-1} P as Super phosphate at 17 years in 2006

3. 200 kg ha^{-1} N as LAN (28%) at 17 years in 2006

4. 200 kg ha^{-1} N as LAN (28%) and 100 kg ha^{-1} P as Super phosphate (10.5%) at 17 years in 2006.

3.4 Sampling and Measurements

3.4.1 Sampling and measurements of tree growth: basal area, tree height and litter depth

***Pinus patula* plantations**

The inner 466.6 m^2 plot was measured. All trees within this area were measured between the end of January and the first week in February from 2001 to 2007 for diameter at breast height (DBH, 1.3 m above ground) and 18 tree heights (trees 28 to 36 and 46 to 54) were measured using a vertex hypsometer. Forest litter depth was measured annually using a meter stick adjacent to where the tree height was measured in each plot.

***Pinus elliottii* plantations**

The inner 765.45 m^2 plot was measured. Eighteen-twenty-one trees within this area were measured for diameter at breast height (DBH, 1.3 m above ground) and tree heights using a vertex hypsometer in all the sites across the different fertilizer treatments. The tree measurements were first done on the 1st February 2006 shortly before the fertilizer was applied, and the final tree measurements were done in May 2007, before the fire that burnt the entire site. The forest litter depth was first measured in July 2006, but could not be measured again due to the fire incident that burnt the site in July 2007.

3.4.2 Sampling and measurements of foliar nutrient concentrations

Four dominant and co-dominant trees were selected from each plot of *P. patula* and *P. elliottii*. The foliage sampling was conducted in the winter period, July 2006 for *P. elliottii* and in May/June, 2007 for *P. patula*. Mature needles of the previous season's growth were collected from the upper third of the canopy of each tree and samples taken at different positions on the branches (tip, middle and the base). The samples from the four trees in each plot were bulked, oven dried at 60 ºC for 72 hours, ground and used for chemical analyses. Total N was determined from the ground samples using the Kjeldahl digestion method and total P was extracted with boiling *aqua regia* and the concentrations determined using a Leco FP528 N analyzer (Horneck and Miller, 1998) and Inductively Coupled Plasma Spectrophotometer (ICP-OES) (Kunze, 1965) respectively. Total organic carbon (C) was measured using the loss on ignition technique (Davies, 1974). Total cations Ca^{2+}, Mg^{2+} and K^+ were extracted with 1 Molar (M) ammonium acetate and manganese (Mn^{2+}) extracted with citrate-bicarbonate dithionite (CBD) and the cation concentrations were determined (ICP-OES) (Kunze, 1965).

3.4.3 Soil sampling and analyses

Soil samples were collected in May 2006 and 2007 from both the *P. patula* and *P. elliottii* sites. Twenty soil samples were randomly collected from each plot at a depth of 0-20 cm using a soil auger and bulked in each plot. The soil was air-dried, sieved through a 2-mm sieve and analysed. Total N was determined from the samples, using the Kjeldahl digestion method and total P was extracted with boiling *aqua regia* and the concentrations determined using a Leco FP528 N analyzer (Horneck and Miller, 1998) and ICP-OES (Kunze, 1965) respectively, while Available P was determined using the Bray-2 method (Bray and Kurtz, 1945). Total organic C was measured using the loss on ignition technique (Davies,1974); total cations (Ca^{2+}, Mg^{2+} and K^+) were extracted with 1M ammonium acetate and Mn^{2+} was extracted with CBD and the cation concentrations were determined by ICP-OES (Kunze (1965). Exchangeable acidity was determined with standard sodium hydroxide (NaOH) using the titrometric method (Reeve and Sumner, 1971); particle size distribution was determined using the hydrometer method (Day, 1965); pH was determined in both distilled water and 1 M KCl (Soil and Plant Analysis Council, 1998). Effective cation exchange capacity (ECEC) was calculated by summing the concentration of the cations (Ca^{2+}, Mg^{2+} and K^+) converted from mg kg^{-1} to $cmol_c$ kg^{-1} and the exchangeable acidity ($cmol_c$ kg^{-1}) values in each plot. Sodium (Na^+) was not determined in this study.

3.4.4 Ammonification, nitrification and N mineralization rates

Ammonification, nitrification and net N mineralization rate was determined using the *in situ* (field incubation) method from May 2006 to March 2007 for *P. patula* and from May 2006 to May 2007 for *P. elliottii* at intervals of six to seven weeks. At the start of the sampling, five and ten pairs of stainless steel cores (size 5 cm diameter and 25 cm long) were randomly located and driven into the mineral soil to a depth of 20 cm in each plot of *P. patula* and *P. elliottii* respectively. One sample of each pair of the soil cores was removed, placed in cooler boxes and transported to the laboratory for determination of the initial (Time t_o) N concentrations, ammonium (NH_4^+) and nitrate, (NO_3^-). The remainder of the steel cores were covered with plastic caps to prevent leaching, and incubated for six to seven weeks under field conditions. After incubation, the soils from the remaining steel cores (Final time, t_1) were analyzed for NH_4^+ and NO_3^-. Ammonium and NO_3^- concentrations were determined as soon as possible using the colorimetric method, after extraction of the soil samples with a 0.5 M K_2SO_4 solution (Anderson and Ingram, 1993).

Ammonification and nitrification rates were calculated using the following equations:

$$\text{Ammonification: } = \frac{\left[\text{Final NH}_4{}^+\ (t_1) - \text{Initial NH}_4{}^+\ (t_0)\right]}{\text{Incubation period (day) } (t_1\text{-}t_0)} \qquad [1]$$

$$\text{Nitrification: } = \frac{\left[\text{Final N0}_3{}^-\ (t_1) - \text{Initial N0}_3{}^-\ (t_0)\right]}{\text{Incubation period (day) } (t_1\text{-}t_0)} \qquad [2]$$

While net N mineralization rate was calculated by summing the net ammonification and the net nitrification rates for each soil core over the incubation period using the following equations:

Net N mineralization rate:

$$= \frac{\left[\text{Final NH}_4{}^+ (t_1) - \text{ Initial NH}_4{}^+ (t_0) + (\text{Final N0}_3{}^-\ (t_1) - \text{ Initial N0}_3{}^- (t_0)\right]}{\text{Incubation period (day) } (t_1 - t_0)} \qquad [3]$$

Where Time t_1 is the end of incubation

Initial Time t_o is the beginning of incubation

Incubation period is the period between the beginning and end of incubation

The fresh soil samples from each steel tube were analyzed separately and the mean per plot determined, the analyses were carried out at the laboratory of the School of Animal, Plant and Environmental Sciences, University of the Witwatersrand and the results are expressed in µg N g dry soil $^{-1}$ day $^{-1}$.

3.4.5 Litter fall and forest floor litter sampling

Sampling and measurements of litter fall and nutrient concentrations

A total of 192 litter traps were used for this study, 144 at the *P. patula* and 48 at the *P. elliottii* site. The traps (1 m x 1 m x 30 cm) were made from shade cloth with a mesh size of 1 mm.

Figure 3.5 Photograph of a litter trap as located in each of the study sites

The study commenced in May, 2006 and lasted for one year. Three litter traps were randomly located in each plot, 1 m above the ground to avoid contamination of the litter samples with soil. The litter samples were emptied every six to seven weeks for the period of the study, then transported back to the laboratory and sorted into needles, wood (small branches), and sporangia (includes micro and megasporangia) and cones. The samples were oven dried at 60 ºC for 72 hours to a constant mass, ground and sub-samples taken for chemical analyses. Total N was determined from the ground samples using the Kjeldahl digestion method and total P was extracted with boiling *aqua regia* and the concentrations determined using a Leco FP528 N analyzer (Horneck and Miller, 1999) and ICP-OES (Kunze, 1965) respectively. Total organic C was determined using the loss on ignition technique (Davies, 1974); total cations (Ca^{2+}, Mg^{2+} and K^{+}) were extracted with 1 M ammonium acetate and Mn^{2+} was extracted with CBD and the concentrations were determined by ICP-OES (Kunze, 1965).

Sampling of forest floor litter and measurements of nutrient concentrations

Standing forest floor litter was sampled at the beginning of the study at the same time the first litter fall samples were collected. Forest floor litter was randomly collected from three points in each plot (from the surface of the litter to the surface of the mineral soil layer) using a quadrat size of 0.5 m by 0.5 m (surface area 0.25 m^2). A sharpened long-bladed knife was used to cut into the litter and this was guided by the quadrat. The litter was transported to the laboratory, and sorted into needles, wood (small branches), and sporangia and cones, oven dried at 60 ºC for 72 hours to a constant mass, ground and sub-samples were taken for analyses. Total N was determined in the ground samples using the Kjeldahl digestion method and total P was extracted with boiling *aqua regia* and the concentrations determined using a Leco FP528 N analyzer (Horneck and Miller, 1998) and ICP-OES (Kunze,1965) respectively. Total organic C was determined using the loss on ignition technique (Davies, 1974); total cations (Ca^{2+}, Mg^{2+} and K^{+}) were extracted with 1 M ammonium acetate and Mn^{2+} was extracted with CBD and the concentrations were determined by ICP-OES (Kunze, 1965).

Litter decomposition and measurement of nutrient concentrations

Litter decomposition rate was determined using the litter bag method. The litter bags of size, 20 cm × 30 cm were made from shade cloth with a mesh size of 1 mm. The study commenced from July 2006 to May 2007 in both *P. patula* and *P. elliottii* plots. A total of 108 litter bags, 18 in each plot of *P. patula* and 144 litter bags, 36 in each plot of *P. elliottii* were randomly placed in each plot respectively. One set of treatment (replicate) plots was used in both *P. patula* and *P. elliottii*; the objective of the decomposition study was to evaluate the nutrient turnover rate in the two species. Twenty grams of the freshly fallen needle litter were weighed into each of the litter bags, closed at the end, labelled, numbered and randomly placed on the litter layer in the plots close to the surface. Representative freshly fallen litter was also collected and taken to the laboratory for soil moisture correction and oven dried at 60 ºC to a constant mass. Three litter bags were recovered from each plot at intervals of six to seven weeks at the same time the litter fall samples were collected. The litter bags were carefully placed in paper packets to prevent any loss of material, and taken to the laboratory. The content of each litter bag was emptied carefully so as not to lose any material e.g. micro-fauna and fine-roots were removed. The litter samples were oven dried at 60 ºC to a constant mass, and weighed to determine the mass loss (decomposition). The litter collected at each sampling site and the samples collected for initial moisture determination were ground and analyzed for total N and P, total organic C and total cations (Ca^{2+}, Mg^{2+} and K^{+}). Total N was determined in the ground samples using the Kjeldahl digestion method and total P was extracted with boiling *aqua regia* and the concentrations determined using a Leco FP528 N analyzer (Horneck and Miller, 1998) and ICP-OES (Kunze, 1965) respectively. Total organic C was determined using the loss on ignition technique (Davies, 1974); total cations (Ca^{2+}, Mg^{2+} and K^{+}) were extracted with 1 M ammonium acetate and Mn^{2+} was extracted with CBD and the concentrations were determined by ICP-OES (Kunze, 1965). The rate of litter decomposition was calculated as a function of mass loss over time (difference between the final and initial mass over the period of incubation).

3.5 Climatic Data

Rainfall data for the *P. patula* study sites were provided by the South Africa Pulp and Paper Industry (Sappi) weather station at monthly intervals for the study period (2001-2007). Rainfall data for the Mamre and Grootgeluk sites were not complete for all the years and because of this, the data for Elandshoogte and Mooifontein were used for Mamre and Grootgeluk respectively since their altitudes are similar and the sites are nearby to each other. The temperature data were not available for the *P. patula* study sites, therefore, mean monthly and annual temperatures of Lydenburg at an altitude of 1436 m above seal level, and latitude 25° 11' 0" S and longitude 30° 48' 0" E were used. This being the closest data set available in terms of altitude and location to the study sites. The rainfall and temperature data for the *P. elliottii* study site at Graskop, together with the temperature data from Lydenburg, were obtained from the South African Weather Service (SAWS).

3.6 Calculations and Statistical Analyses

Allometric equations were used to calculate stand volume using tree height and basal area data. The volume equation used is based on the Schumacher and Hall model, it is normally written as:

$$\ln V = b_0 + b_1 \ln(DBH + f) + b_2 \ln H \qquad [4]$$

Where: ln = natural logarithm to the base e

V = stem volume (m^3, under bark), usually to 75 mm tip diameter

DBH = breast height diameter (cm, over-bark)

for *P. patula*:

f = 8 correction factor

H = tree height (m)

b_0 = -13.4694

b_1 = 2.4396

b_2 = 1.3254

and for *P. elliottii*:

f	=	0 correction factor
b_0	=	-10.6771
b_1	=	1.9306
b_2	=	1.1567

Coefficients for the equation were supplied by Bredenkamp (2000).

The basal-area ($m^2\ ha^{-1}$) was calculated using the equation provided by Von Gadow and Bredenkamp, (1992).

$$\text{Basal area } (m^2\ ha^{-1}) = \left[\left(\frac{Dq}{200}\right)^2 \text{ x } \pi\right] \text{x} \left[\frac{1}{plot\,area}\right] \text{x } n \quad where\ \ Dq = \sqrt{\frac{\Sigma_{i=1}^{n}\ d_i^2}{n}} \qquad [5]$$

Where d	=	individual tree DBH measurements on plots
n	=	number of live trees on plot
Plot area	=	plot area in hectare (ha)
Dq	=	Quadratic mean

The plot tree volume and the basal area values were converted to hectare values. The quadratic mean diameter and not the arithmetic mean diameter was used since it is better related to basal area and tree volume (Bredenkamp, 1994).

The percentage of the remaining litter mass was calculated using the equation described by Alhamd *et al*., (2004):

$$\frac{L_t}{L_0} \times 100 \qquad [6]$$

Where L_t = the final litter dry mass after a given month of decomposition

L_0 = the litter dry mass at the beginning of the decomposition

Nutrient pool sizes (kg ha^{-1}) in the litter fall and forest floor litter in *P. patula* and in *P. elliottii* were calculated by multiplying the mass of litter fall and the nutrient concentrations in %.

In addition, soil nutrient pools (kg ha^{-1}) were calculated using the equation:

$$\frac{NC}{100} \times BD \times D \qquad [7]$$

Where NC = nutrient concentrations (%)

BD = bulk density in kg m^{-3} (1180 kg m^{-3}, Morris, 1986)

D = soil depth in m (to a depth of 1cm)

All statistical procedures were performed using STATISTICA (StatSoft, version 6, 2002). Absolute tree growth values were used for the statistical analyses and the values were first tested for normality and assumption of constant variance, the concentration of Mn^{2+} in the soil across the sites was log transformed to normalize the distribution. Data for *P. patula* were analyzed using a number of tests. The orthogonal contrasts method was used in testing the main and the interaction effects. The general linear model (GLM) nested design analysis of variance (ANOVA)**,** with replicates nested within the site to test for significant difference between, fertilizer treatments and sites for stem density, tree heights, basal area and stand volume. The significant differences between treatments, sites, year of sampling, with replicate nested within the sites for soil properties were also determined. Nutrient concentrations of different components, foliage, litter fall, forest floor litter, and litter decomposition were tested for significant differences between treatments, site and months for litter fall and litter decomposition**.** The effects of treatment, site, and months of sampling on N mineralization, ammonification and nitrification rates were tested using the GLM method. A repeated measure ANOVA was used to test for significant differences in amount of litter fall and litter depth between the plots across the sites and between the treatments. Correlation tests were used to determine the relationships between the stem density, tree heights, basal area and stand volume and quadratic DBH (using tree growth increment), soil properties, amount (concentration) of cations present in different nutrient pools (soil, litter and foliage) across the sites, as well as the relationships between ammonification, nitrification and N mineralization rate and tree growth parameters. Post-hoc testing was carried out using Fisher's least significant difference (LSD) technique.

Data for *P. elliottii* were analyzed using a number of tests. The significant differences between the fertilizer treatments and the replicates, and the basal area, stand volume, tree heights and quadratic mean DBH were tested using factorial ANOVA. The significant differences between treatments and year (2006 and 2007) of sampling for soil properties; and treatments and months for litter fall, litter decomposition, N mineralization, nitrification and ammonification rate were tested using a factorial ANOVA design. Nutrient contents of different components, foliage, litter fall, forest floor litter, and litter decomposition were also tested for significant differences between treatments and the sampling period. Correlation tests were used to determine the relationships between tree height, volume, basal-area and quadratic mean DBH (using tree growth increment) and soil properties; concentrations of cations present in the different pools (soil, litter and foliage) across the different fertilizer treatments, as well as the relationships between ammonification, nitrification and N mineralization rate and tree growth parameters. Post-hoc testing was carried out using a Fisher (LSD) test technique. The results are presented as means plus confidence intervals at 5% significant level except where otherwise stated.

3.7 The Physiological Principles Predicting Growth (3-PG) model

The 3-PG model described by Landsberg and Warring (1997) was used to predict the tree growth (quadratic DBH, basal area and stand volume) parameters across the sites following late rotation fertilization. The model simulation was initialized when the trees were at age two because the accuracy for young trees prior to canopy closure has been reported not to be high (Landsberg, 2003a; Landsberg and Waring, 1997). The model runs were conducted for 17 years (planting date, 1989 to 2007, end of the study) for *P. patula*; from 1989 to 2007, and to 2017 (28 years), which would be the end of the rotation for *P. elliottii*.

The model parameters used for this study were mostly the parameters described by Dye (2001) for *P. patula* and *P. elliottii* (unpublished), except where otherwise stated (Table 3.3 and 3.4). Long-term mean monthly solar radiation, temperature, vapour pressure deficit (VPD), frost days and rainy days were obtained from a new version of 3-PG (named 3-PG Sim-A-Tree) described by Peter Dye (Dye 2005). The Sim-A-tree model compiles long-term climatic data for different weather stations in South Africa from 1957 to 2000. Climatic data from 1989 (when the trees were planted) to 2000 were extracted from the model based on the locations and altitude of the study sites, while the climatic data from 2001 to 2007 were obtained from the South Africa Weather services. Solar radiation and VPD from 2001 to 2007 were calculated using the Penman-Monteith equation in the GC_PM Spreadsheet model. The mean of the last ten years of monthly climatic data, 1998-2007 was calculated, and used repeatedly from 2008 to 2017, the end of the rotation for *P. elliottii*. This is one way to estimate climate variables into the future. The 3-PG model calculates mean air temperature and vapour pressure deficit (D) from mean minimum and maximum air temperatures. In *P. patula,* the rainfall data from the Elandshoogte and Mooifontein sites were used for the Mamre and Grootgeluk sites. This set being the closest available in terms of altitude and location, since there was no complete set available for the Mamre and Grootgeluk sites. The climatic data from Graskop were used for the *P. elliottii* study site, where the site is located.

The mean maximum available soil water content was obtained using the method described by Smith *et al*., (2005), calculated as the product of soil depth and the texture-derived available water capacity. A fertility rating (FR) value of 0.8 was used based on the fact that treatments had no significant effect on the tree growth parameters at the *P. patula* and *P. elliottii* sites, which indicates that the soils are fertile. The average monthly litter fall value used in this study was calculated by dividing the annual litter fall by 12. Other parameter values used in the model simulations are the ones described by Dye (2001) for *P. patula* and *P. elliottii* (unpublished) except where otherwise stated (Table 3.3 and 3.4). Thinning values in the model were adjusted to account for the stem number at age 8 years (557 #stems), 12 years (395 #stems), and 16 years (285 #stems) before wind damage; and 17 years after wind damage (230 #stems) for *P. elliottii*. Soil textural class was determined from the site, while the latitude, initial tree stock and planting date data and other information were supplied for both *P. patula* (Table 3.1) and *P. elliottii* (Table 3.2) by the forestry industry that established the trial. A flow chart of 3-PG illustrating the model structure as described by Dye, 2001 is shown in (Figure 3.5)

3.8 Model Performance

3-PG model-performance was evaluated for *P. patula* using the correlation (r) between observed and simulated values (Almeida *et al.*, 2004b; Esprey and Smith, 2002; Landsberg *et al.*, 2003; Stape *et al.*, 2004). This was however, not possible for *P. elliottii* since the 2-year (2006-2007) data set (n = 2) was too small to estimate the correlation between observed and simulated values. Therefore, model predictions of tree growth parameters in *P. elliottii* were assessed in terms of percent bias (Campion *et al*., 2005), calculated as:

$$\frac{\text{Observed}(\text{O}) - \text{Predicted}(\text{P})}{\text{Predicted}(\text{P})} \qquad [8]$$

The negative values indicate model over-prediction.

The predicted results obtained in 2017, the end of rotation in *P. elliottii*, were compared with the conventional/empirical growth yield table for South Africa (Kassier and Kotze, 2000).

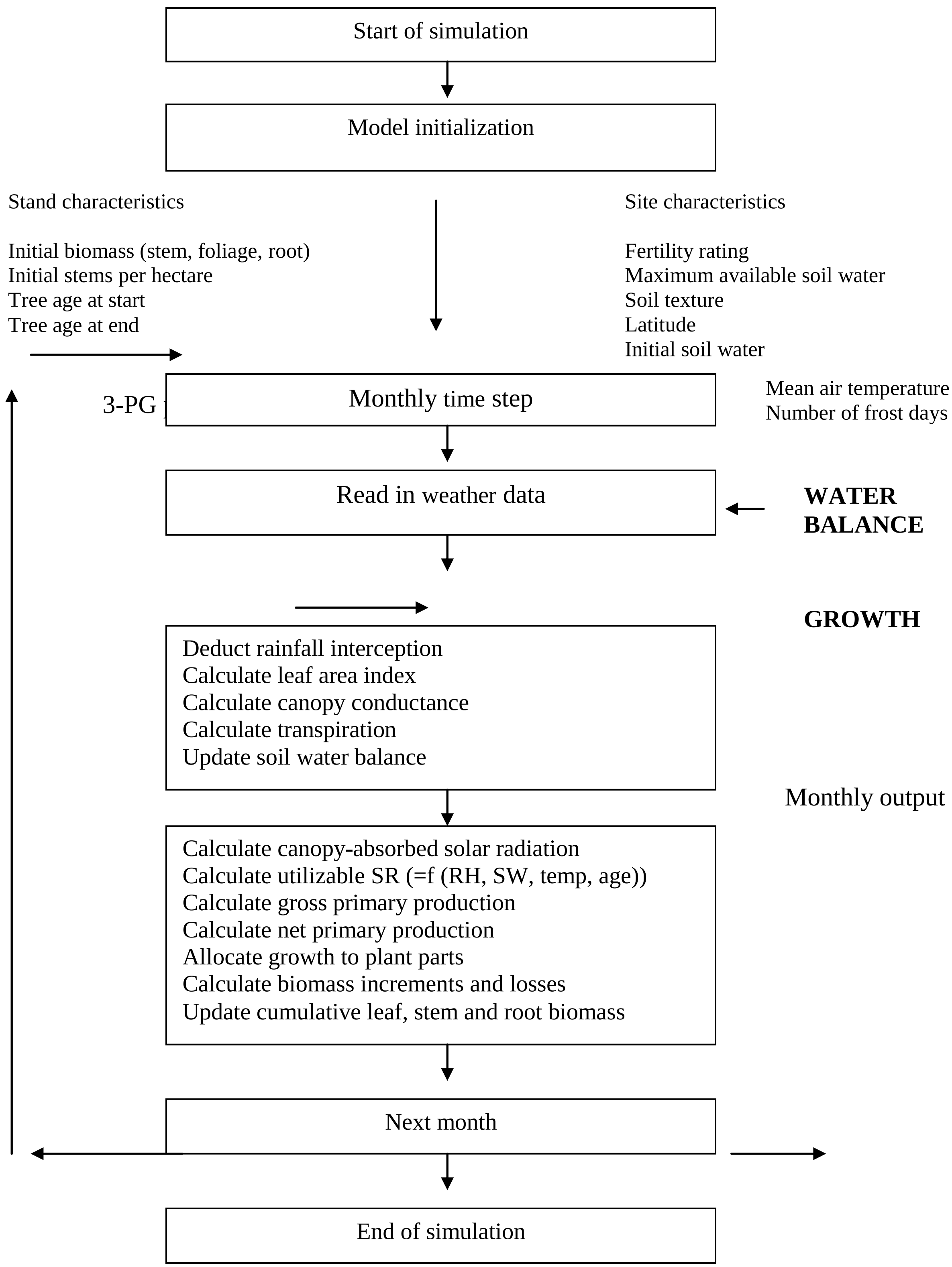

Figure 3.6 A flow chart of 3-PG illustrating the model structure as described by Dye (2001)

Table 3.3: *Pinus patula* model parameters as described by Dye (2001) except where otherwise stated

Parameters	Value used
Biomass partitioning and turnover	
Allometric relationships & partitioning	
Foliage:stem partitioning ratio @ D=2 cm	1
Foliage:stem partitioning ratio @ D=20 cm	0.2
Constant in the stem mass v. diam. Relationship	0.01
Power in the stem mass v. diam. Relationship	3.112
Maximum fraction of NPP to roots	0.4
Minimum fraction of NPP to roots	0.2
Litterfall and root turnover	
*Maximum litterfall rate	0.02 This study. 0.035 (Dye, 2001)
Litterfall rate at t = 0	0.001
Age at which litterfall rate has median value	24
Average monthly root turnover rate	0.02
NPP & conductance modifiers	
Temperature modifier (fT)	
Minimum temperature for growth	3
Optimum temperature for growth	23
Maximum temperature for growth	35
Frost modifier (fFRost)	
Days production lost per frost day	1
Soil water modifier (fSW)	
Moisture ratio deficit for f□ = 0.5	0.5
Power of moisture ratio deficit	5
Fertitlity effects	
Value of 'm' when FR = 0	0
Value of 'fNutr' when FR = 0	1
Power of (1-FR) in 'fNutr'	0
Age modifier (fAge)	
Maximum stand age used in age modifier	80
Power of relative age in function for fAge	4
Relative age to give fAge = 0.5	0.95
Stem mortality and self-thinning	
Mortality rate for large t	0
Seedling mortality rate (t = 0)	0
Age at which mortality rate has median value	2
Shape of mortality response	1
Max. stem mass per tree @ 1000 trees/hectare	340
Power in self-thinning rule	1.5
Fraction mean single-tree foliage biomass lost per dead tree	0
Fraction mean single-tree root biomass lost per dead tree	0.2

*Monthly litter fall was calculated by dividing the annual litter fall in this study by 12.

Table 3.3 continued: *Pinus patula* model parameters as described by Dye (2001) except where otherwise stated

Parameters	Value used
Fraction mean single-tree stem biomass lost per dead tree	0.2
Canopy structure and processes	
Specific leaf area	
Specific leaf area at age 0	5
Specific leaf area for mature leaves	5
Age at which specific leaf area = (SLA0+SLA1)/2	2.5
Light interception	
Extinction coefficient for absorption of PAR by canopy	0.5
Age at canopy cover	0
Maximum proportion of rainfall evaporated from canopy	0.13
LAI for maximum rainfall interception	5
Production and respiration	
Canopy quantum efficiency	0.052
Ratio NPP/GPP	0.47
Conductance	
Maximum canopy conductance	0.02
LAI for maximum canopy conductance	3.33
Defines stomatal response to VPD	0.05
Canopy boundary layer conductance	0.2
Wood and stand properties	
Branch and bark fraction (fracBB)	
Branch and bark fraction at age 0	0.75
Branch and bark fraction for mature stands	0.19
Age at which fracBB = (fracBB0+fracBB1)/2	7
Basic Density	
Minimum basic density - for young trees	0.470
Maximum basic density - for older trees	0.380
Age at which rho = (rhoMin+rhoMax)/2	7
Conversion factors	
Intercept of net v. solar radiation relationship	-90
Slope of net v. solar radiation relationship	0.8
Molecular weight of dry matter	24
Conversion of solar radiation to PAR	2.3

Table 3.4: *Pinus elliottii* model parameters as described by Dye (unpublished) except where otherwise stated

Parameters	**Value used**
Biomass partitioning and turnover	
Allometric relationshipspartitioning	
Foliage:stem partitioning ratio @ D=2 cm	0.934 Johnson, 1990
Foliage:stem partitioning ratio @ D=20 cm	0.2
Constant in the stem mass v. diam. Relationship	0.04
Power in the stem mass v. diam. Relationship	2.65
Maximum fraction of NPP to roots	0.8 Sands and Landsberg, 2002
Minimum fraction of NPP to roots	0.2 Sands and Landsberg, 2002
Litterfall and root turnover	
* Maximum litterfall rate	0.02 This study 0.032 Dye, 2001
Litterfall rate at t = 0	0.001
Age at which litterfall rate has median value	24
Average monthly root turnover rate	0.02
NPP and conductance modifiers	
Temperature modifier (fT)	
Minimum temperature for growth	3
Optimum temperature for growth	23
Maximum temperature for growth	35
Frost modifier (fFRost)	
Days production lost per frost day	1
Soil water modifier (fSW)	
Moisture ratio deficit for f□ = 0.5	0.5
Power of moisture ratio deficit	5
Fertility effects	
Value of 'm' when FR = 0	0
Value of 'fNutr' when FR = 0	1
Power of (1-FR) in 'fNutr'	0
Age modifier (fAge)	
Maximum stand age used in age modifier	80
Power of relative age in function for fAge	4
Relative age to give fAge = 0.5	0.95
Stem mortality and self-thinning	
Mortality rate for large t	0
Seedling mortality rate (t = 0)	0
Age at which mortality rate has median value	2
Shape of mortality response	1
Max. stem mass per tree @ 1000 trees/hectare	340
Power in self-thinning rule	1.5
Fraction mean single-tree foliage biomass lost per dead tree	0
Fraction mean single-tree root biomass lost per dead tree	0.2
Fraction mean single-tree stem biomass lost per dead tree	0.2

*Monthly litter fall was calculated by dividing the annual litter fall in this study by 12

Table 3.4 continued: *Pinus elliottii* model parameters as described by Dye (unpublished) except where otherwise stated

Parameters	**Value used**
Specific leaf area at age 0	5
Age at which specific leaf area = (SLA0+SLA1)/2	2.5
Light interception	
Extinction coefficient for absorption of PAR by canopy	0.5
Age at canopy cover	0
Maximum proportion of rainfall evaporated from canopy	0.13 Dye and Versfeld, 1992
LAI for maximum rainfall interception	6
Production and respiration	
Canopy quantum efficiency	0.05
Conductance	
Maximum canopy conductance	0.018 Landsberg and Gower,1997
LAI for maximum canopy conductance	3.33
Defines stomatal response to VPD	0.05
Canopy boundary layer conductance	0.3 Ford and Bassow, 1979 used by Dye, 2001
Wood and stand properties	
Branch and bark fraction (fracBB)	
Branch and bark fraction at age 0	0.75
Branch and bark fraction for mature stands	0.19
Age at which fracBB = (fracBB0+fracBB1)/2	7
Basic Density	
Minimum basic density - for young trees	0.380
Maximum basic density - for older trees	0.400
Age at which rho = (rhoMin+rhoMax)/2	7
Conversion factors	
Intercept of net v. solar radiation relationship	-90
Slope of net v. solar radiation relationship	0.8
Molecular weight of dry matter	24
Conversion of solar radiation to PAR	2.3

CHAPTER 4

RESULTS

The results in this study are presented in three sections, firstly, *P. patula* followed by *P. elliottii* and lastly, the 3-PG modelling results for both *P. patula* and *P. elliottii* species.

4.1 *Pinus patula*

4.1.1 Tree growth data

Results of the analysis of variance are presented in Tables 4.1 and 4.2. These results are then interpreted, together with the data collected on stem density, tree height, basal area and stand volume. Drought damage occurred at the Elandshoogte site between 2005 and 2006 and wind damage at the Grootgeluk and Mooifontein sites in August 2006, these events impacted tree growth measurements in 2006 and 2007 respectively. The drought occurred after the 2005 measurements had been taken but before the 2006 measurements. The wind damage affected the measurements in 2007 since the tree measurement were done at the end of January in 2007 after the damage in August 2006. There is evidence that the damage was limited to small areas within the trials, but the major impact was evident in the control plots. Due to there being only two replicates it became extremely difficult to separate the treatment effects from the wind and drought damage, this is especially true for stem density and basal area.

Between 2001 (age 11 years) when the fertilizer was first applied and 2003 (age 13 years) when the final application of fertilizer was made, each treatment occurred twice within each replication. Thus, the trial was analysed as having four replications of the three initial treatments (LAN, Urea and Control). Results from the analysis of variance of the tree growth measurements and the growth increment between the periods of 2001-2003 are presented in Table 4.1.

Between 2003 (age 13 years) when the final dose of fertilizer was applied and the end of the study in 2007 (age 17 years), each treatment occurred twice within each replication. Thus, the trial was analysed as having two replications of the six treatments. Results from the analysis of variance, of the tree growth measurements from 2003 (age 13 years), when the final application of fertilizers were made, to 2007 (age 17 years), which was at the end of the study; as well as the results of the analysis of variance of the growth increments for the periods 2003-2005 (ages 13 to 15 years), 2001-2005 (ages 11 to 15 years) and 2001-2007 (ages 11 to 17 years), are presented in Table 4.2.

Table 4.1: ANOVA table showing the probability values of tree growth measurements and the tree growth increment between the first application of fertilizer in 2001 at age 11 years and the second fertilizer application in 2003 at age 13 years

Source of variation	df	Year of measurements			Growth increment from 2001-2003
		2001	2002	2003	
Stem density (#stem ha^{-1})					
Treatment	2	0.210	0.221	0.246	0.361
Fertilizer vs. control	1	0.893	0.560	0.537	0.168
Site.Rep.Plots stratum					
*Rep (site)	4	0.003	0.010	0.015	0.762
Site	3	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Error	38				
Total	47				
Tree height (m)					
Treatment	2	0.257	0.333	0.482	0.868
Fertilizer vs. control	1	0.110	0.157	0.298	0.842
Site.Rep.Plots stratum					
*Rep (site)	4	0.210	0.001	0.475	0.882
Site	3	**0.001**	**<0.001**	**<0.001**	**<0.001**
Error	38				
Total	47				
Basal area (m^2 ha^{-1})					
Treatment	2	**0.080**	0.267	**0.065**	**0.050**
Fertilizer vs. control	1	0.378	0.241	0.161	**0.018**
Site.Rep.Plots stratum					
*Rep (site)	4	0.033	0.012	0.025	0.404
Site	3	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Error	38				
Total	47				
Stand volume (m^{3}ha^{-1})					
Treatment	2	0.397	0.293	0.412	0.704
Fertilizer vs. control	1	0.201	0.155	0.203	0.411
Site.Rep.Plots stratum					
*Rep (site)	4	0.0474	0.001	0.147	0.878
Site	3	**<0.001**	**<0.001**	**<0.001**	**0.005**
Error	38				
Total	47				

Bold values indicate significant differences (at the 5% level and 1% level) for the variable site, while bold and highlighted values show significance at the 10% significant level for the treatment variable.

Rep (site) = replicate nested within sites.

Table 4.2: ANOVA table showing the probability values of tree growth measurements from the final applications of fertilizer in 2003 (age 13 years) to the end of study in 2007 (age 17 years) and the tree growth increments for the periods of 2003-2005, 2001-2005 and 2001-2007

Source of variation	Df	Year of measurements					Growth increment from		
		2003	2004	2005	2006	2007	2003-2005	2001-2005	2001-2007
Stem density (#stem ha^{-1})									
Treatment	5	0.279	0.139	0.147	**0.084**	0.106	0.528	**0.093**	0.199
Fertilizer vs. control	1	0.310	0.289	0.237	**0.039**	**0.065**	0.612	0.736	0.120
Site.Rep.Plots stratum									
*Rep (site)	4	0.015	0.016	0.014	0.190	0.576	0.740	0.790	**0.088**
Site	3	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.228	**0.001**	**0.025**
Error	35								
Total	47								
Tree height (m)									
Treatment	5	0.358	0.384	0.530	0.681	0.251	0.630	0.643	0.127
Fertilizer vs. control	1	0.105	0.240	0.538	0.863	0.392	0.337	0.972	0.959
Site.Rep.Plots stratum									
*Rep (site)	4	0.461	0.319	0.088	0.004	0.001	0.494	0.002	<0.000
Site	3	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.004**	**<0.001**
Error	35								
Total	47								
Basal area (m^2 ha^{-1})									
Treatment	5	0.239	0.206	0.239	**0.065**	**0.030**	0.780	0.465	**0.059**
Fertilizer vs. control	1	0.169	0.166	0.170	**0.015**	**0.007**	0.474	**0.076**	**0.003**
Site.Rep.Plots stratum									
*Rep (site)	4	0.024	0.027	0.014	0.030	0.022	0.442	0.118	0.018
Site	3	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0001**	**0.005**	0.458	**<0.001**
Error	35								
Total	47								
Stand volume (m^3 ha^{-1})									
Treatment	5	0.345	0.243	0.504	0.322	**0.091**	0.899	0.864	0.152
Fertilizer vs. control	1	**0.089**	0.111	0.270	**0.079**	**0.015**	0.470	0.470	**0.009**
Site.Rep.Plots stratum									
Site	3	**<0.001**	**<0001**	**0.001**	**0.012**	**0.001**	0.564	0.384	0.105
*Rep (site)	4	0.140	0.080	0.897	0.198	0.021	0.042	0.354	0.006
Error	35								
Total	47								

Bold values indicate significant differences (at the 5% level and 1% level) for the variables: treatment, fertilizer vs. control and across the sites, while bold and highlighted values show significance at the 10% significant level for replicate, treatment and fertilizer vs. control.
* Rep (site) = replicate nested within sites.

Stem density

The ANOVA results indicated there was no evidence of significant differences between treatments from 2001 (age 11 years) to 2003 (age 13 years) (Table 4.1), as well as from 2003 till 2005 (Table 4.2). However, a 10% significant treatment effect (p=0.084) was observed in 2006 (Table 4.2). When comparing the fertilizer treatments with the control there were significant differences in 2006 (p=0.039) and in 2007 (p=0.065). There was weak evidence of a significant treatment effect in stem density increment between 2001 and 2005 (p=0.093) (Table 4.2). A drought occurred in 2005 (Elandshoogte) and severe wind storms in 2006 (Grootgeluk and Mooifontein) at all of the sites except Mamre, measurements taken in 2006 and 2007 could be misinterpreted to be as a result of treatment (Figure 4.1).

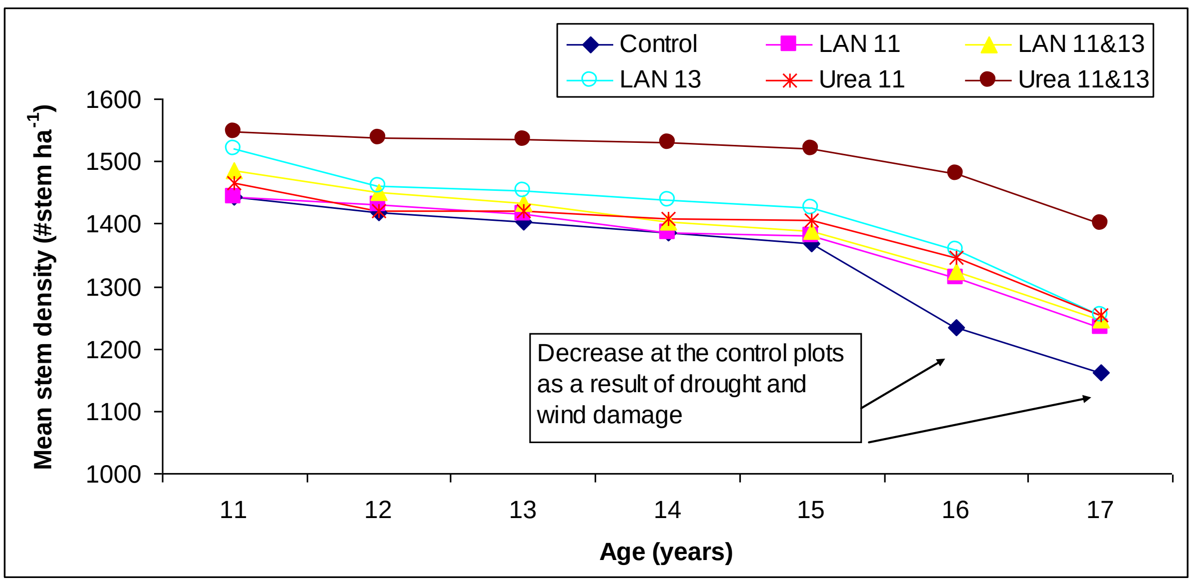

Figure 4.1 Mean stem density per treatment across all four sites showing the impact of wind and drought on control plots in 2006 and 2007

To understand the effects of the treatments vs. the abiotic perturbations the data were analysed by comparing the measured variables by subtracting the control values (in this thesis the subtraction of the control values allowed for a relative change to be assessed. This procedure was used for any reference to relative change in the entire thesis). In order to compare treatment responses with each other across all years, the stem densities were adjusted to zero by subtracting the number of stems in the control treatments from themselves for each of the years. In addition, the treatments in 2001 were adjusted to zero by subtracting the control from each of the treatments. Thereafter, for each of the subsequent years the 2001 values were subtracted from each of the treatment values in order to obtain a relative response. The results indicate that the stem density increased up to 45.5 (#stem ha^{-1}) in 2005. Increases in 2006 and 2007 are not due to treatment effects but due to the drought and the wind storms (Figure 4.2).

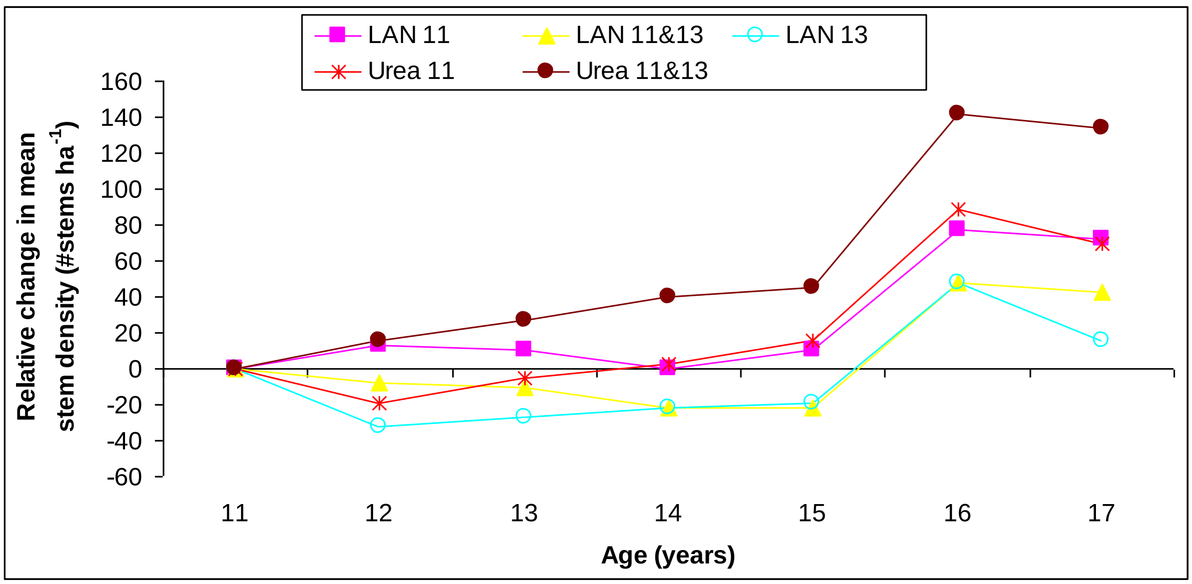

Figure 4.2 Mean stem density differences relative to the initial mean stem density per treatment in 2001 at 11 years (the beginning of the study) and the control in subsequent years in all the four sites

ANOVA results showed that there were site significant differences in the stem density over the years (2001-2007) (Table 4.1 and Table 4.2). Stem density remained steady or decreased over time due to die off of some of the trees over the years (Figure 4.3). It should be noted that the number of stems (#stems ha^{-1}) was not the same across the different sites at the beginning of the study, the initial number at the Mooifontein site was 1693 (#stems ha^{-1}); Mamre was 1414 (#stems ha^{-1}); Grootgeluk was 1409 (#stems ha^{-1}) and Elandshoogte was 1420 (#stems ha^{-1}). The number of stems was significantly higher at the Mooifontein site compared with other sites, while the Mamre site was significantly lower compared to the other sites over the years except in 2006 and 2007, where the Mamre site was not affected by drought and wind damage. The Elandshoogte site experienced drought in 2005 which impacted negatively on the 2006 measurements, while the Grootgeluk and Mooifontein sites experienced wind damage in 2006 that impacted negatively on 2007 measurements.

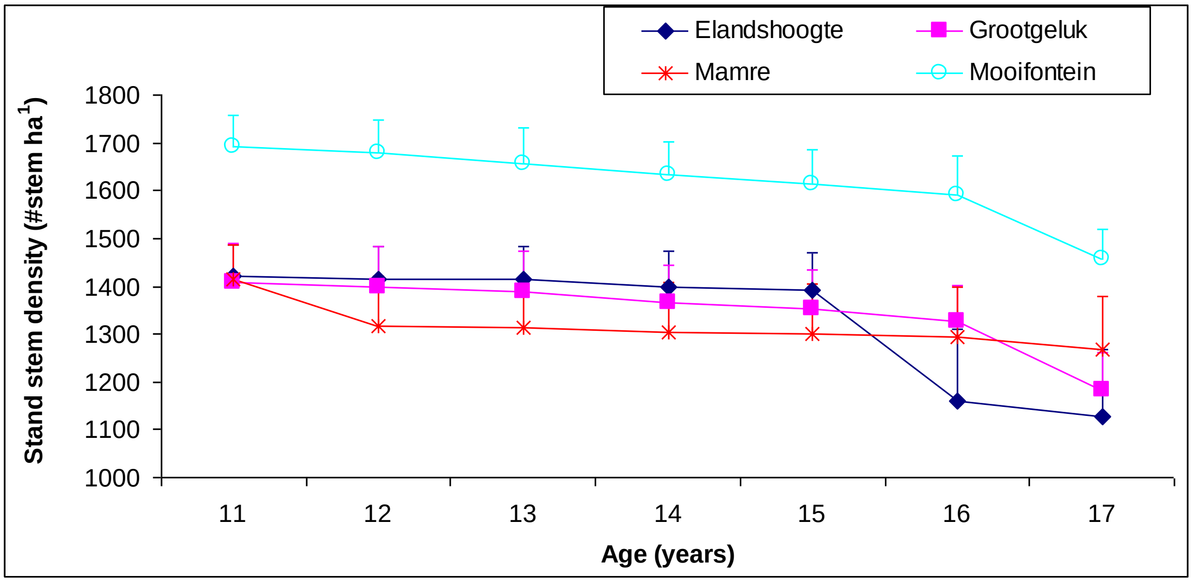

Figure 4.3 Stem density measured across the study sites for the period of seven years after fertilization (2001-2007). Values are presented as means and the vertical bars indicate confidence intervals at the 5% significance level, n = 12

Tree height

Treatment had no significant effect on tree height or tree height increment (Table 4.1 and 4.2). When the mean relative change between the fertilizer treatments and the control plots were calculated, using the approach described above, the increased of 0.7m recorded in the LAN 13 treatment was not significantly different (Figure 4.4).

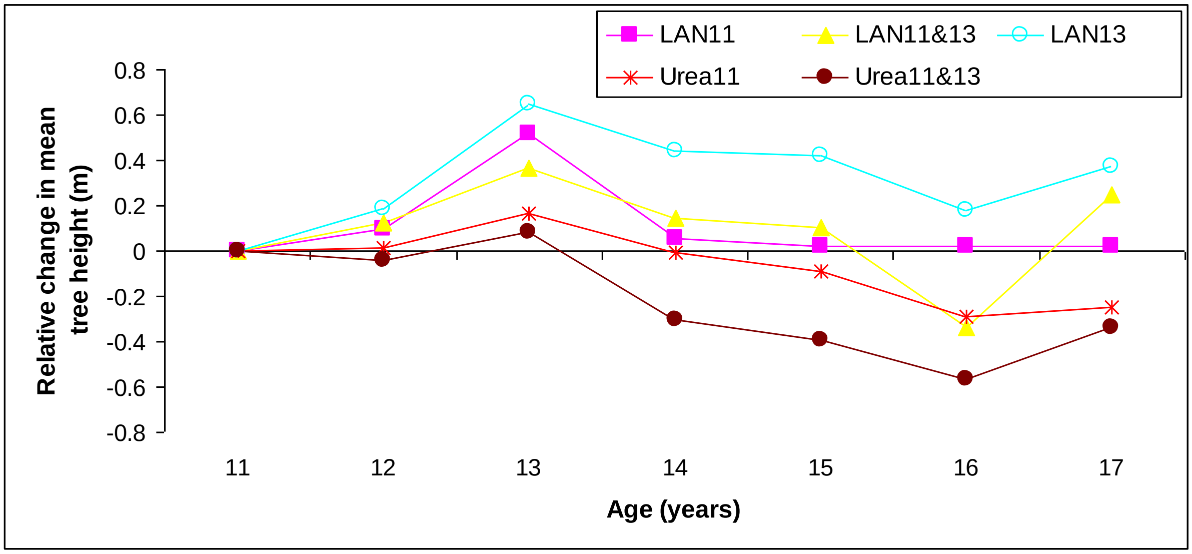

Figure 4.4 Mean tree height differences relative to the initial mean tree height per treatment in 2001 at 11 years (the beginning of the study) and the control in subsequent years in all the four sites

However, there were site significant differences in the tree height over the years (Table 4.1 and 4.2). The mean tree height across the trial sites of the same trees measured over the study period (excluding the trees that died or additional trees that were measured as the trials progressed) indicated that the mean tree height increased from 14.3 m in 2001 (age 11 years) at the Mamre site to 21.7 m in 2007 (age 17 years) at the Elandshoogte site (Figure 4.5). Tree height was significantly higher at the Elandshoogte and Grootgeluk sites compared with the other sites over the years except in 2002, where the Elandshoogte and Mooifontein sites were higher. Mooifontein and Mamre sites were significantly lower in 2001, 2003 and 2007 compared with the other sites, in addition the Mooifontein site was significantly lower in 2005 and 2006.

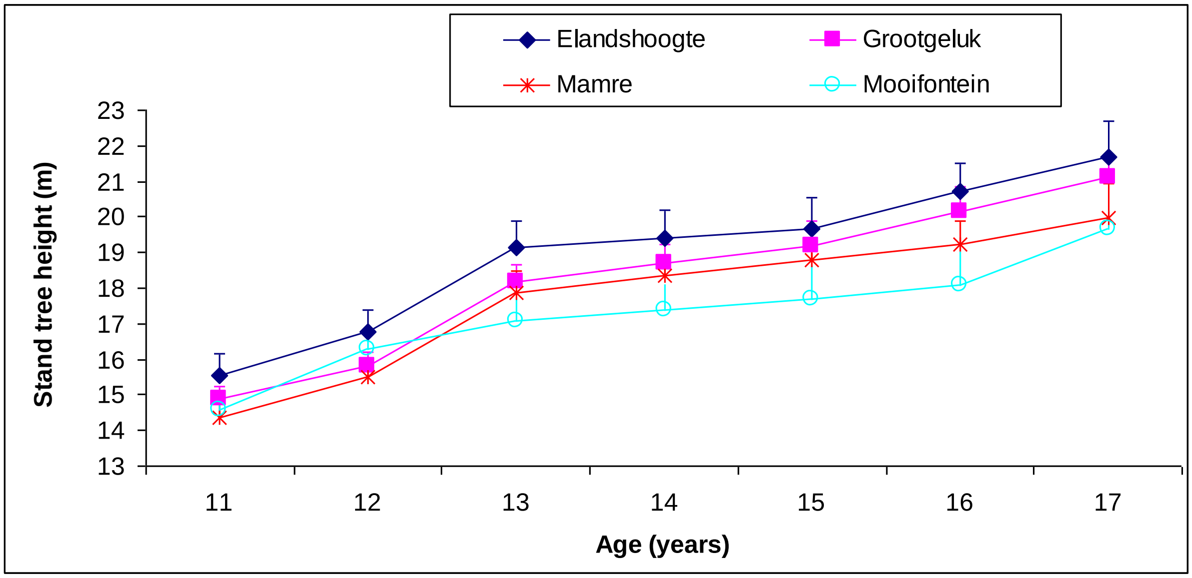

Figure 4.5 Tree height measured across the study sites for the period of seven years after fertilization (2001-2007). Values are presented as means and the vertical bars indicate confidence intervals at the 5% significance level, n = 12

Basal area

Basal area measurement has been shown to be a better parameter to assess tree growth response following fertilization than tree height because of the error associated with tree height measurements. The ANOVA results showed that there were significant treatment effects in 2001 and 2003 (at the 10% level, p=0.080 and p=0.065) (Table 4.1), the significant effect in 2001 cannot be related to the fertilizer application since the application and the tree measurements in that year were done at the same time. There was a weak significant (p=0.050) treatment effect on the growth increment between 2001 and 2003, as well a significant (p=0.018) difference in basal area increment when comparing the fertilizer treatments with the control over the two year period (2001-2003) (Table 4.1), the increase was however very small (Figure 4.6).

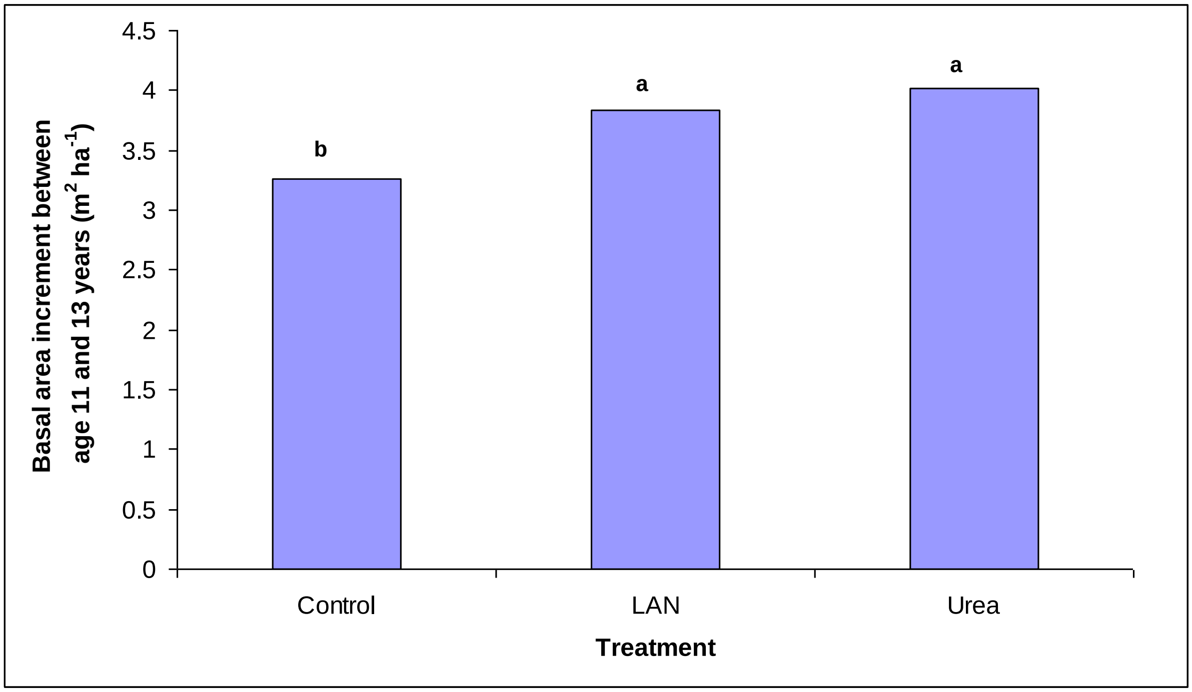

Figure 4.6 Basal area increment from 2001 (age 11 years) when fertilizer was first applied to 2003 (age 13 years) when the second fertilizer application was applied. Values with the same letter are not significantly different from each other

The ANOVA results showed there was no significant treatment effect in basal area between 2003 (age 13 years) and 2005 (age 15 years) (Table 4.2) however, there were significant treatment effects in 2006 (p=0.065) and in 2007 (p=0.030) and basal area increment between 2001 and 2007 (p=0.059). The comparison between the fertilizer treatments with the control plots showed there were significant differences in basal area in 2006 (p=0.015) and in 2007 (p=0.007), as well as evidence of significant differences in basal area increments from 2001-2005 (p=0.076) as shown in Figure 4.7 with the increment being 1.19 m^2 ha^{-1}, and between 2001 to 2007 (p=0.003) (Table 4.2).

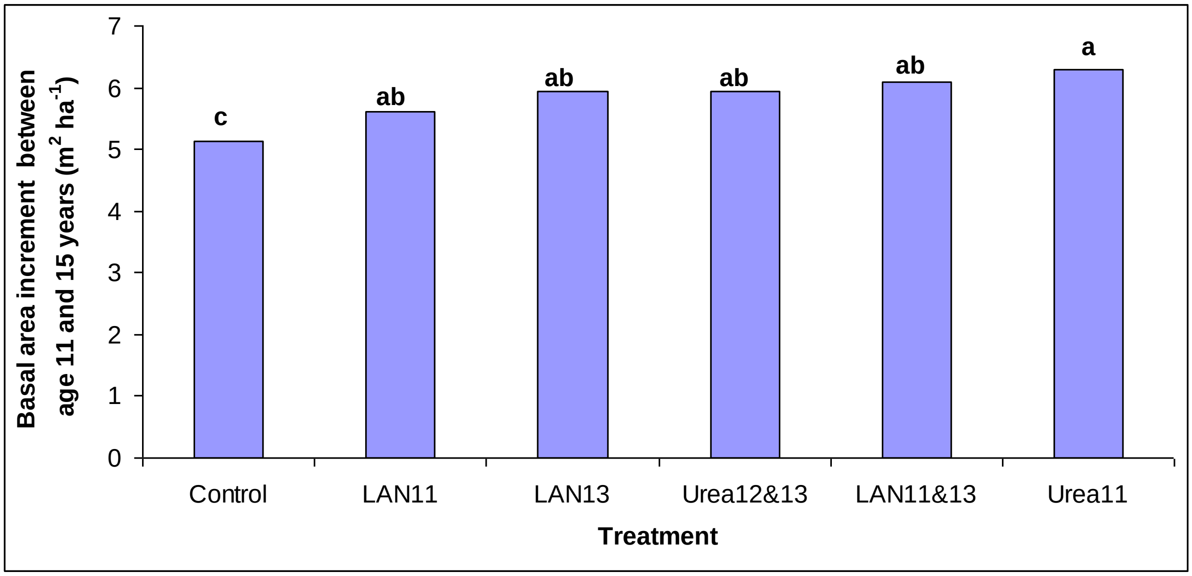

Figure 4.7 Basal area increment from 2001 (age 11 years) when fertilizer was first applied to 2005 (age 15 years) across the treatments in all the sites. Values with the same letter are not significantly different from each other

When the trial was established in 2001 at age 11, there was already a difference in absolute terms between the fertilized and the control plots (Figure 4.8). It was only the LAN 11 treatment that had a smaller basal area than the control treatment at the start of the trial. Up to 2005 (age 15 years) the relative difference between all the treatments remained the same. However, from 2006 (age 16 years) the mean basal area in all the treatments decreased, but the greatest decrease occurred in the control treatment.

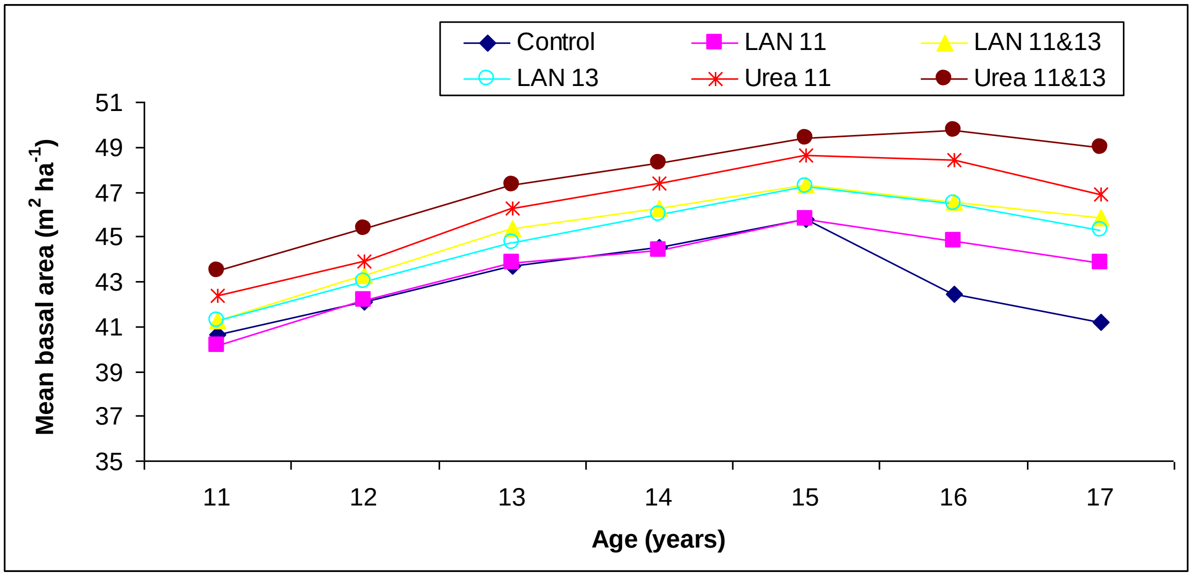

Figure 4.8 Mean Basal area per treatment across all four sites from 2001 (age 11 years) when the application of N fertilizer was done to 2007 (age 17 years), end of study

In order to compare treatment responses with each other across all years, the same approach as for stem density was adopted. The results indicated that the basal area was increased by 0.5 to 1.2 $m^2\ ha^{-1}$, (not significant) in the fertilized plots as opposed to the control plot at age 15 years (Figure 4.9). This increase became significant at 16 and 17 years (Figure 4.9), but the effect can be explained by the drought and wind-related mortality in the control plots and not by the additional basal area growth in the fertilized plots.

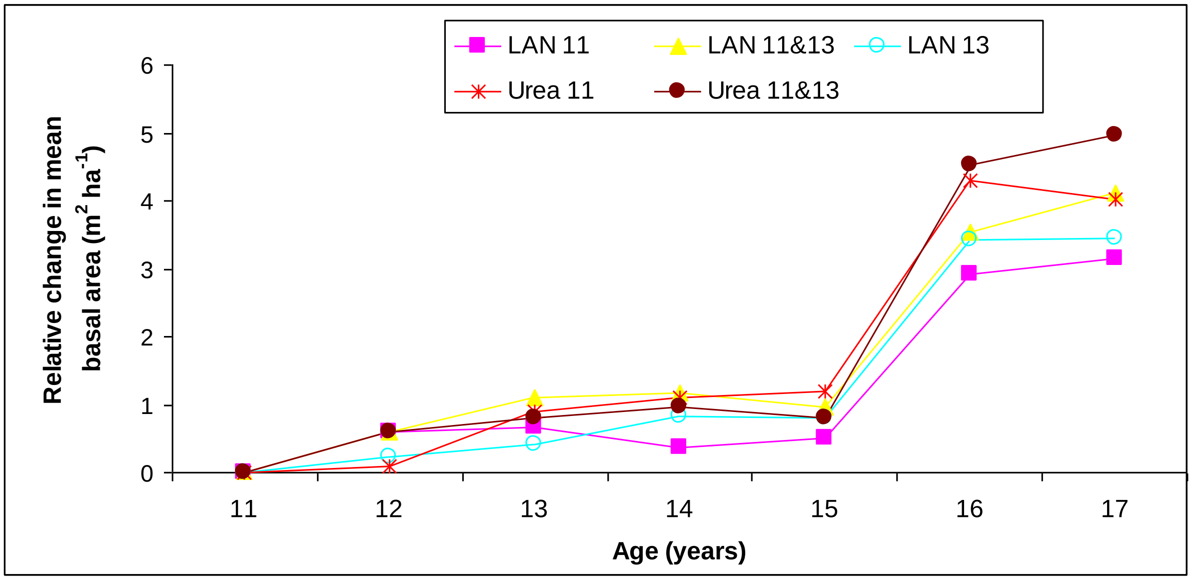

Figure 4.9 Mean basal area differences relative to the initial basal area per treatment in 2001 at 11 years (the beginning of the study) and the control in subsequent years in all the four sites

Basal area (m^2 ha^{-1}) was found to be significantly ($p<0.0001$) different over the years across the sites (Table 4.1 and Table 4.2). The basal area recorded at the Mooifontein site was found to be significantly higher than at the other sites across the years while the Mamre site was significantly lower compared to other sites (Figure 4.10). It should however be noted that at the start of the trial, the basal area at Mooifontein was 15 m^2 ha^{-1} higher than the Mamre site. The declines in stem density and basal area in 2006 and 2007 at the Elandshoogte and Grootgeluk sites were due to drought that occurred between 2005 and 2006 and wind damage in August 2006 respectively in 2006 and 2007 as explained above.

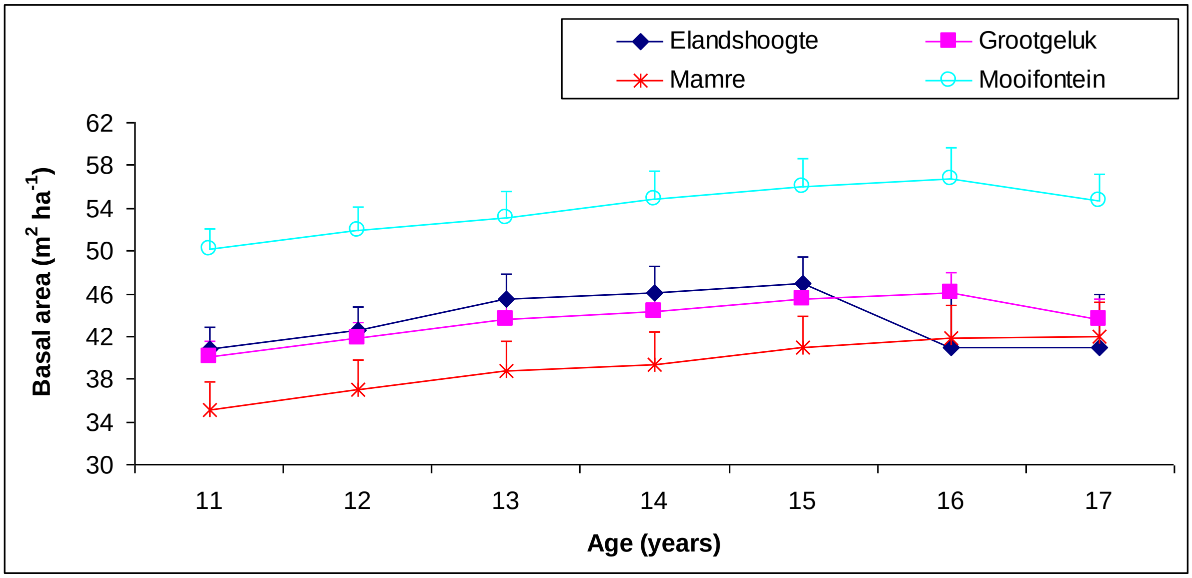

Figure 4.10 Basal area measured across the study sites for the period of seven years after fertilization (2001-2007). Values are presented as means and the vertical bars indicate confidence intervals at the 5% significance level, n = 12

Stand volume

The stand volume measurements and volume increment between 2001 (age 11 years) and 2003 (age 13 years) and volume increments between the periods were not affected by fertilizer treatments (Table 4.1). There were no significant differences in stand volume over the years except a weak significant treatment effect (p=0.091) in 2007 (Table 4.2 and Figure 4.11). When comparing the fertilizer treatments with the control plots there were weak significant treatment effects in 2003 (p=0.089), 2006 (p=0.079) and a strong treatment effect in 2007 (p=0.015) (Table 4.2). There was a significant (p=0.009) difference in volume increment from 2001 to 2007 (ages 11 to 17 years) when fertilized and control plots were compared (Table 4.2).

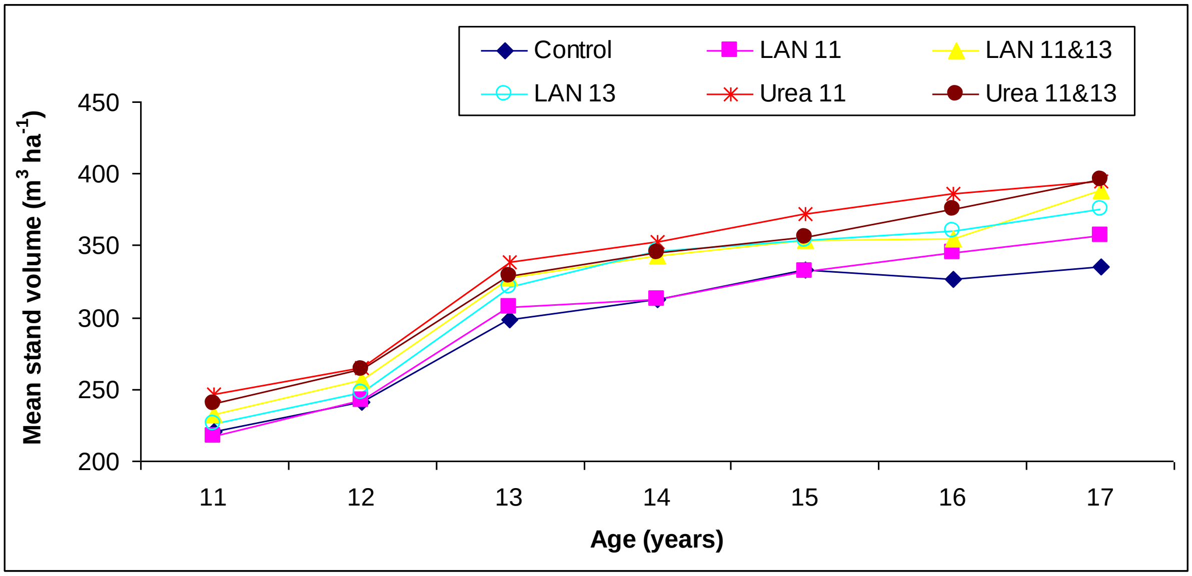

Figure 4.11 Mean stand volume per treatment across all four sites from 2001 (age 11 years) when the application of nitrogen fertilizer was done to 2007 (age 17 years), end of study

When the mean relative change in stand volume between the fertilizer treatments and the control plots were calculated (Figure 4.12), the stand volume became significant in 2006 and 2007 but this cannot be attributed to treatment effects but rather to drought and wind effects as explained earlier.

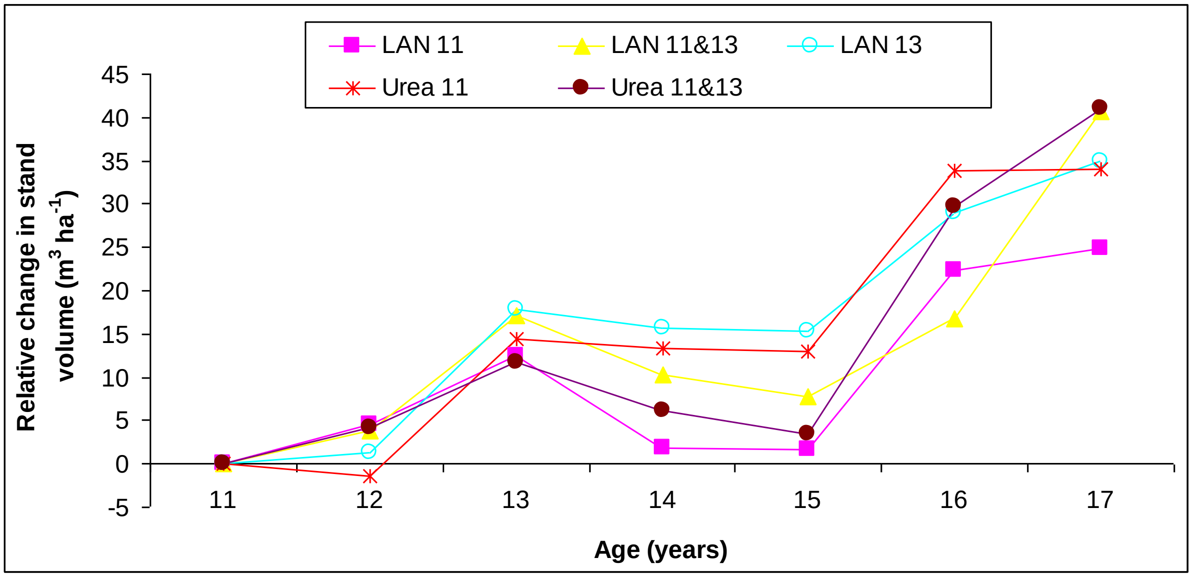

Figure 4.12 Mean stand volume differences relative to the initial mean tree volume per treatment in 2001 at age 11 years (the beginning of the study) and the control in subsequent years in all the four sites

The stand volume (m^3 ha^{-1}) increased gradually over the 7 years (Figure 4.13), and it was found to be significantly ($p<0.001$) different across the sites (Tables 4.1 and 4.2). The stand volume was higher at the Mooifontein site than at the other sites over the years (2001-2007), while the lowest tree volume response was recorded at the Mamre site.

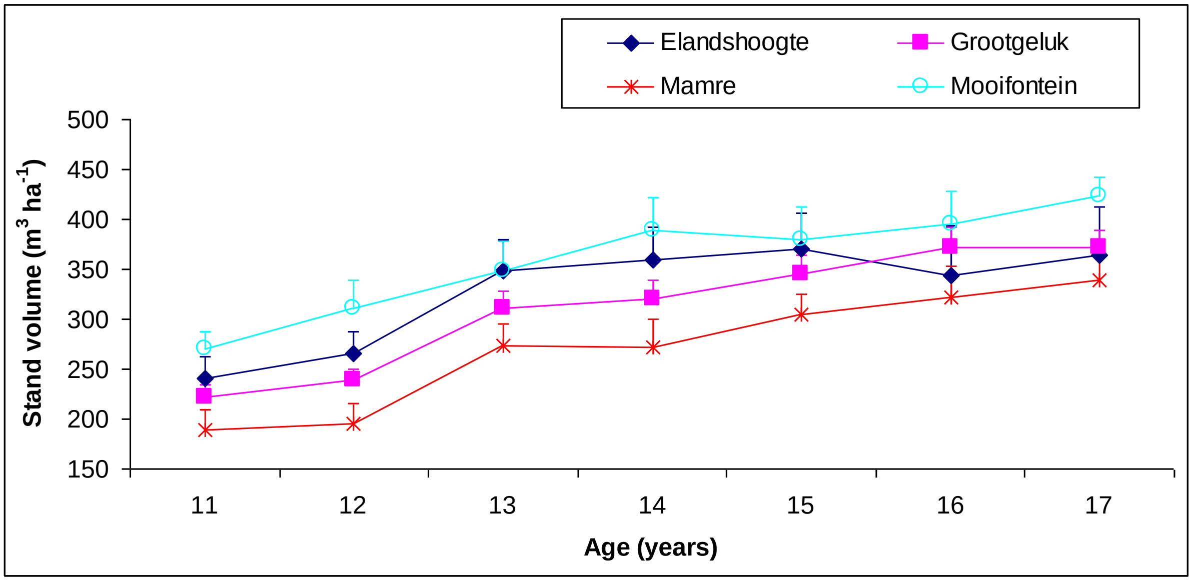

Figure 4.13 Stand volume measured across the study sites for the period of seven years after fertilization (2001-2007). Values are presented as means and the vertical bars indicate confidence intervals at the 5% significance level, n = 12

4.1.2 Soil properties

The results of soil properties across the sites are shown for 2006 and 2007 in Tables 4.3 and 4.4. Values for treatments, amounts and types of fertilizers are not shown because they are not significantly different ($p>0.05$). The results of the soil nutrient analyses showed that within a site and for each chemical element analyzed, there were no significant treatment ($p>0.05$) effects in both 2006 and 2007 for all elements. However, there were significant ($p<0.001$) differences in the soil properties across the sites (Table 4.3 and 4.4). The following soil properties; K^+ ($p=0.002$), C ($p=0.0001$), available P ($p=0.0001$), Al^{3+} ($p=0.0001$), exchangeable acidity ($p=0.0334$), pH (KCl) ($p=0.0001$) and water ($p=0.0001$) differed across the two years.

Table 4.3: Soil properties sampled at 0-20 cm across the study sites in 2006. Values are presented as means and standard errors (n = 12). Results for treatments, amounts and types of fertilizer are not shown because they were not significantly different

	Study sites			
Soil Properties	**Elandshoogte**	**Grootgeluk**	**Mamre**	**Mooifontein**
Ca^{2+} (mg kg^{-1})	947.7 ± 136.9^{a}	46.0 ± 16.4^{b}	19.0 ± 5.7^{b}	38.9 ± 15.7^{b}
Mg^{2+} (mg kg^{-1})	301.5 ± 36.7^{a}	11.9 ± 0.9^{b}	4.8 ± 0.4^{c}	5.4 ± 0.6^{c}
K^{+} (mg kg^{-1})	80.2 ± 6.0^{a}	46.6 ± 1.4^{b}	35.2 ± 1.5^{c}	35.5 ± 1.4^{c}
***ECEC ($cmol_c$ kg^{-1})**	8.6 ± 0.6^{a}	4.8 ± 0.1^{b}	4.5 ± 0.1^{c}	2.8 ± 0.1^{c}
Mn^{2+} (mg kg^{-1})	30.7 ± 4.9^{a}	2.1 ± 0.2^{b}	0.9 ± 0.1^{c}	1.6 ± 0.1^{bc}
N (%)	0.3 ± 0.0^{b}	0.4 ± 0.0^{a}	0.3 ± 0.0^{b}	0.3 ± 0.0^{b}
Carbon (%)	4.9 ± 0.5^{b}	9.3 ± 0.3^{a}	5.8 ± 0.3^{b}	5.7 ± 0.4^{b}
Total P (mg kg^{-1})	126.0 ± 20.7^{c}	515.6 ± 76.1^{a}	234.6 ± 31.5^{b}	179.6 ± 6.5^{c}
Available P (mg kg^{-1})	4.0 ± 0.5^{c}	8.7 ± 0.5^{a}	7.5 ± 0.4^{b}	4.4 ± 0.4^{c}
Al^{3+} (mg kg^{-1})	4.4 ± 0.5^{d}	7.1 ± 0.2^{a}	5.2 ± 0.2^{b}	4.4 ± 0.2^{c}
Exchangeable acidity ($cmol_c$ kg^{-1})	1.2 ± 0.4^{d}	4.3 ± 0.1^{a}	4.3 ± 0.1^{b}	2.5 ± 0.1^{c}
pH (1 M KCl)	4.9 ± 0.1^{a}	4.1 ± 0.0^{b}	4.0 ± 0.0^{b}	4.0 ± 0.0^{b}
pH (distilled H_20)	4.2 ± 0.1^{a}	4.4 ± 0.0^{b}	4.5 ± 0.0^{b}	4.6 ± 0.0^{b}
$^{+}$Clay (%)	30.1 ± 7.6^{a}	34.9 ± 2.7^{a}	40.7 ± 1.8^{a}	27.7 ± 0.8^{a}
$^{+}$Silt (%)	47.2 ± 1.9^{b}	54.7 ± 1.8^{a}	49.9 ± 2.7^{ab}	55.0 ± 4.8^{a}
$^{+}$Sand (%)	22.7 ± 9.5^{a}	12.3 ± 0.9^{a}	9.3 ± 0.9^{a}	17.3 ± 4.0^{a}

Values with the same letter are not significantly (p>0.05) different for each element across the row for that year

*ECEC = Effective cation exchange capacity

$^{+}$ For the soil particle distribution values, n = 3 because of the limitation of soil mass.

Table 4.4: Soil properties sampled at 0-20 cm across the study sites in 2007. Values are presented as means and standard errors (n = 12). Results for treatments, types and amounts of fertilizer are not shown because they were not significantly different

	Study sites			
Soil Properties	**Elandshoogte**	**Grootgeluk**	**Mamre**	**Mooifontein**
Ca^{2+} (mg kg^{-1})	875.4 ± 88.8^{a}	36.8 ± 15.5^{b}	25.5 ± 2.8^{b}	15.9 ± 4.5^{b}
Mg^{2+} (mg kg^{-1})	295.9 ± 21.9^{a}	7.7 ± 0.8^{b}	5.8 ± 2.9^{b}	4.6 ± 01.9^{b}
K^{+} (mg kg^{-1})	62.1 ± 4.8^{a}	42.6 ± 1.7^{b}	30.9 ± 1.8^{c}	31.9 ± 0.9^{c}
***ECEC ($cmol_c$ kg^{-1})**	7.9 ± 0.6^{a}	4.4 ± 0.1^{b}	4.2 ± 0.2^{c}	2.5 ± 0.1^{c}
Mn^{2+} (mg kg^{-1})	21.5 ± 4.5^{a}	1.5 ± 0.1^{b}	0.9 ± 0.1^{c}	1.2 ± 0.1^{bc}
N (%)	0.2 ± 0.1^{b}	0.4 ± 0.0^{a}	0.3 ± 0.0^{b}	0.3 ± 0.0^{b}
Carbon (%)	4.4 ± 0.2^{c}	7.9 ± 0.3^{a}	4.8 ± 0.3^{b}	4.9 ± 0.4^{b}
Total P (mg kg^{-1})	131.7 ± 14.6^{c}	434.5 ± 10.1^{a}	216.5 ± 27.6^{b}	155.5 ± 17.9^{c}
Available P (mg kg^{-1})	2.4 ± 0.2^{b}	5.9 ± 0.7^{a}	5.2 ± 0.5^{a}	2.8 ± 0.3^{b}
Al^{3+} (mg kg^{-1})	1.9 ± 0.3^{d}	6.0 ± 0.9^{a}	4.4 ± 0.2^{b}	4.7 ± 0.2^{c}
Exchangeable acidity ($cmol_c$ kg^{-1})	0.9 ± 0.2^{d}	4.0 ± 0.1^{a}	4.0 ± 0.1^{b}	2.3 ± 0.1^{c}
pH (1 M KCl)	4.2 ± 0.1^{a}	4.4 ± 0.0^{b}	4.2 ± 0.1^{b}	4.3 ± 0.0^{b}
pH (distilled H_20)	4.5 ± 0.1^{a}	4.8 ± 0.0^{b}	4.8 ± 0.0^{b}	4.9 ± 0.0^{b}
$^{+}$Clay (%)	31.3 ± 1.2^{b}	32.0 ± 1.5^{b}	37.7 ± 1.3^{a}	24.9 ± 1.7^{c}
$^{+}$Silt (%)	47.7 ± 0.3^{c}	57.3 ± 0.7^{a}	50.7 ± 0.3^{bc}	54.0 ± 2.1^{ab}
$^{+}$Sand (%)	21.0 ± 1.6^{a}	10.7 ± 0.9^{b}	11.6 ± 1.2^{b}	21.1 ± 4.5^{a}

Values with the same letter are not significantly ($p>0.05$) different for each element across the row for each year

*ECEC = Effective cation exchange capacity

$^{+}$ For the soil particle distribution vales, n = 3 because of the limitation of soil mass.

The levels of Ca^{2+}, Mg^{2+}, K^{+}, effective cation exchange capacity, $Mn^{2+}$and pH (KCl and water) were found to be significantly ($p<0.0001$) higher at the Elandshoogte site than at the other sites in both 2006 and 2007 (Table 4.3 and 4.4); percentage sand was also higher at the site than at the Grootgeluk and Mamre sites in 2007 (Table 4.4); total P and soil available P (Bray-2) were found to be significantly lower at the Elandshoogte site than at the Grootgeluk and Mamre sites in both years (Table 4.3 and 4.4); Al^{3+} and exchangeable acidity were ($p<0.001$) lower at the Elandshoogte site compared with the other sites in both years; percentage silt was found to be significantly ($p<0.0001$) lower at the Elandshoogte site than at the Grootgeluk and Mooifontein sites in both years (Table 4.3 and 4.4). At the Grootgeluk site, effective cation exchange capacity was significantly higher at the site than at the Mamre and Mooifontein sites in both years; N, C, total P, Al^{3+} and exchangeable acidity were significantly ($p<0.001$) higher at the site than at the other sites in both years

(Table 4.3 and Table 4.4); available P was significantly ($p<0.001$) higher at the site than at the other sites in 2006 (Table 4.3) and higher than the Elandshoogte and Mooifontein sites in 2007 (Table 4.4); percentage clay was higher at the site compared with the Mooifontein site in 2007 (Table 4.4); percentage silt was significantly ($p<0.001$) higher than at the Elandshoogte site in 2006 (Table 4.3), and at the Elandshoogte and Mamre sites in 2007 (Table 4.4). At the Mamre site, total P and available P (Bray-2) were significantly higher at the site than the Elandshoogte and Mooifontein sites in both years (Table 4.3 and 4.4); percentage clay was higher at the Mamre site than at the other sites in 2007 (Table 4.4). At the Mooifontein site, percentage clay was significantly ($p<0.001$) lower at the site than at the other sites in 2007 (Table 4.4); percentage silt was significantly ($p<0.001$) higher than at the Elandshoogte site in both years (Table 4.3 and 4.4); while, percentage sand was significantly ($p<0.0001$) higher at the site compared with Grootgeluk and Mamre sites in 2007 (Table 4.4). The pH of the sites is acidic and varied from 4.0 (pH 1 M KCl) at the Mamre and Mooifontein sites in 2006 (Table 4.3) to 4.5 (distilled water) in 2007 at the Elandshoogte site (Table 4.4), with the Elandshoogte site having a higher pH in the range of 4.9-4.5 compared with other sites of 4.0-4.9 across the two years. The sites are rich in organic carbon, ranging from 4.9-9.3% in 2006 and 4.4-7.9% in 2007 across the sites (Table 4.3 and 4.4).

4.1.3 Relationship between soil properties and tree growth parameters

Although the soil properties differed in both years across the sites, the mean values were used to evaluate the relationship between the soil properties and tree growth parameters at each site. The growth increment between 2001 and 2005 was used being the closest to 2006 and 2007 when the soil samples were analyzed because the tree growth measurements in 2006 and 2007 were affected by wind and drought. The results showed generally that there were no strong relationships between soil properties and the tree growth increments except in a few cases. In summary (data not shown), at the Elandshoogte site, stem density increment was strongly negatively correlated with Mn^{2+} ($r = -0.61$, $p=0.023$) and positively correlated with percentage clay ($r = -0.99$, $p=0.008$), while basal area increment was negatively correlated with pH (KCl) ($r = -0.63$, $p=0.027$). There were no correlations between the tree height, stand volume increment and soil properties at the site. At the Grootgeluk site, there were only negative correlations between basal area increment and K^+ (r = -0.64, p=0.026); and available P (r = -0.65, p=0.023). At the Mamre site, stem density increment showed strong negative correlations with C (r = -0.59, p=0.045), Al^{3+} (r = -0.64, p=0.024) and exchangeable acidity (r = -0.60, p=0.039), and a positive correlation with pH (KCl) (r = 0.60, p=0.038); tree height increment was negatively correlated with Ca^{2+} (r = -0.90, p=0.000), and positively correlated with total P (r = 0.76, p=0.004), pH (water) (r = 0.67, p=0.002) and clay (r = 0.99, p=0.000); stand volume was negatively correlated with Ca^{2+} (r = -0.62, p=0.033), and exchangeable acidity (r = -0.58, p=0.049), and positively correlated with total P (r = 0.68, p=0.014), pH (KCl) (r = 0.69, p=0.013) and pH (water) (r = 0.66, p=0.019). There were no correlations between the basal area increment and soil properties at this site, while stand volume increment was negatively correlated with pH in KCl (r = 0.69, p=0.013), and pH in water (r = 0.66, p=0.013). At the Mooifontein site, stem density increment was negatively correlated with Mn^{2+} (r = -0.75, p=0.005); there was no correlation between tree height increment and soil properties; basal area increment was strongly negatively correlated with Mg^{2+} (r = -0.70, p=0.011), K^+ (r = -0.70, p=0.011) and Mn^{2+} (r = -0.62, p=0.032).

The tree growth values from all the sites using the growth increment data from 2001-2005, were pooled and analyzed together with the mean soil properties (across sites) in order to evaluate the relationships between the soil properties and the tree growth parameters measured. This was done to increase the sample size from 12 (two replicates and six treatments) in each site to 48 when combined. Correlations showing relationships at the 5% and 1% levels and the probability values between the tree growth increments and soil properties are shown in Table 4.5. There were generally weak or no relationships except for: stem density was weakly positively correlated with Mg^{2+} (r = 0.34, p=0.017), K^+ (r = 0.32, p=0.027) and pH in (KCl) (r = 0.30, p=0.041) and in water (r = 0.39, p=0.007); tree height increment was weakly positively correlated with total P (r = 0.29, p=0.044) and available P (r = 0.31, p=0.030) and strongly negatively correlated with percentage silt (r = -0.71, p=0.009); basal area was negatively correlated with N (r = -0.36, p=0.012) and C (r = -0.35, p=0.016); while stand volume showed no relationships with the soil properties (Table 4.5).

Table 4.5: Table showing correlations (r) between tree growth increments between 2001 and 2005, and soil properties measured across all the study sites at 0-20cm (mean of the 2006 and 2007 soil properties). Marked correlations *, ** are significant at the probability values of 5% and 1%, n = 48

Soil properties	Stem density Increment	Tree height Increment	Basal area increment	Stand volume Increment
Ca^{2+} (mg kg^{-1})	.2565	-.1674	.1830	.0952
	p=.078	P=.255	p=.213	p=.520
Mg^{2+} (mg kg^{-1})	.3426	.0460	.1250	.1836
	p=.017*	P=.756	p=.397	p=.212
K^{+} (mg kg^{-1})	.3183	.1362	-.1212	.1879
	p=.027*	P=.356	p=.412	p=.201
Mn^{2+} (mg kg^{-1})	.2585	.0007	.0063	.0843
	p=.076	P=.996	p=.966	p=.569
N (%)	-.0561	.2269	-.3606	.0691
	p=.705	P=.121	p=.012*	p=.641
C (%)	-.0717	.1938	-.3457	.0197
	p=.628	P=.187	p=.016*	p=.895
Total P (mg kg^{-1})	-.0001	.2917	-.2247	.1017
	p=.999	P=.044*	p=.125	p=.492
Available P (mg kg^{-1})	-.1872	.3136	-.1450	.0269
	p=.203	P=.030*	p=.326	p=.856
Al^{3+}(mg kg^{-1})	-.1334	.1797	-.2078	-.0234
	p=.366	P=.222	p=.156	p=.875
Exchangeable acidity ($cmol_c$ kg^{-1})	-.2095	.1625	-.2121	-.0815
	p=.153	P=.270	p=.148	p=.582
pH (KCl)	.2963	-.0900	.0036	.0358
	p=.041*	P=.543	p=.981	p=.809
pH (Water)	.3875	.0509	.0863	.1602
	p=.007**	P=.731	p=.560	p=.277
+Clay (%)	-.5202	.2815	-.0048	.1121
	p=.083	P=.375	p=.988	p=.729
+Silt (%)	.3688	-.7123	.2044	-.3263
	p=.238	P=.009**	p=.524	p=.301
+Sand (%)	.0730	.5731	-.2369	.2798
	p=.822	P=.051	p=.458	p=.378

+For soil particle distribution values, n = 12 because of the limitation of soil mass

Positively significant probability values are shown in deep bold (pink) while negative values are in light bold (yellow)

Details of the relationships between the soil properties and the tree growth parameters that were hypothesized in this study are shown in Figure 4.14 to 4.18. There were weak or no relationships between the soil properties; soil organic C, total N, Mn^{2+}, Al^{3+}, and exchangeable acidity and tree growth responses. Increments (2001-2005) of stem density (#stems ha^{-1}), tree height (m), and basal area (m^2 ha^{-1}) and stand volume (m^3 ha^{-1}) were generally found not to be related to organic C concentration (Figure 4.14), total N concentration (Figure 4.15), log mean Mn^{2+} (Figure 4.16), Al^{3+} concentration (Figure 4.17) and the level of exchangeable acidity (Figure 4.18).

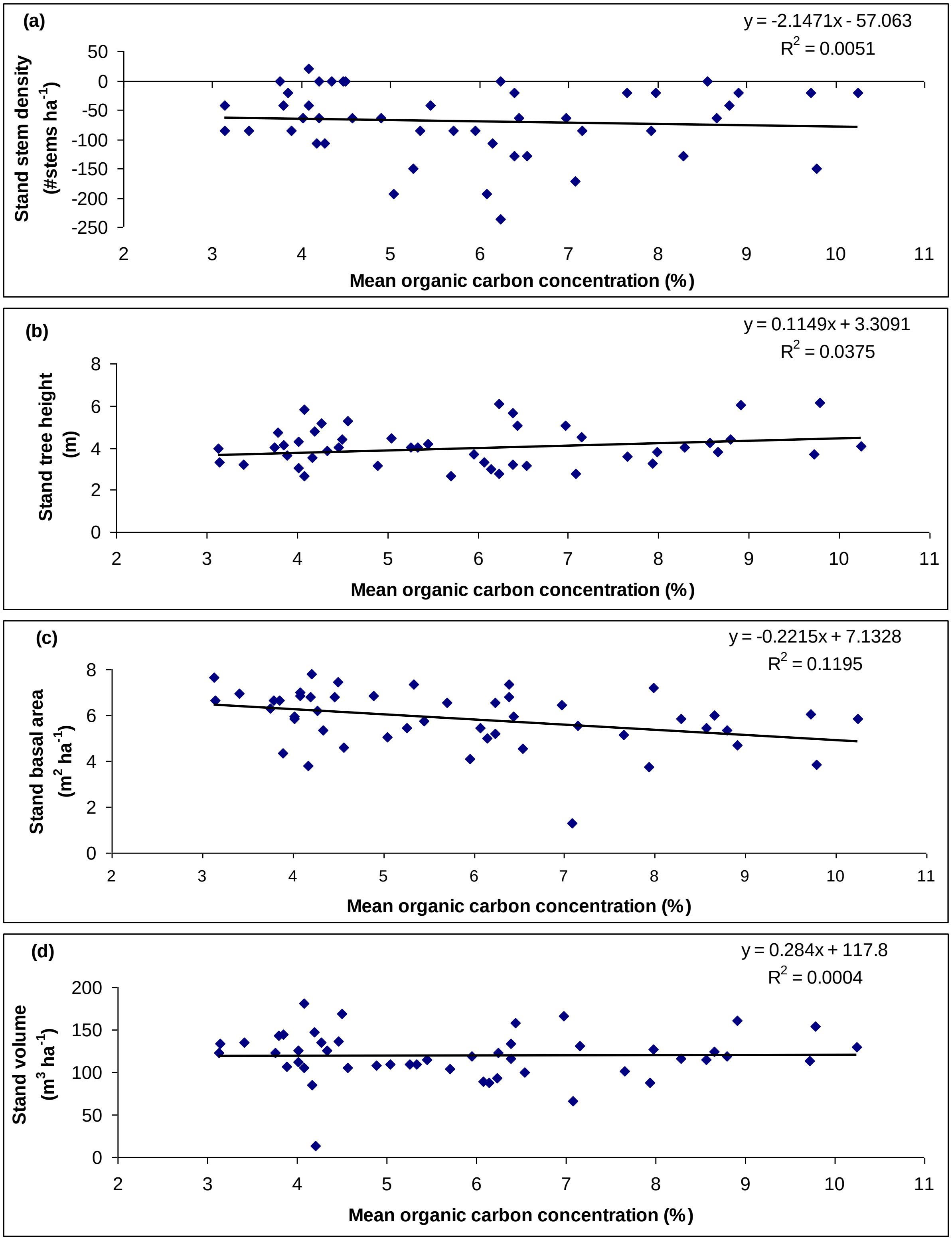

Figure 4.14(a-d) Tree growth increments and mean organic carbon concentration (%) across the study sites. The site soil data were pooled and tree growth increment between 2001 and 2005 were used

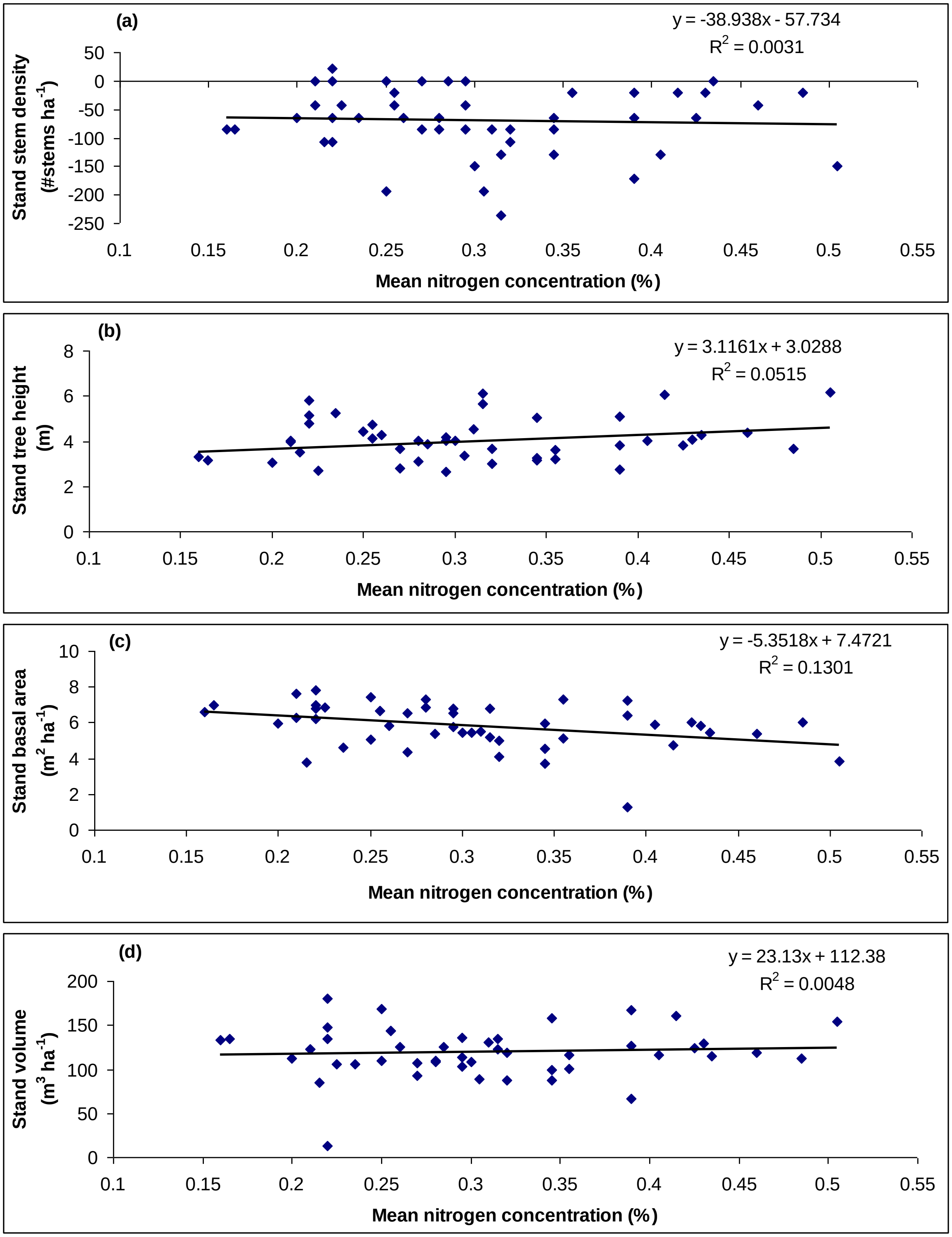

Figure 4.15(a-d) Tree growth increments and mean nitrogen concentration (%) across the study sites. The site soil data were pooled and tree growth increment between 2001 and 2005 were used

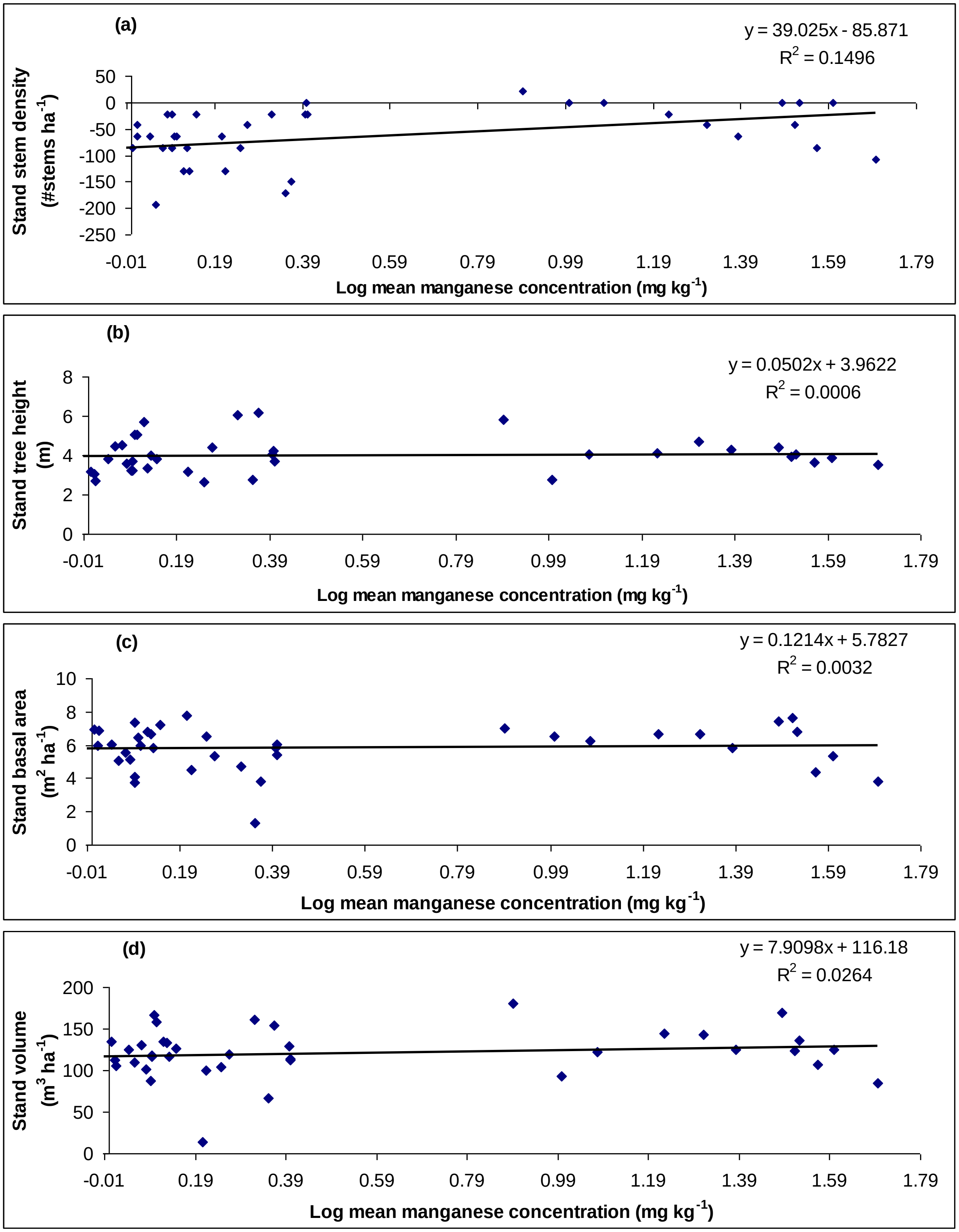

Figure 4.16(a-d) Tree growth increments and log manganese concentration (mg kg^{-1}) across the study sites. The site soil data were pooled and tree growth increment between 2001 and 2005 were used

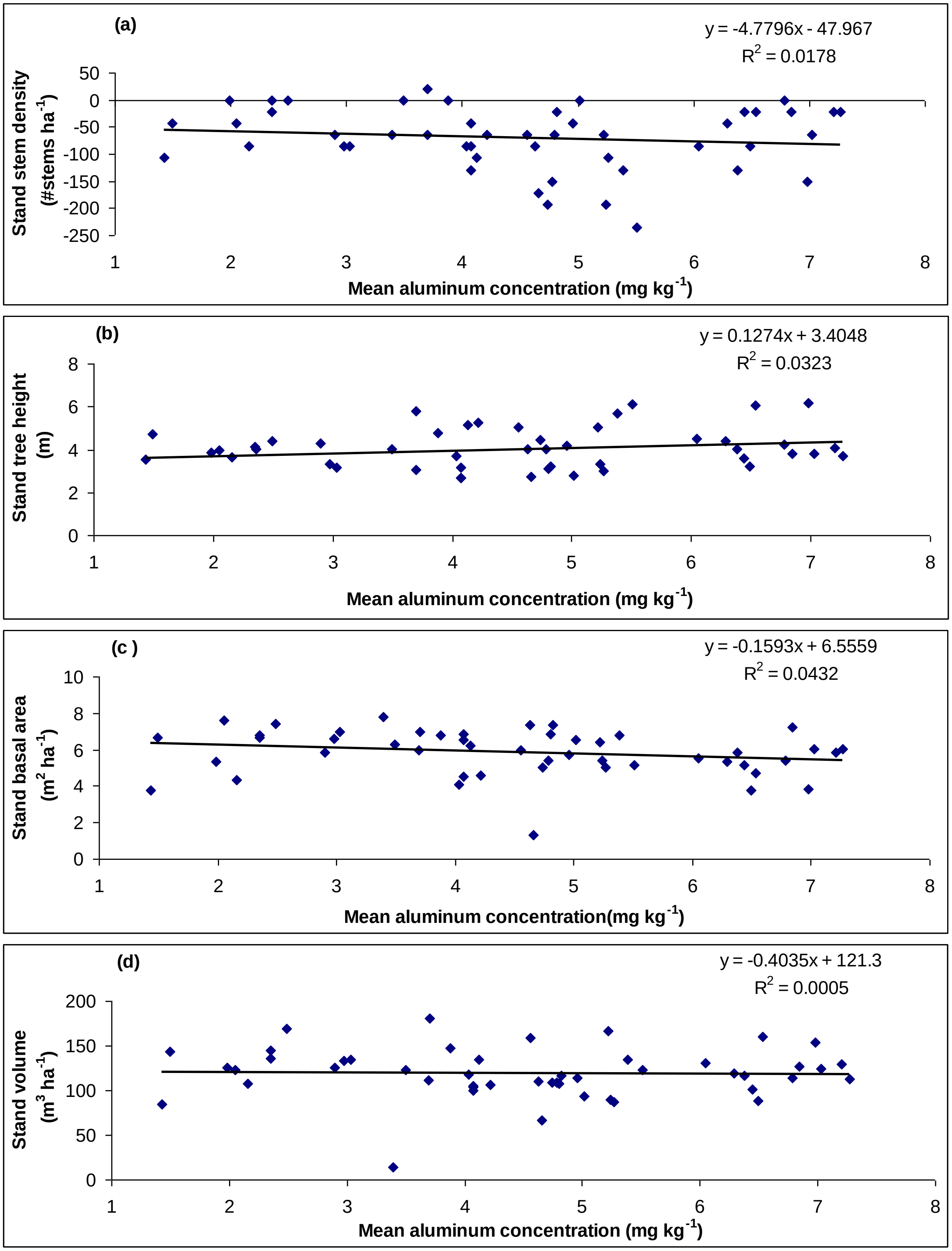

Figure 4.17(a-d) Tree growth increments and mean aluminum concentration (mg kg^{-1}) across the study sites. The site soil data were pooled and tree growth increment between 2001 and 2005 were used

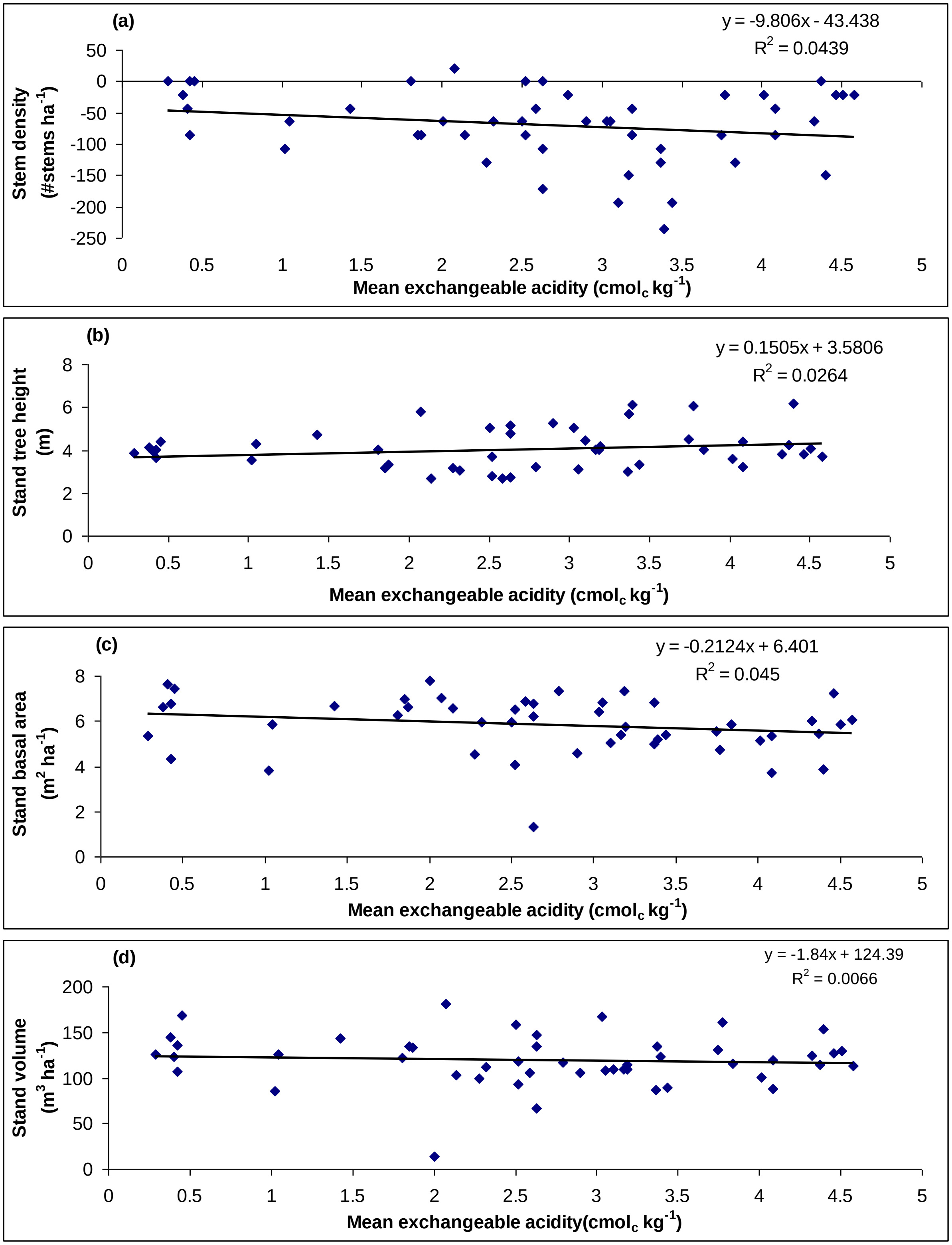

Figure 4.18(a-d) Tree growth increments and mean exchangeable acidity concentration ($cmol_c$ kg^{-1}) across the study sites. The site soil data were pooled and tree growth increment between 2001 and 2005 were used

4.1.4 Litter production

Annual litter fall production

The mean total litter production calculated by summing all the litter fraction values at each site over the sampling period, from May 2006 to May 2007 are: 1.25 t ha^{-1} yr^{-1} at the Elandshoogte site, 2.03 t ha^{-1} yr^{-1} at the Grootgeluk site, 1.24 t ha^{-1} yr^{-1} at the Mamre site and 2.17 t ha^{-1} yr^{-1} at the Mooifontein site (Figure 4.19). Needle litter fall accounted for 0.81 t ha^{-1} yr^{-1} (64.8%), 1.16 t ha^{-1} yr^{-1} (57.1%), 0.75 t ha^{-1} yr^{-1} (60.5%) and 1.22 t ha^{-1} yr^{-1} (56.2%) at the Elandshoogte, Grootgeluk, Mamre and Mooifontein sites respectively; wood litter accounted for 0.31 t ha^{-1} yr^{-1} (24.8%) at the Elandshoogte site, 0.61 t ha^{-1} yr^{-1} (30.1.%) at the Grootgeluk, 0.27 t ha^{-1} yr^{-1} (21.8%) at the Mamre site and 0.66 t ha^{-1} yr^{-1} (30.4%) at the Mooifontein site, and sporangia and cones contributed 0.13 t ha^{-1} yr^{-1} (10.4%) at the Elandshoogte, 0.26 t ha^{-1} yr^{-1} (12.8%) at the Grootgeluk site, 0.22 t ha^{-1} yr^{-1} (17.7%) at the Mamre site and 0.29 t ha^{-1} yr^{-1} (14.4%) at the Mooifontein site, of the total.

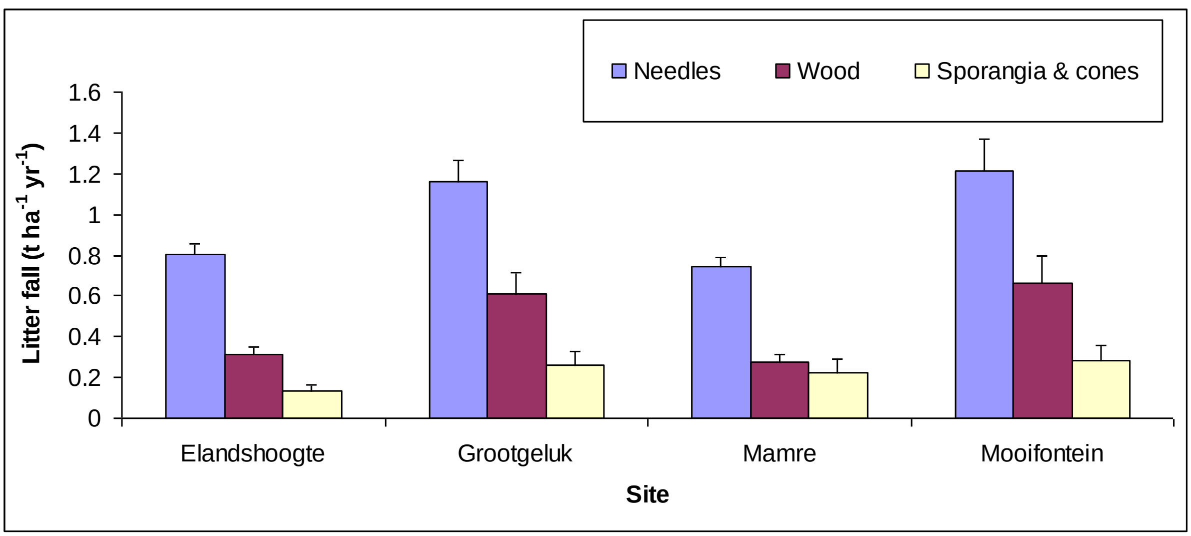

Figure 4.19 Litter fall fractions (t ha^{-1} yr^{-1}) recorded across the study sites. Values are presented as means and the vertical bars indicate the confidence intervals at the 5% significance level, n = 36

There were site significant differences for all the litter fall components. The amount of needle and wood litter fall recorded at the Mooifontein and Grootgeluk sites were higher (p=0.0001) than the values obtained at the Elandshoogte and Mamre sites (Figure 4.19). The sporangia and cones litter fall rate was found to be lower at the Elandshoogte site compared with the other sites.

Results of the analysis of variance showed that there were significant (p=0.0001) differences for needle, wood and sporangia and cones litter fall across the fertilizer treatments in each of the sites. However, sporangia and cones could not be analyzed at the Grootgeluk and Mooifontein sites because the data were too sparse in some treatment plots at these sites. At the Elandshoogte site, the needle litter fall was significantly lower in the control and the Urea 11&13 treatments than the other treatments (Figure 4.20). The highest rate of wood litter fall was recorded in the LAN 11 and LAN 11&13 treatments and the lowest values occurred in the control plots. Sporangia and cones were higher at the LAN 11&13 and LAN 11 compared with Urea 11&13, Urea 11 and LAN 13 treatment plots. The comparison between the fertilized and control (unfertilized) plots showed that there were no significant differences in needle (p=0.5861), wood (p=0.5085) and sporangia and cones (p=0.8530) litter fall at this site (Figure 4.20).

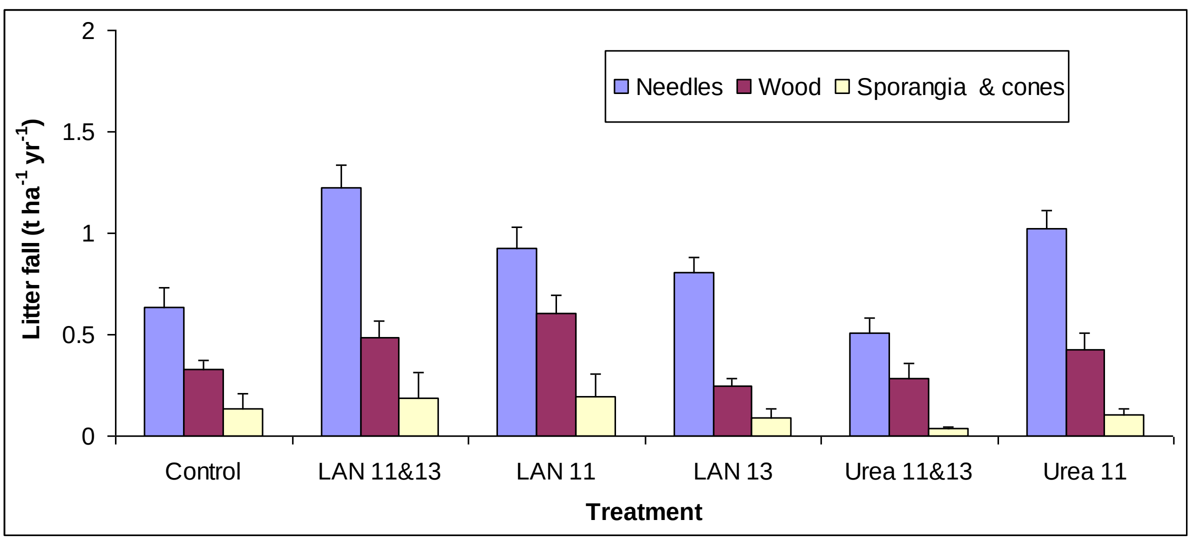

Figure 4.20 Litter fall (t ha^{-1} yr^{-1}) in different fertilizer treatments at the Elandshoogte site. Values are presented as means and vertical bars indicate the confidence intervals at the 5% significance level, n = 36

At the Grootgeluk site, the needle litter fall recorded at the LAN 11, LAN 13 and Urea 11 was higher than at the other treatments (Figure 4.21). The rate of wood litter fall recorded in the control plots was significantly lower than in the other treatment plots (Figure 4.21). Sporangia and cones could not be analyzed at this site because there were too few data points for some of the treatments. The comparison between the fertilized and control plots showed no significant differences in the rate of needle (p=0.061) and wood (p=0.3491) litter fall.

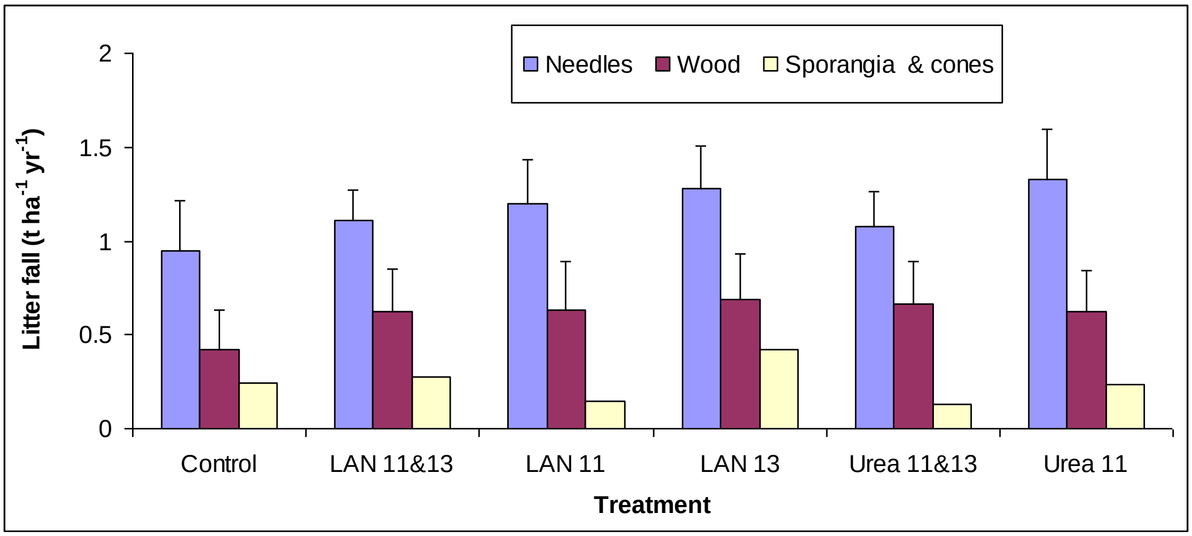

Figure 4.21 Litter fall (t ha^{-1} yr^{-1}) in different fertilizer treatments at the Grootgeluk site. Values are presented as means and vertical bars indicate the confidence intervals at the 5% significance level, n = 36

At the Mamre site, the highest needle fall was recorded in all of the treatments except in the Urea 11&13 treatment (Figure 4.22). The highest rate of wood litter fall was recorded in the control and Urea 11&13 treatment plots. The highest sporangia and cones litter fall rates were measured in the control and the LAN 11 treatment (Figure 4.22). The comparison between the fertilized and control plots showed that there was no significant difference in needle litter fall rate (p=0.7485), however, there were significant differences in wood (p=0.0044), sporangia and cones (p=0.0001) litter fall rate.

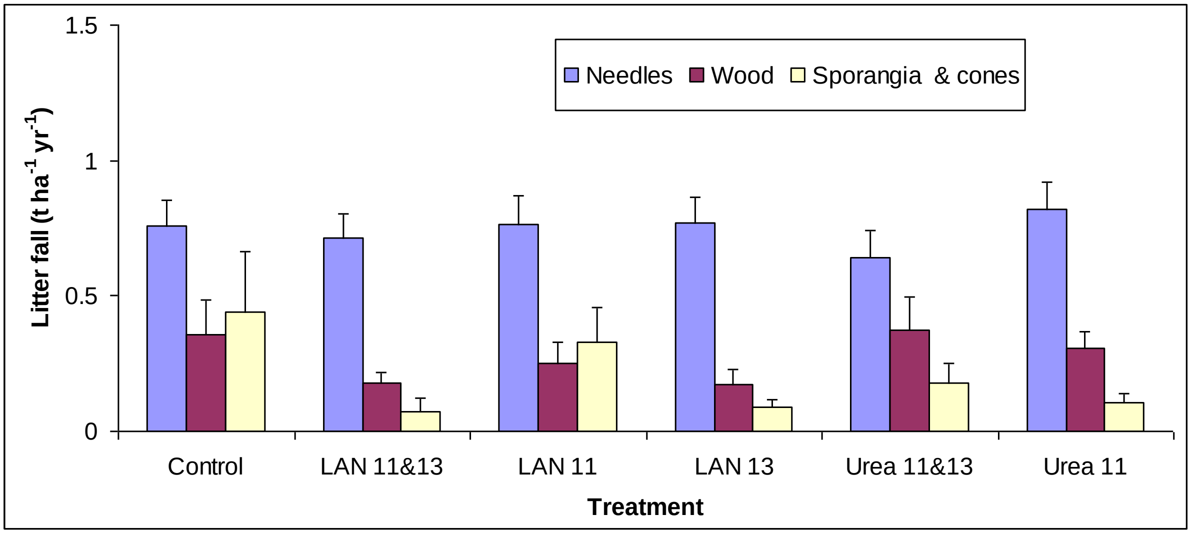

Figure 4.22 Litter fall (t ha^{-1} yr^{-1}) under different fertilizer treatments at the Mamre site. Values are presented as means and vertical bars indicate the confidence intervals at the 5% significance level, n = 36

At the Mooifontein site, treatment had no significant effect on the rate of needle litter fall, whilst the highest wood litter fall occurred in the LAN 11 treatment (Figure 4.23). Sporangia and cones could not be analyzed at this site due to a lack of data (Figure 4.23). The comparison between the fertilized and control treatment plots showed that there were no significant differences in needle (p=0.9627) and wood (p=0.2098) litter fall.

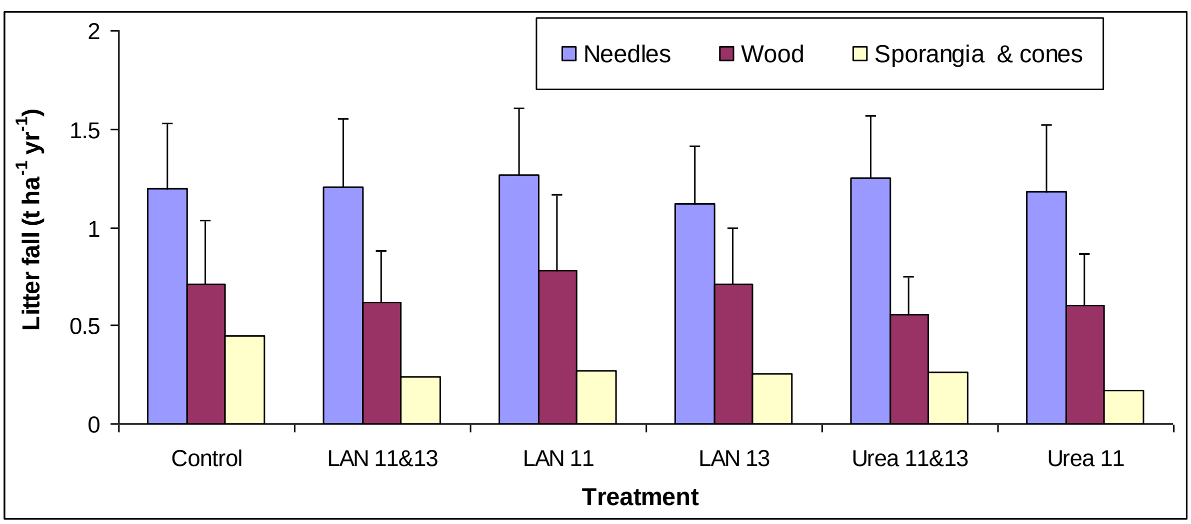

Figure 4.23 Litter fall (t ha^{-1} yr^{-1}) in different fertilizer treatments at the Mooifontein site. Values are presented as means and vertical bars indicate the confidence intervals at the 5% significance level, n = 36

Seasonal litter fall

There were bi-monthly differences which were significant; these being the needle litter fall, ($p<0.0001$) and the wood litter fall ($p=0.0001$) (Figure 4.24a, 4.24b and 4.24d). It should be noted that sporangia and cones could not be analyzed at the Mooifontein and Grootgeluk sites because of the limited data set. The patterns at Mamre were different to the other three sites, with the highest and lowest needle litter fall occurring in July 2006 and May 2007 respectively (Figure 4.24c). The highest needle litter fall rate was recorded in September 2006 at the Elandshoogte, Grootgeluk and the Mooifontein sites (Figure 4.24a, 4.24b and 4.24d). The lowest rate of needle litter fall was recorded in January 2007 at the Elandshoogte, Grootgeluk and the Mooifontein sites (Figure 4.24a, 4.24b and 4.24d). Grootgeluk and Mooifontein were the only two sites which showed reasonably high rates of wood litter fall (Figure 4.24b and 4.24d). The rate of sporangia and cones litter fall was low across the year.

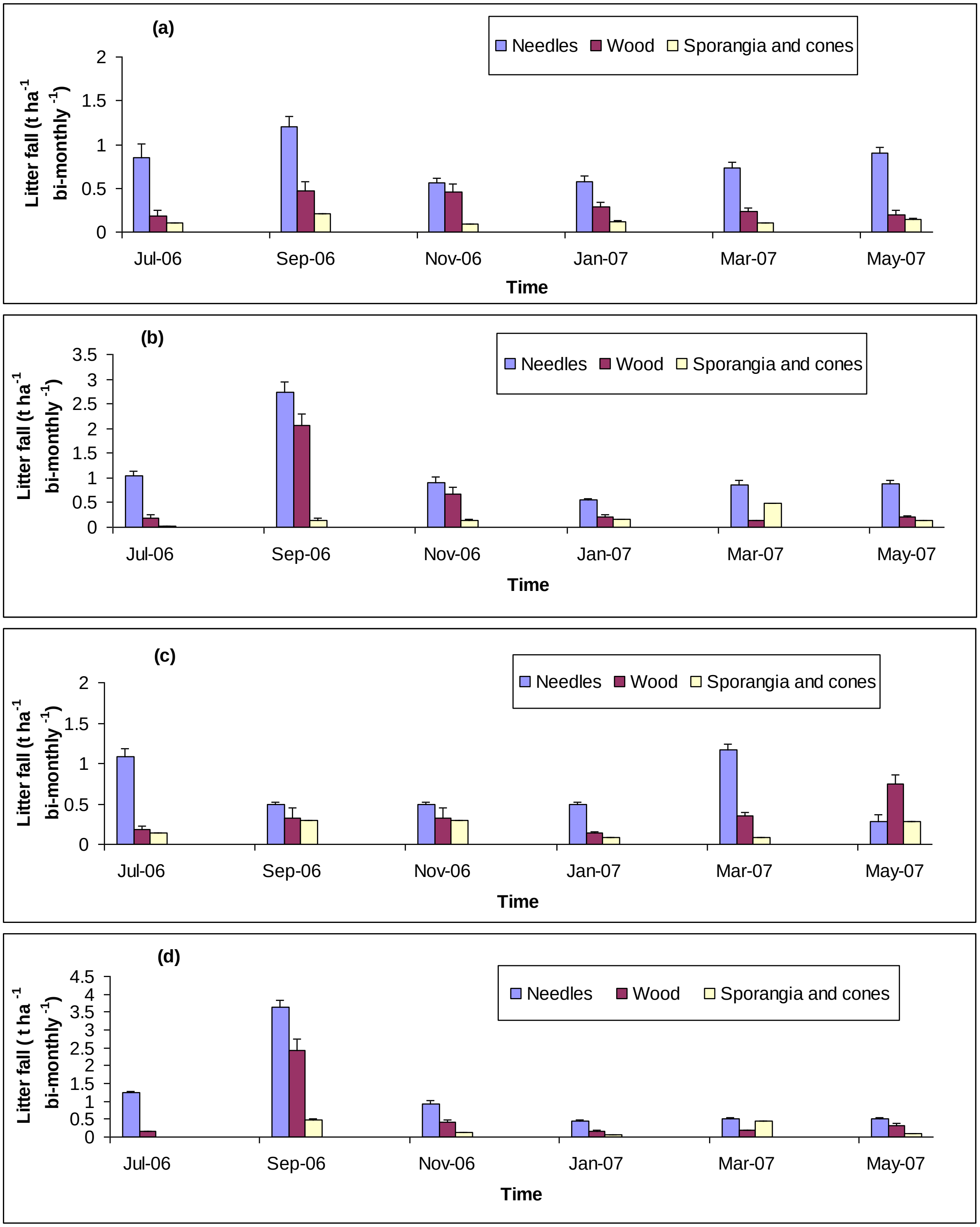

Figure 4.24 Bi-monthly litter fall fractions (t ha^{-1} bi-monthly $^{-1}$) from May 2006 to May 2007. Values are presented as means and the vertical bars indicate the confidence intervals at the 5% significance level, n = 36. In the Figure "a" stands for the Elandshoogte site, b = the Grootgeluk site, c = the Mamre site and d = the Mooifontein site.

4.1.5 Forest floor litter accumulation and depth

Forest floor litter accumulation

Results of the analysis of variance showed that there was a significant difference in the amount of needle litter ($p<0.0001$) accumulated since the establishment of the plantation across the treatments. At the Elandshoogte site, the amount of litter (needle, wood and sporangia and cones) accumulated in the LAN 11 and Urea 11 treatments were significantly higher, while the lowest values were recorded in the control and LAN 11&13 treatments (Figure 4.25). The comparison between the control and fertilized plots showed that there were significant differences in needle forest litter ($p=0.003$) and wood forest litter ($p=0.023$) accumulation, while and sporangia and cones litter were not significantly different ($p=0.2943$).

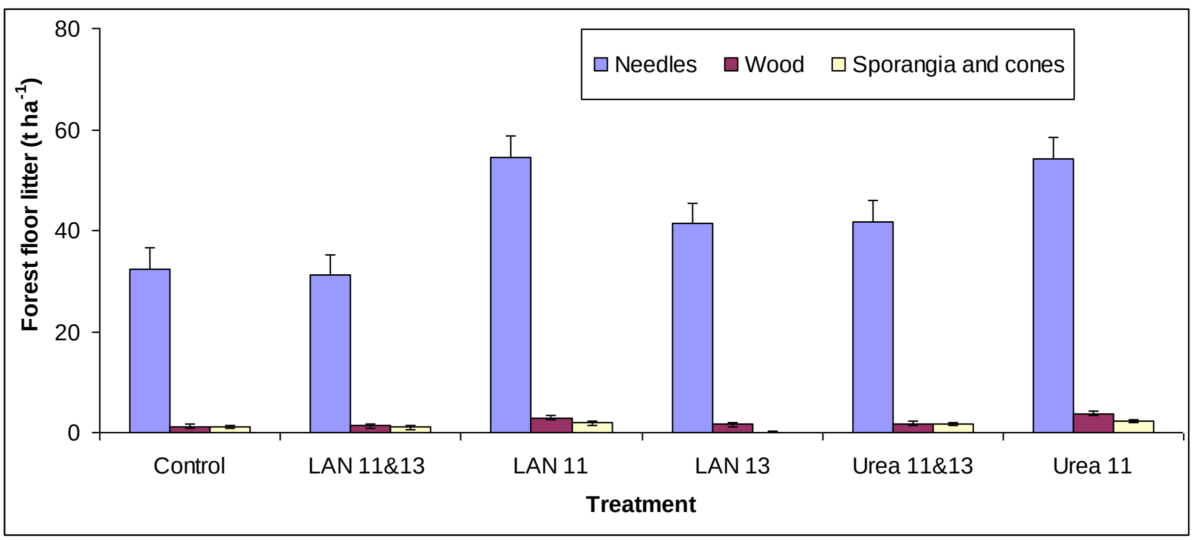

Figure 4.25 Forest floor litter accumulated in different fertilizer treatments at the Elandshoogte site. Values are presented as means and the vertical bars indicate the confidence intervals at the 5% significance level, n = 36

At the Grootgeluk site, the highest needle accumulation occurred in the LAN 11 treatment and the lowest in the LAN 13; wood litter accumulated in the Urea 11&13; sporangia and cone litter had the highest value in the Urea 11 and control treatment (Figure 4.26). Results of ANOVA showed that there were no differences between the fertilized and control plots in all the litter fractions, needles (p=0.8360), wood (p=0.5821) and sporangia and cones (0.8091).

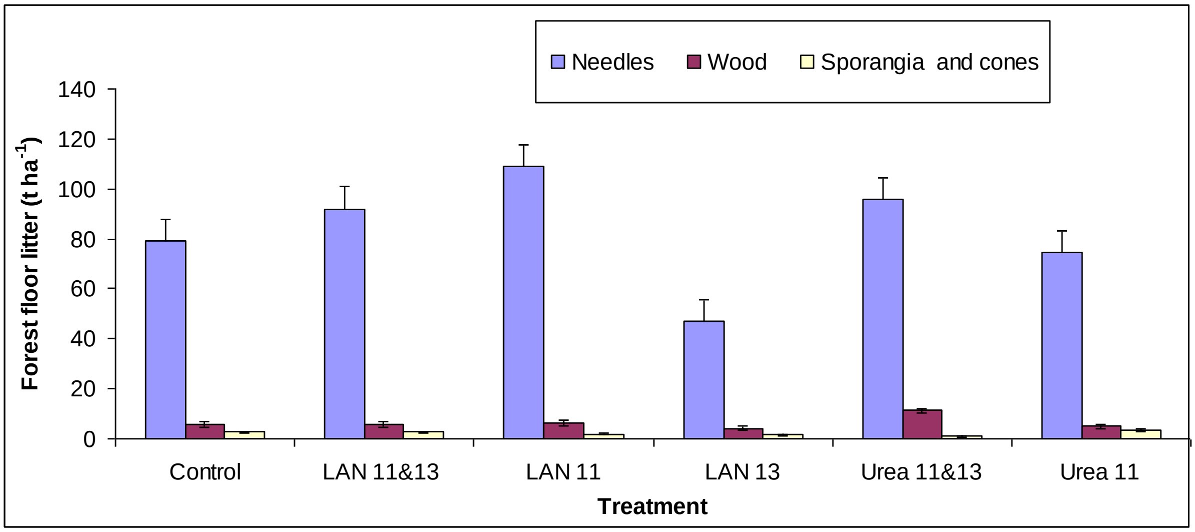

Figure 4.26 Forest floor litter accumulated in different fertilizer treatments at the Grootgeluk site. Values are presented as means and the vertical bars indicate the confidence intervals at the 5% significance level, n = 36

The greatest needle accumulation occurred in the LAN 11&13 treatments at the Mamre site, while the LAN 13 and control treatments had the lowest needle litter accumulation at this site. There was no difference in the wood litter accumulated across the treatments; sporangia and cones were higher in the Urea 11&13 treatments compared with the LAN 11, LAN 13 and control treatments (Figure 4.27). The comparison between fertilized and unfertilized plots showed a significant difference in the needles accumulation on the forest floor (p=0.0001), while there were no differences in wood (p=0.9068) and sporangia and cones (p=0.3834) litter on the forest floor.

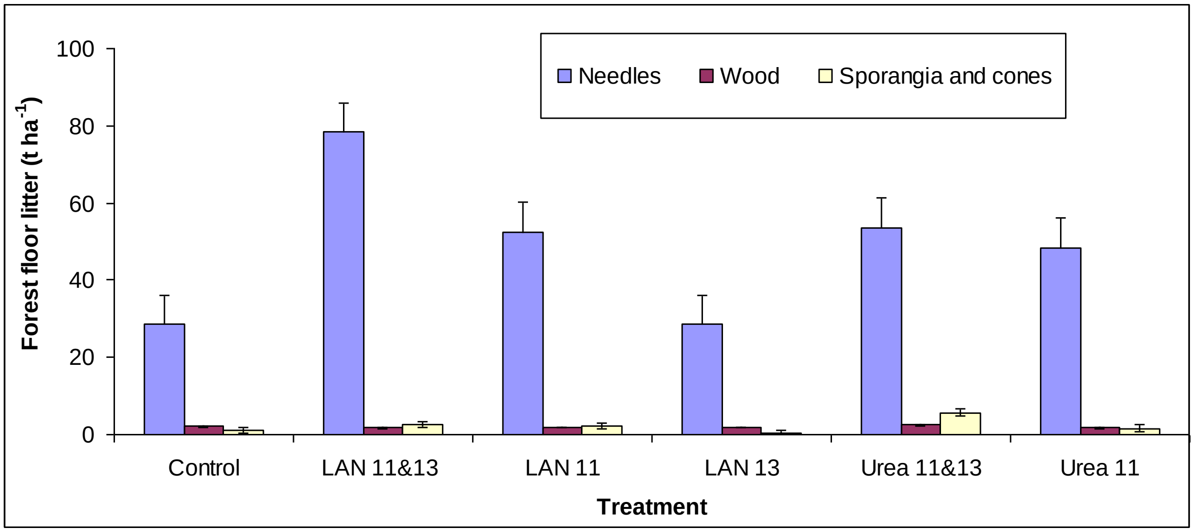

Figure 4.27 Forest floor litter accumulated in different fertilizer treatments at the Mamre site. Values are presented as means and the vertical bars indicate the confidence intervals at the 5% significance level, n = 36

At the Mooifontein site, there were no differences in needle and wood litter accumulated across the treatments, however, in the sporangia and cones, LAN 11&13 and control treatments were significantly higher than the other plots (Figure 4.28). The comparison between the fertilized and unfertilized plots showed no differences.

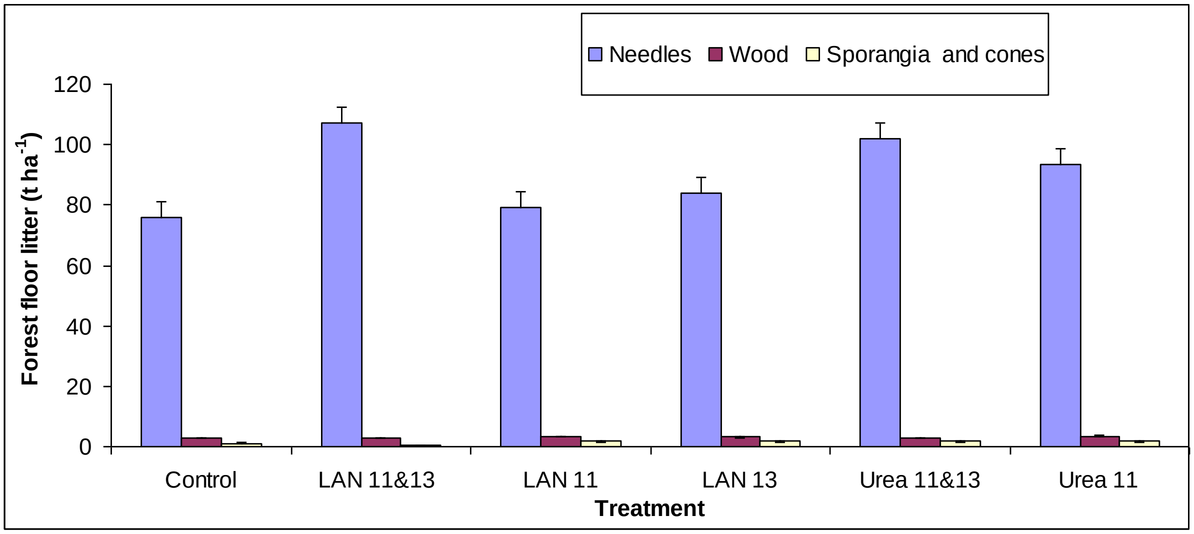

Figure 4.28 Forest floor litter accumulated in different fertilizer treatments at the Mooifontein site. Values are presented as means and the vertical bars indicate the confidence intervals at the 5% significance level, n = 36

The amount of litter accumulated on the forest floor since the establishment of the trial differed significantly ($p<0.0001$) across the study sites. The amount of litter accumulated on the forest floor varied from 42.5-90.2 t ha^{-1} for needles, 1.7-6.1 t ha^{-1} for wood and 0.9-1.9 t ha^{-1} for sporangia and cones across the sites (Table4.6). The needle litter accumulated at the Mooifontein and Grootgeluk sites was found to be significantly ($p<0.001$) higher than at the other sites, while the wood litter accumulation was highest at the Grootgeluk site.

Table 4.6: Forest floor litter accumulation (July 2006) since the establishment of the *Pinus patula* trial across the study sites

Trial site	**Forest floor litter accumulation (t ha^{-1})**			
	Needles	**Wood**	**Sporangia and cones**	**Total**
Elandshoogte	42.54^{b}	2.09^{c}	0.95^{c}	45.58^{b}
Grootgeluk	82.84^{a}	6.10^{a}	1.92^{a}	90.86^{a}
Mamre	48.35^{b}	1.73^{c}	1.22^{ab}	51.3^{b}
Mooifontein	90.24^{a}	4.08^{b}	1.04^{bc}	94.36^{a}

Values are presented as means and values with the same letter are not significantly ($p>0.05$) different within each column.

Litter depth

Results of the analysis of variance showed that the fertilizer treatments had no significant ($p=0.1762$) effect on the forest litter depth across the years (2001-2007). There was a sharp increase in litter depth from 2003 to 2004 across the treatments, this could be attributed to higher amounts of rainfall in 2004 compared to 2003, and rainfall at these sites can be accompanied by strong winds. Litter depths were not measured in 2002 across the sites (Figure 4.29).

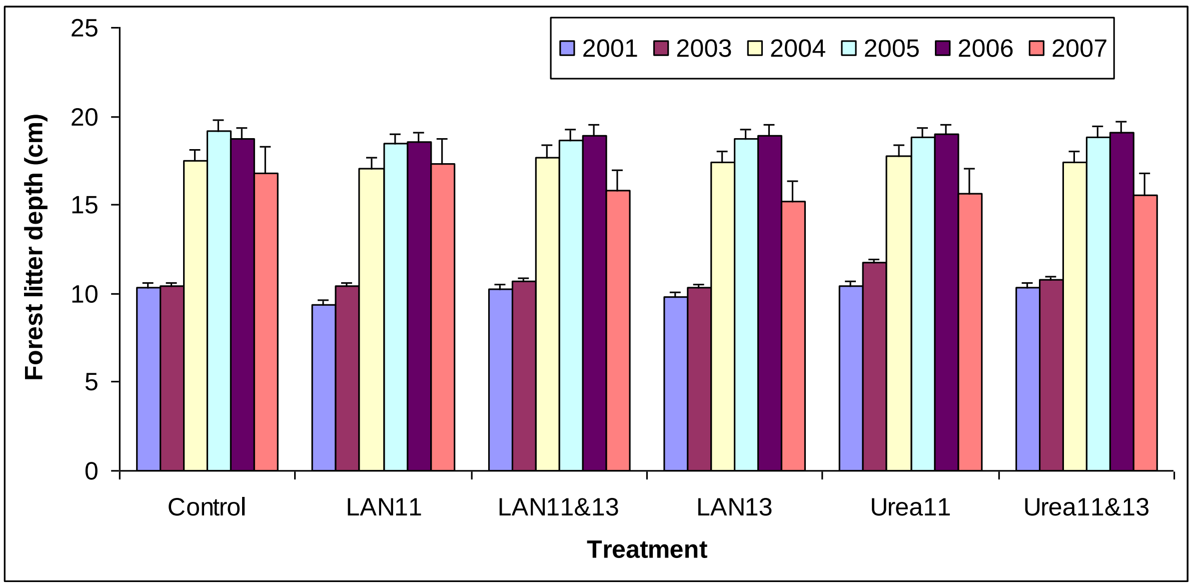

Figure 4.29 Forest floor litter depth measured over the years (2001-2007) in the different fertilizer treatments. Values are presented as means and the vertical bars indicate the confidence intervals at the 5% significance level, n = 84

However, there were site significant ($p<0.0001$) differences over the years (Figure 4.30). Litter depth at the Grootgeluk site was significantly ($p<0.0001$) higher than at the other sites over the years except in 2003 where Mooifontein was higher. Litter depth at the Elandshoogte site was significantly lower over the years compared with other sites.

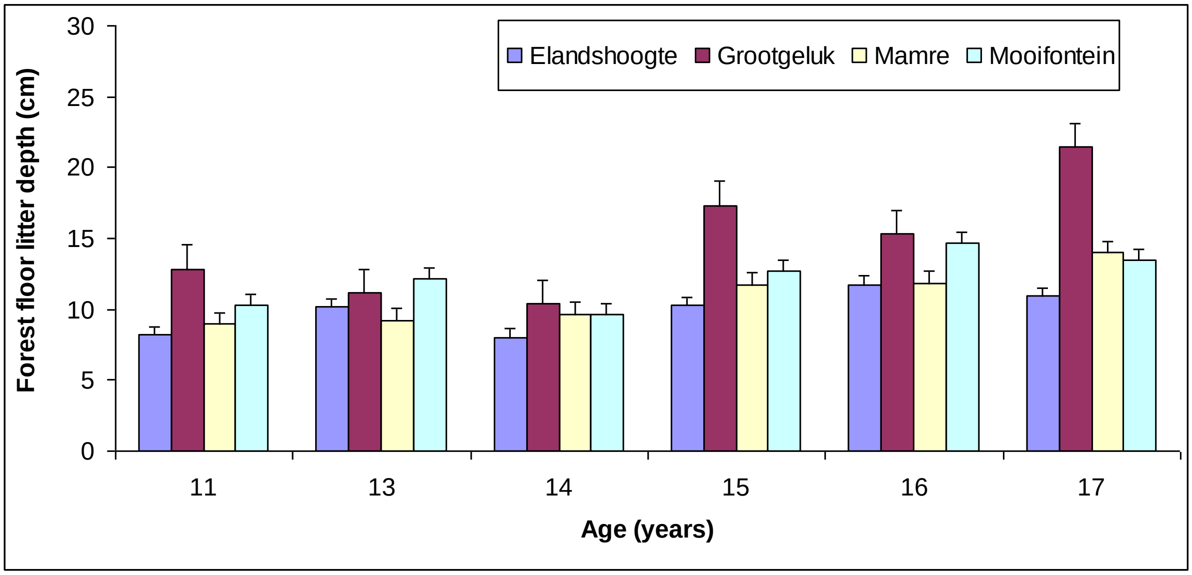

Figure 4.30 Forest floor litter depth measured over the years across the study sites in *Pinus patula*. Values are presented as means and the vertical bars indicate the confidence intervals at the 5% significance level, n = 84

4.1.6 Foliage, litter fall and forest floor litter nutrient concentrations

Results of the analysis of variance showed that there were no significant treatment effects on the foliar nutrient concentrations at each of the sites (Elandshoogte, p=0.1856), Grootgeluk (p=0.4056), Mamre site (p=0.2957) and at the Mooifontein site (p=0.5588) except for the concentration of Mn^{2+} at the Elandshoogte site, where the Urea 11 treatment was significantly higher than the LAN 11&13 treatment; the concentration of K^{+} at both the Grootgeluk and Mamre sites were higher in the Urea 11 than in the LAN 11&13 treatments; at the Mooifontein site, N and C concentrations were higher in the LAN 11&13 treatment than in the control treatment; the nutrient concentration ratios of C:N and P:N were higher in the control than in all the other treatments (Data not shown). There were no correlations between foliar nutrient concentration except for a weak positive relationship between tree height and concentration of Ca^{2+} (r = 0.46, p=0.001), Mg^{2+} concentration (r = 0.42, p=0.003) and C:N ratio (r=0.47, p=0.001).

The details of the nutrient concentrations and nutrient concentration ratios in the foliage, litter fall, forest floor; and litter fractions (needles and branch wood) across the sites in *P. patula* are presented in Table 4.7. In Table 4.7, the data under the heading “litter fall” are the combined needle and wood data but do not include the sporangia and cones data due to the small number of samples in this fraction; the data under the headings “litter fractions” give the concentrations by litter fraction. There were significant differences in the nutrient concentrations at each of the sites. The concentrations of Ca^{2+} in foliage, litter fall and forest floor litter were significantly ($p<0.001$) higher at the Elandshoogte site compared to other sites, however nutrient ratios for P:N were lower. In a few cases the elemental concentrations were lower at the Mooifontein site. The mean concentration of Mg^{2+}, K^{+}, P, N and the nutrient concentration ratios of P:N and K:N were found to be significantly higher ($p<0.001$) in the foliage than in the litter fall and forest floor litter; concentrations of Ca^{2+} and C, and nutrient concentration ratios of Ca:N were higher in litter fall than in the other fractions. Nutrient concentrations were significantly higher ($p<0.0001$) in the needle litter than in the branch wood in both litter fall (by fraction and forest floor (by fraction) except for C:N and Ca:N.

Table 4.7: Nutrient concentrations in foliar, litter fall, forest floor litter across the study sites and in litter components in *Pinus patula*. Values are presented as the means ± standard deviations (n = 4). * P:N, K:N and Ca:N ratios were multiplied by 100

Site and nutrient pools	**Nutrient concentrations (%)**						**Nutrient concentration ratios**			
	Ca^{2+}	Mg^{2+}	K^{+}	P	N	C	C:N	*P:N	*K:N	*Ca:N
Foliage										
Elandshoogte	0.58±0.17	0.22±0.03	0.61±0.09	0.10±0.01	1.39±0.19	48.34±0.85	34.78±4.50	7.19±1.11	43.88±5.43	41.73±14.74
Grootgeluk	0.40±0.06	0.16±0.03	0.74±0.12	0.14±0.01	1.50±0.14	48.08±0.40	32.05±2.87	9.33±0.79	49.33±6.93	26.67±5.40
Mamre	0.34±0.04	0.15±0.02	0.69±0.08	0.13±0.01	1.36±0.12	48.18±0.38	35.43±4.13	9.56±0.47	50.74±6.31	25.00±4.10
Mooifontein	0.26±0.08	0.13±0.03	0.72±0.08	0.13±0.01	1.50±0.11	48.19±0.68	32.13±2.24	8.67±0.95	48.00±8.45	17.33±6.97
Mean	**0.40±0.15**	**0.16±0.04**	**0.69±0.10**	**0.12±0.02**	**1.44±0.15**	**48.20±0.60**	**33.47±4.57**	**8.33±0.13**	**47.92±7.12**	**27.78±12.49**
Litter fall										
Elandshoogte	0.54±0.19	0.13±0.07	0.16±0.08	0.03±0.02	0.66±0.24	48.75±0.79	73.86±59.48	4.55±1.35	24.24±9.24	81.82±32.84
Grootgeluk	0.49±0.17	0.12±0.06	0.18±0.12	0.06±0.02	0.73±0.24	48.65±0.73	66.64±19.94	8.22±11.90	24.66±104.07	67.12±166.71
Mamre	0.43±0.15	0.10±0.05	0.16±0.11	0.06±0.02	0.70±0.21	48.88±0.59	69.83±27.40	8.57±1.07	22.86±12.25	61.43±29.89
Mooifontein	0.39±0.13	0.10±0.05	0.16±0.10	0.06±0.02	0.74±0.29	48.72±0.66	65.84±36.53	8.11±0.97	21.62±11.72	52.70±25.78
Mean	**0.46±0.17**	**0.11±0.06**	**0.17±0.10**	**0.05±0.02**	**0.71±0.25**	**48.75±0.70**	**68.66±106.68**	**7.04±6.17**	**23.94±0.25**	**64.79±87.72**
Forest floor litter										
Elandshoogte	0.45±0.16	0.12±0.05	0.07±0.05	0.04±0.02	0.82±0.37	46.60±1.61	56.83±37.40	4.88±0.60	8.54±15.45	54.88±12.87
Grootgeluk	0.17±0.06	0.06±0.03	0.08±0.07	0.05±0.02	0.76±0.34	48..66±1.10	64.03±39.63	6.58±0.96	10.53±5.73	22.37±8.08
Mamre	0.15±0.06	0.05±0.03	0.07±0.04	0.04±0.02	0.70±0.27	48.88±1.25	69.83±34.48	5.71±1.29	10.00±2.64	21.43±6.24
Mooifontein	0.11±0.05	0.05±0.03	0.06±0.04	0.03±0.02	0.75±0.30	48.40±4.08	64.53±34.12	4.00±1.39	8.00±4.24	14.67±6.93
Mean	**0.22±0.16**	**0.07±0.05**	**0.07±0.05**	**0.04±0.02**	**0.76±0.32**	**48.14±2.48**	**63.34±35.85**	**5.26±1.31**	**9.21±8.49**	**28.95±19.17**
Litter fractions (Litter fall)										
Needles	0.48±0.11	0.16±0.02	0.25±0.08	0.07±0.01	0.88±0.15	48.76±0.65	55.41±26.88	7.95±1.19	28.41±4.18	54.55±21.09
Branch wood	0.44±0.17	0.06±0.04	0.09±0.02	0.04±0.01	0.54±0.16	48.74±0.78	90.26±88.30	7.41±8.29	16.67±9.37	81.48±120.0
Mean	**0.46±0.17**	**0.11±0.03**	**0.17±0.05**	**0.06±0.01**	**0.71±0.16**	**48.75±0.72**	**68.66±57.59**	**8.45±4.74**	**23.94±6.78**	**64.79±70.55**
Litter fractions (Forest floor litter)										
Needles	0.28±0.19	0.10±0.05	0.10±0.03	0.06±0.01	1.05±0.14	47.67±1.73	45.40±10.79	5.71±0.85	9.52±2.88	26.67±15.02
Branch wood	0.15±0.11	0.04±0.03	0.05±0.05	0.02±0.01	0.46±0.10	48.60±4.00	105.65±21.44	4.35±1.48	10.87±11.71	32.61±22.05
Mean	**0.22±0.16**	**0.07±0.04**	**0.07±0.04**	**0.04±0.02**	**0.76±0.12**	**48.13±2.37**	**63.33±16.12**	**5.26±1.17**	**9.21±0.7.30**	**28.95±18.54**

4.1.7 Litter decomposition

The decomposition study using litter bags was conducted only at Grootgeluk, due to workload demands, the data for that site are displayed in Table 4.8. The mean decomposition rates were calculated for each treatment over the year and were normalized by the initial dry mass of the litter which was placed into the bags. The highest decomposition rate took place in the first three months. The mean decomposition rates were significantly ($p<0.0001$) higher in the LAN 13 treatment than in all the other treatments except for the control. The mean decomposition rate recorded over the months in this study is 0.045 g day^{-1} (Table 4.8).

Table 4.8: Needle litter decomposition rates under different fertilizer treatments over the study period, May 2006-May 2007 in *Pinus patula*. Values are presented as means and confidence intervals at the 5% significance level, n = 3

Month	**Decomposition rate (g day^{-1})**						
	Treatment						
	Control	LAN 11&13	LAN 11	LAN 13	Urea 11&13	Urea 11	**Mean**
May-July 2006	0.084± 0.045	0.064± 0.063	0.067± 0.052	0.103± 0.042	0.084± 0.037	0.072± 0.023	0.079± 0.010^{a}
July-Sep 2006	0.049± 0.038	0.032± 0.013	0.034± 0.043	0.043± 0.012	0.016± 0.015	0.028± 0.018	0.034± 0.007^{d}
Sep-Nov 2006	0.048± 0.015	0.043± 0.013	0.054± 0.026	0.053± 0.030	0.041± 0.031	0.06± 0.005	0.05± 0.005^{b}
Nov-Jan 2007	0.044± 0.009	0.039± 0.002	0.041± 0.010	0.043± 0.012	0.042± 0.011	0.047± 0.013	0.043± 0.002^{c}
Jan-Mar 2007	0.037± 0.003	0.032± 0.00	0.035± 0.010	0.035± 0.008	0.034± 0.009	0.039± 0.005	0.035± 0.002^{d}
Mar-May 2007	0.032± 0.002	0.027± 0.003	0.031± 0.009	0.035± 0.002	0.031± 0.007	0.035± 0.006	0.032± 0.002^{d}
Mean	0.049± 0.015^{ab}	0.039± 0.015^{d}	0.044± 0.017^{bc}	0.052± 0.026^{a}	0.042± 0.023^{cd}	0.047± 0.016^{b}	0.045± 0.004

Values with the same letter within the column (mean) indicate no significant difference for treatment, while values with same letter within the row (mean) indicate no significant difference for month at a probability $p<0.05$.

The percentage mass remaining at the end of the incubation period differed significantly across the ($p<0.0001$) treatments. The litter mass remaining for the Urea 11&13 treatment and the LAN 11&13 treatments were higher than for the other treatments (Figure 4.31). There were monthly significant ($p<0.001$) differences on the percentage remaining mass over time, and post hoc tests showed that July and September were higher than other months.

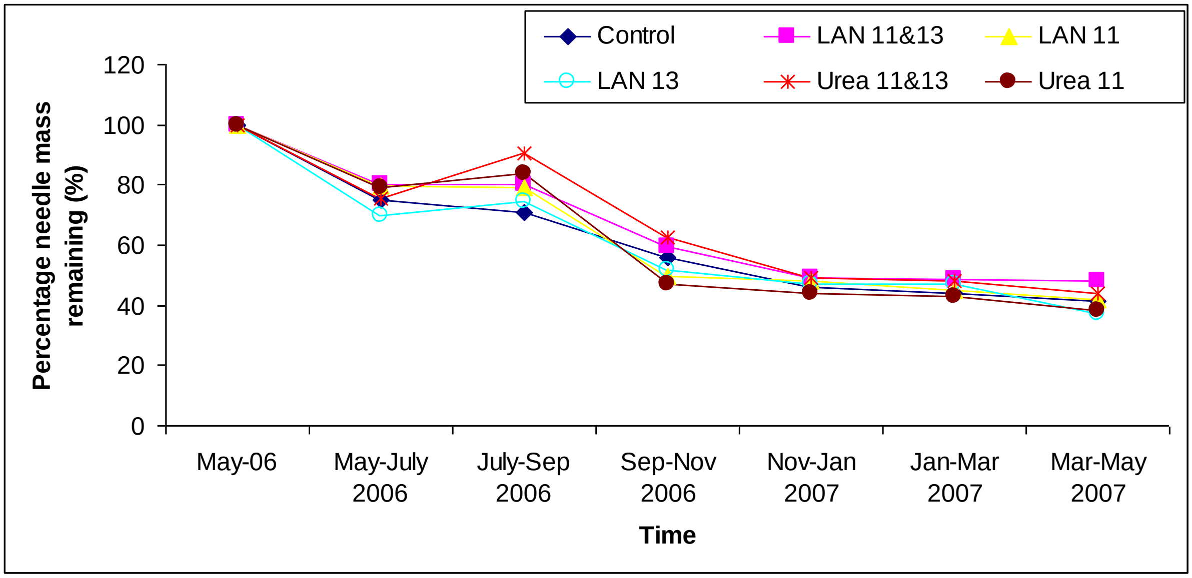

Figure 4.31 Percentage mass remaining in needle litter decomposition under different treatments and over the months

4.1.7 Nutrient concentrations in *Pinus patula* decomposing needle litter

The concentrations of nutrients and nutrient concentration ratios in *P. patula* needle litter at the beginning of the decomposition study are presented in Table 4.9. The concentrations of nutrients did not appear to be affected by the fertilizer treatments.

Table 4.9: Nutrient concentrations and nutrient ratios in the initial needle litter at the beginning of the study in *P. patula* across the treatments. Values are presented as means and confidence intervals at the 5% significant level, n = 3

Nutrient concentrations	**Treatment**					
	Control	LAN 11&13	LAN 11	LAN 13	Urea 11&13	Urea 11
Ca^{2+}(%)	0.46±0.06[ab]	0.30±0.05[bc]	0.28±0.05[c]	0.33±0.07[b]	0.55±0.03[a]	0.33±0.05[b]
Mg^{2+}(%)	0.17±0.03[a]	0.18±0.02[a]	0.14±0.01[a]	0.15±0.03[a]	0.17±0.02[a]	0.14±0.00[a]
K^{+} (%)	0.61±0.05[a]	0.72±0.04[a]	0.67±0.07[a]	0.61±0.09[a]	0.60±0.04[a]	0.56±0.05 [a]
Mn^{2+} (%)	0.07±0.0[ab]	0.06±0.01[b]	0.05±0.01[b]	0.06±0.01[a]	0.10±0.01[a]	0.06±0.01[b]
P (%)	0.11±0.00[b]	0.12±0.01[b]	0.13±0.01[ab]	0.14±0.02[a]	0.12±0.00[b]	0.11±0.01 [b]
N (%)	1.19±0.02[a]	1.23±0.01[a]	1.36±0.13[a]	1.44±0.16[a]	1.28±0.08[a]	1.23±0.06 [a]
C (%)	49.10±0.26 a	48.27±0.24 b	48.70±0.17[a] b	48.67±0.39[a] b	49.00±0.21 a	49.10±0.31 a
Nutrient concentration ratios						
C:N	41.28±0.76	39.35±0.28	36.54±4.34	34.46±4.38	38.59±2.43	40.12±2.03
P:N	8.96±0.18	9.78±0.41	9.68±0.56	9.70±0.16	9.69±0.43	8.95±0.34
K:N	51.21±4.72	58.45±4.57	49.94±6.19	42.05±2.14	47.03±4.20	45.63±2.45
Ca:N	38.81±5.72	24.68±4.08	20.98±4.65	24.5±6.77	44.12±4.97	26.83±4.82

Values are presented as means and values with the same letter are not significantly ($p>0.05$) different across the row.

When the fertilizer treatment data were pooled and analyzed in order to investigate trends across months, the following patterns emerged. The concentrations of Ca^{2+} in the decomposing needle litter remained steady from the beginning up to July 2006 and markedly increased from September 2006 to May 2007 (Figure 4.32a). The concentration of K^{+} increased slightly up to September 2006 and then declined sharply until the end of the study, with the highest decline between September 2006 and January 2007. The concentrations of Mg^{2+}, Mn^{2+} and P increased slightly from the beginning to the end of the study (Figure 4.32a).

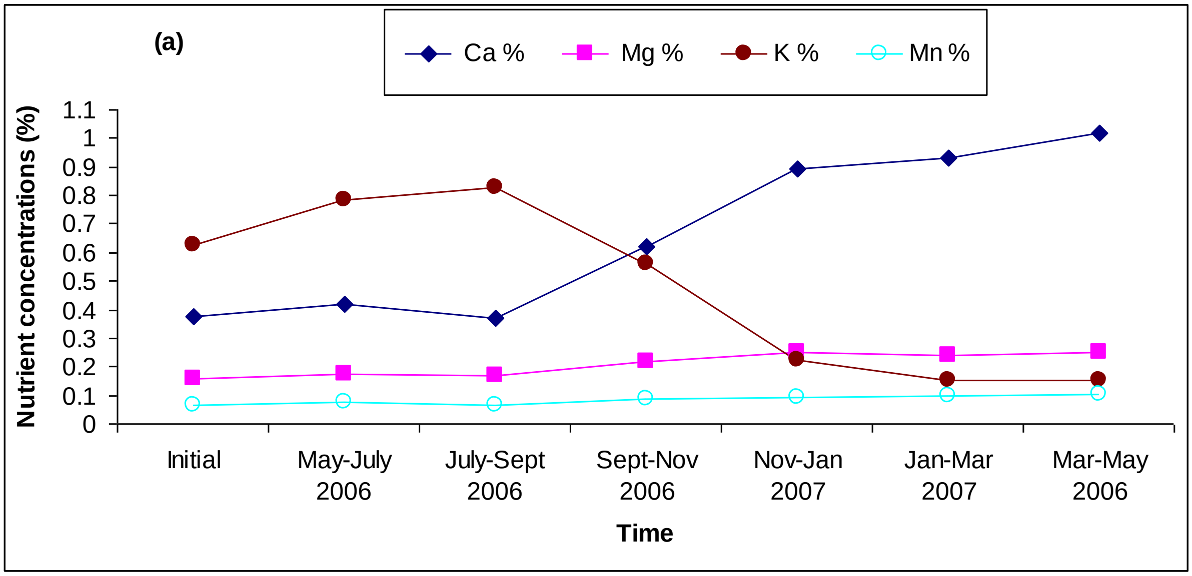

Figure 4.32a Changes in nutrient concentrations in decomposing needle litter over the study period, July 2006 to May 2007

The initial concentration of carbon (48.81%) at the beginning of the decomposition was high and remained more or less constant until the end of the study period (Figure 4.32b). The concentration of N however, increased slightly from the beginning to the end of the study. The initial high rate of litter decomposition is probably driven by the soluble sugar and N concentrations. The C:N ratio decreased rapidly from the start (35.5) of the study until November 2006 (24.0) and then stabilized till the end of the study, while, the P:N ratio decreased slightly from the beginning (9.4) until the end of the study (6.4) (Figure 4.32b).

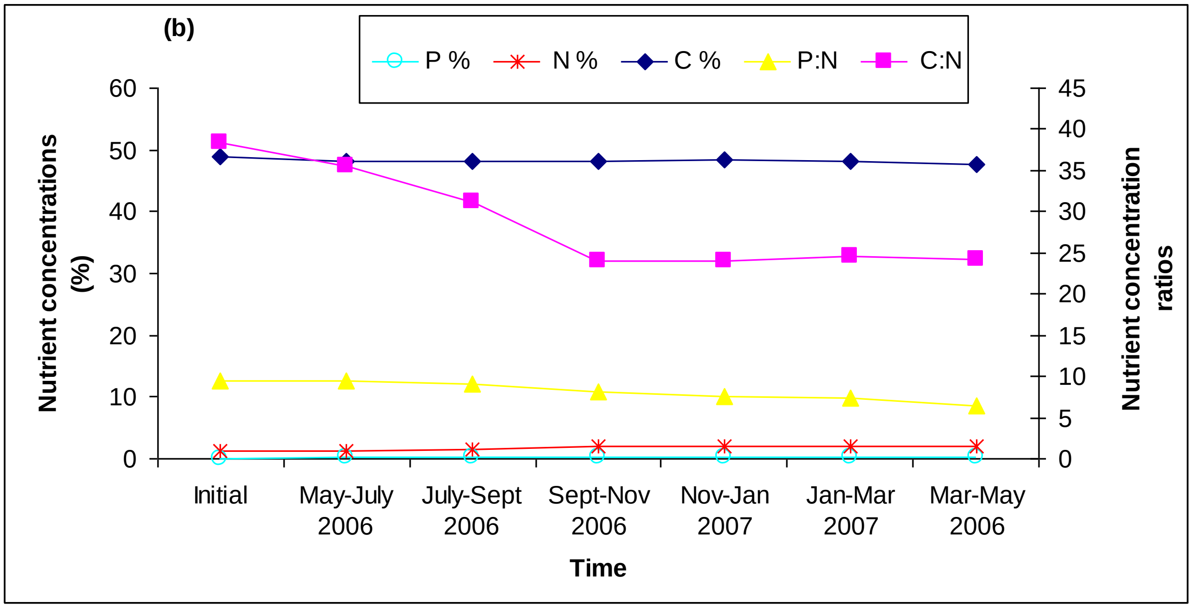

Figure 4.32b Changes in nutrient concentrations and nutrient concentration ratios in decomposing needle litter over the study period, July 2006 to May 2007

4.1.9 Soil ammonification, nitrification and N mineralization rates

There were no significant ($p<0.05$) treatment effects on the rates of ammonification, nitrification and N mineralization at the Elandshoogte (Figure 4.33a), Grootgeluk (Figure 4.33b) and Mooifontein (Figure 4.33d) sites respectively, while they differed at the Mamre site (Figure 4.33c). At the Mamre site, ammonification rate was significantly higher in the control and in the Urea 11 & 13 treatment than in the other treatments, nitrification and N mineralization rates in LAN 11 were higher than in the other treatments, while the lowest ammonification, nitrification and N mineralization rates were recorded at the LAN 11 & 13 treatment compared with the other treatments (Figure 4.33).

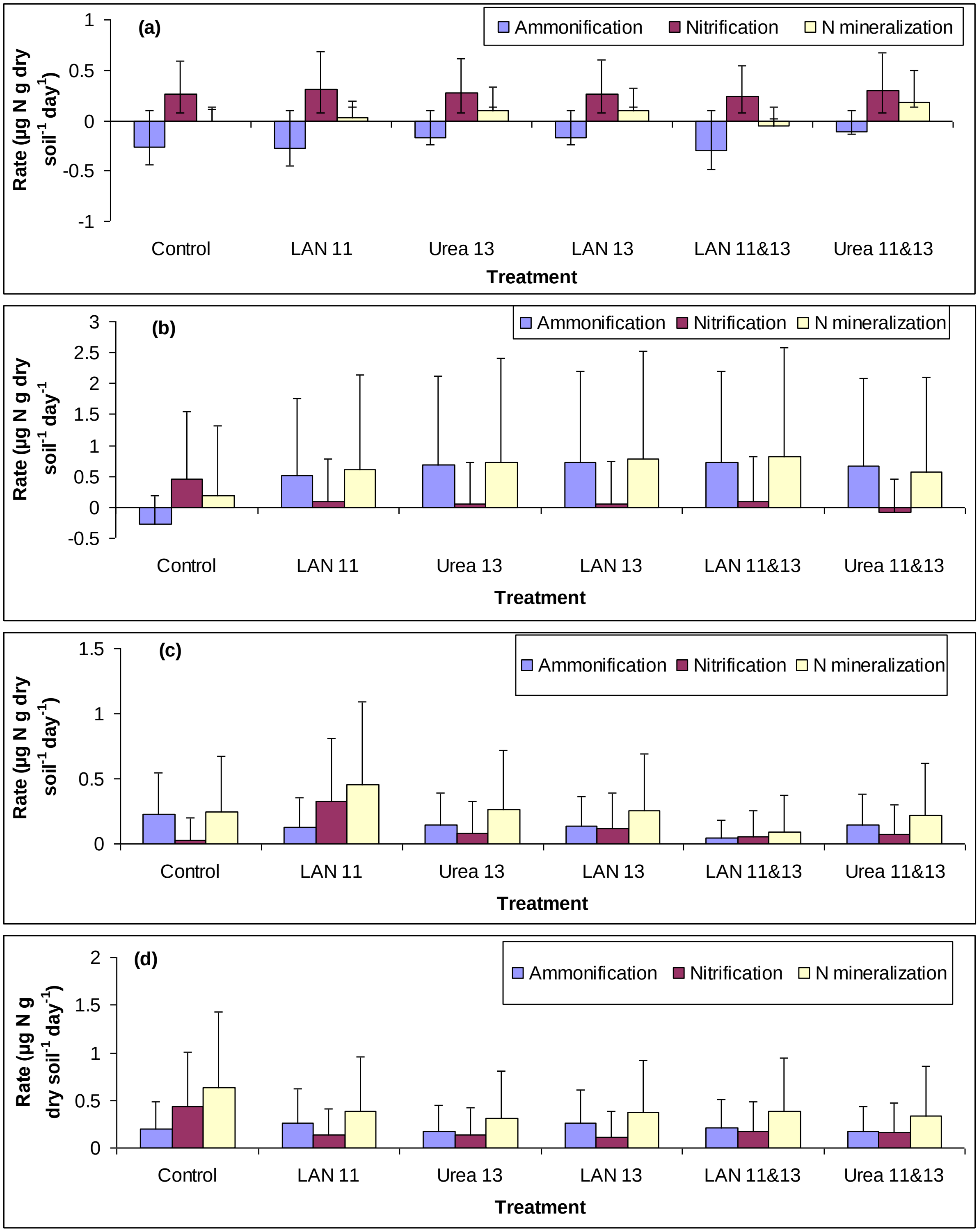

Figure 4.33 Ammonification, nitrification and N mineralization rates in the different fertilizer treatments at each *Pinus patula* site. Values are presented as means and the vertical bars indicate confidence intervals at the 5% significant level, n = 60. In the Figure "a" stands for the Elandshoogte site, b = the Grootgeluk site, c = the Mamre site and d = the Mooifontein site

Result of the ANOVA also showed that there were significant differences in the ammonification ($p=0.00010$), nitrification ($p=0.0004$) and N mineralization ($p=0.0001$) rates across the sites (Figure 4.34). The highest ammonification, nitrification and N mineralization rates occurred at the Mooifontein, Elandshoogte and Grootgeluk sites respectively, while, the lowest ammonification and N mineralization rates occurred at Elandshoogte, and the lowest nitrification at the Mamre site. These differences are as a result mainly of the availability of water and soluble carbon at the sites. There were no differences in the rates between the Grootgeluk and Mooifontein sites across the three processes.

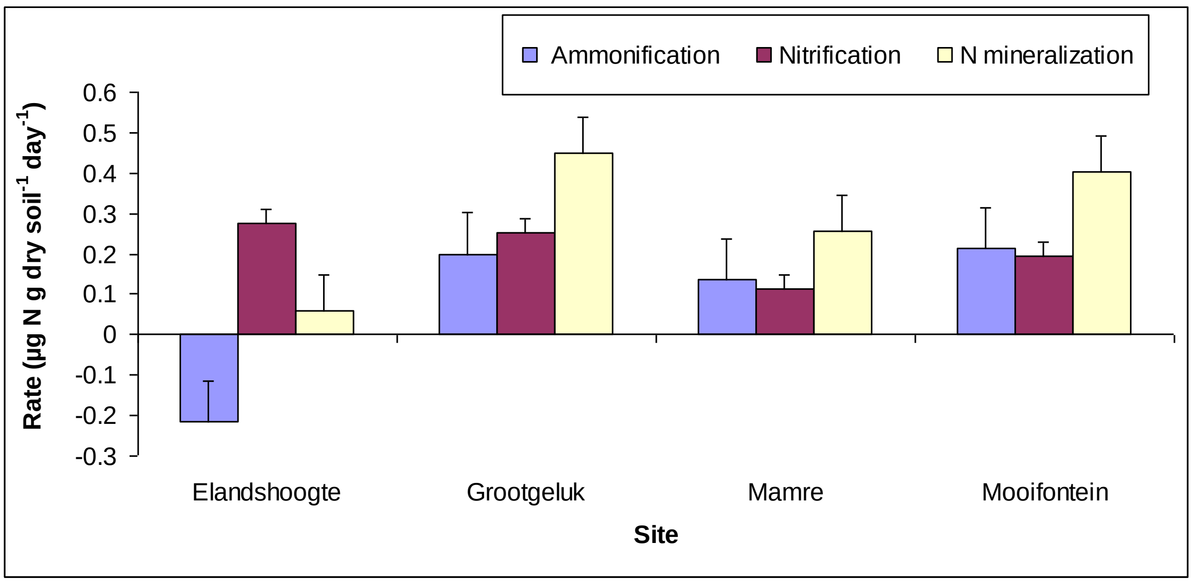

Figure 4.34 Ammonification, nitrification and N mineralization rates across the study sites. Values are presented as means and the vertical bars indicate confidence intervals at the 5% significant level, n = 60

Ammonification, nitrification and N mineralization rates differed significantly ($p<0.0001$) for the different months across the sites (Figure 4.35). Ammonification rate was significantly higher in the month of January, than for all the other months, at the Elandshoogte and Grootgeluk sites. Nitrification and N mineralization rates were highest in the month of March, 2007 at all of the sites. The lowest ammonification and N mineralization rates were recorded in November at the Elandshoogte site (Figure 4.35a), in September 2006 at both the Grootgeluk and Mamre sites (Figure 4.35b and 4.35c), and in July 2006 at the Mooifontein site (Figure 4.35d), while the lowest nitrification rate was recorded at the Elandshoogte and Grootgeluk sites in November, 2006 and in September and July at the Mamre and Mooifontein respectively (Figure 4.35a-d). There was generally higher immobilization of N ions in May, September and November 2006 at the Elandshoogte and Mamre sites.

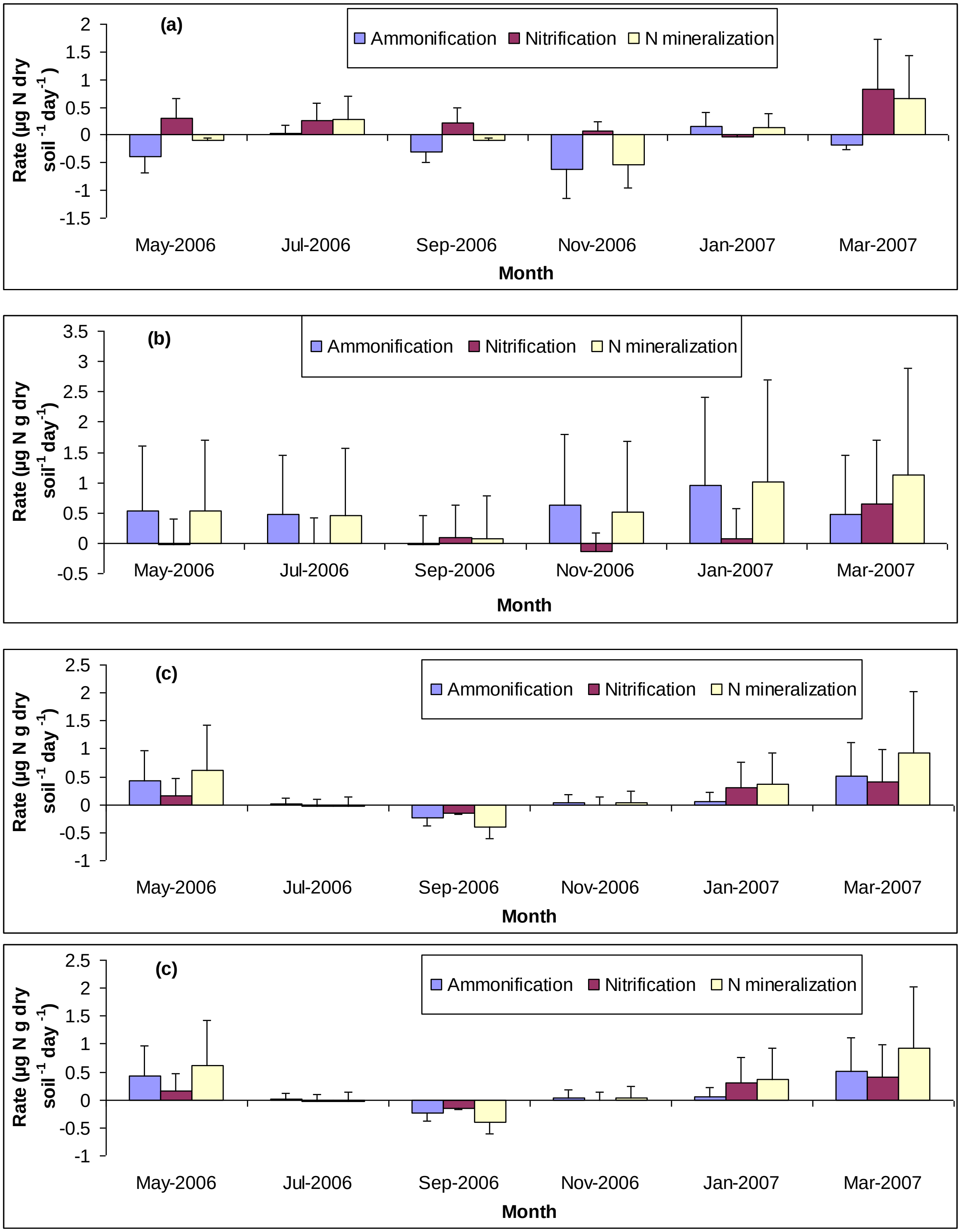

Figure 4.35 Ammonification, nitrification and N mineralization rates for the different months. Values presented as means and the vertical bars indicate confidence intervals at the 5% significant level, n = 60. In the Figure "a" stands for the Elandshoogte site, b = the Grootgeluk site, c = the Mamre site and d = the Mooifontein site.

Results of correlation tests, using combined data sets across treatments and sites, showed that the only positive relationship ($r = 0.47$, $p<0.001$) was between tree height and nitrification rate. A negative relationship ($r = -0.34$, $p<0.02$) was found between tree height and ammonification rates. There was a very weak correlation between other tree growth parameters and any of the three soil N transformation processes.

4.2 *Pinus elliottii*

4.2.1 Tree stand growth

There was a heavy windstorm in the first week of August, 2006, six months after the commencement of the trial (1st of February, 2006), and this damaged some of the trees across the plots especially the P treatment plots. The tree growth parameters (stem density ($p=0.2988$), tree height ($p=0.7321$), basal area ($p= 0.3326$) and stand volume ($p=0.4279$) measured were found not to be significantly affected by the fertilizer treatments.

Stem density

There was a decline in stem density (#stems ha^{-1}) over time (Figure 4.36), the mean number of stems per hectare measured at the start of the study was 256 and these declined to 230 at the time of measurement in May 2007. These declines are not as a result of fertilizer application but due to the wind storm.

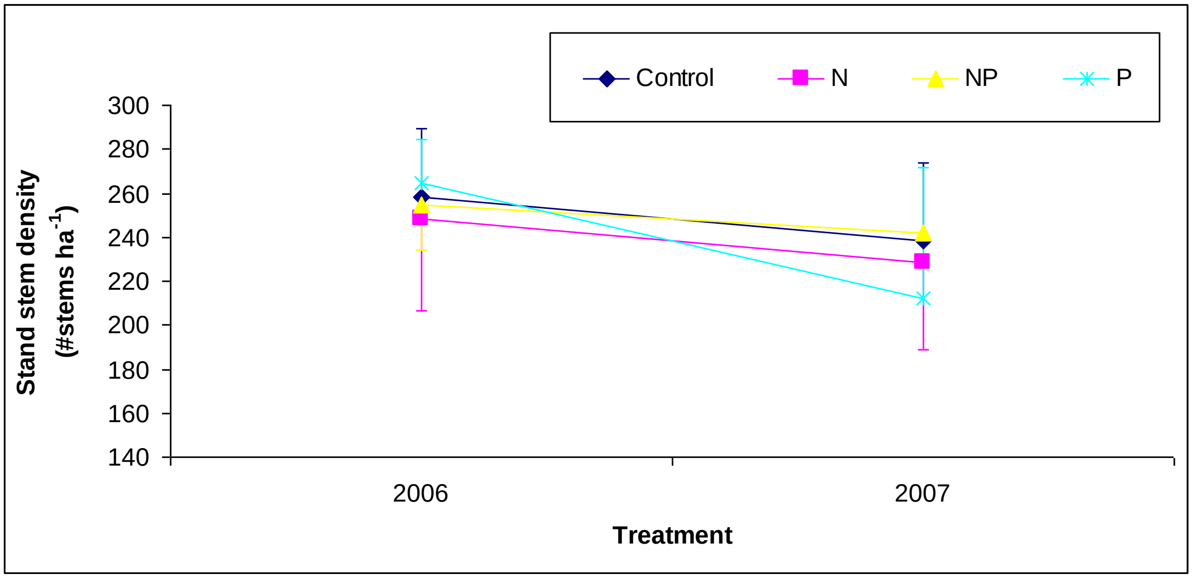

Figure 4.36 Stem density (#stems ha^{-1}) measured in February, 2006 before fertilizer application and in May 2007, 14 months after fertilizer was applied in different fertilizer treatments. Values are presented as means and the vertical bars indicate confidence intervals at the 5% level, n = 4

Tree height

Tree height was not affected by the wind, treatment or time. The variability in tree height data measured in February 2006 was high and resulted in there being no NP treatment effect.

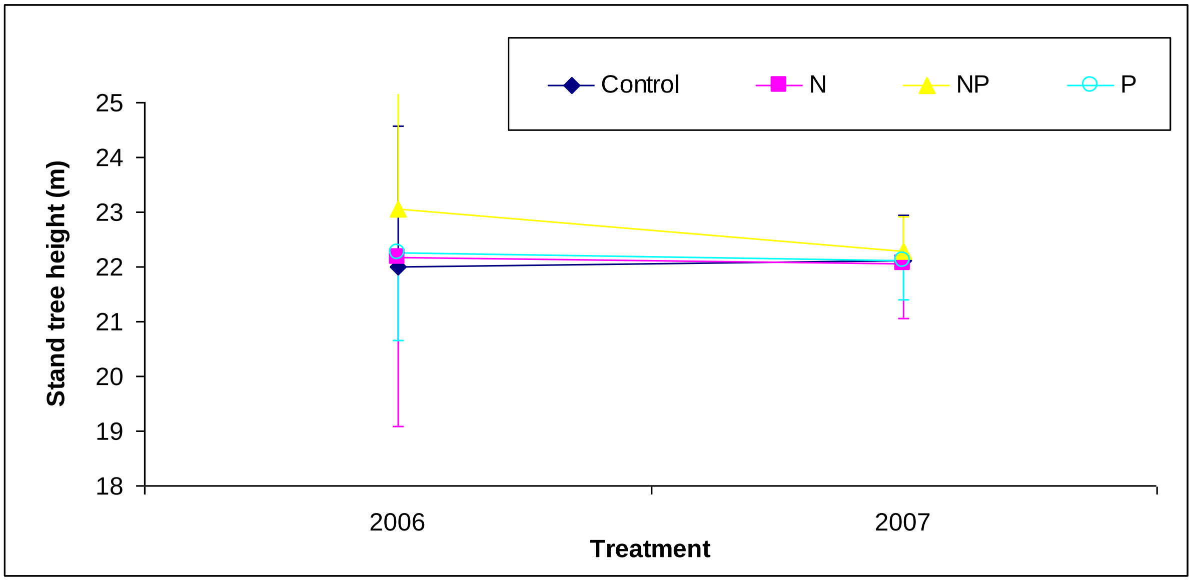

Figure 4.37 Tree height (m) measured in February, 2006 before fertilizer application and in May 2007, 14 months after fertilizer was applied in different fertilizer treatments. Values are presented as means and the vertical bars indicate confidence intervals at the 5% significance level, n = 4

Basal area

There was a slight decline in basal area in the P treatment, though not significant (Figure 4.38). The decline in the P treatment is related to the wind damage as was shown for stem density (see Figure 4.38).

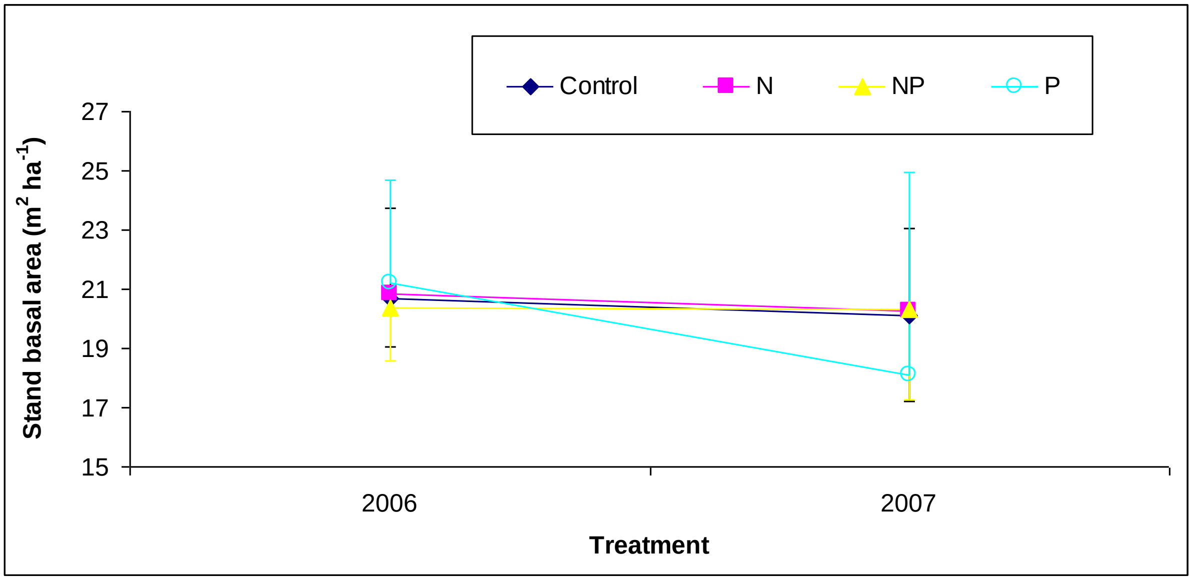

Figure 4.38 Stand basal area (m^2 ha^{-1}) measured in February, 2006 before fertilizer application and in May 2007, 14 months after fertilizer was applied in different fertilizer treatments. Values are presented as means and the vertical bars indicate confidence intervals at the 5% level, n = 4

Stand volume

The general decline in stand volume across the treatments (Figure 4.39) followed the same pattern as was observed in stem density. This decline is more as a result of a decline in stem density and basal area than tree height. The trees in the P treatment were most heavily impacted.

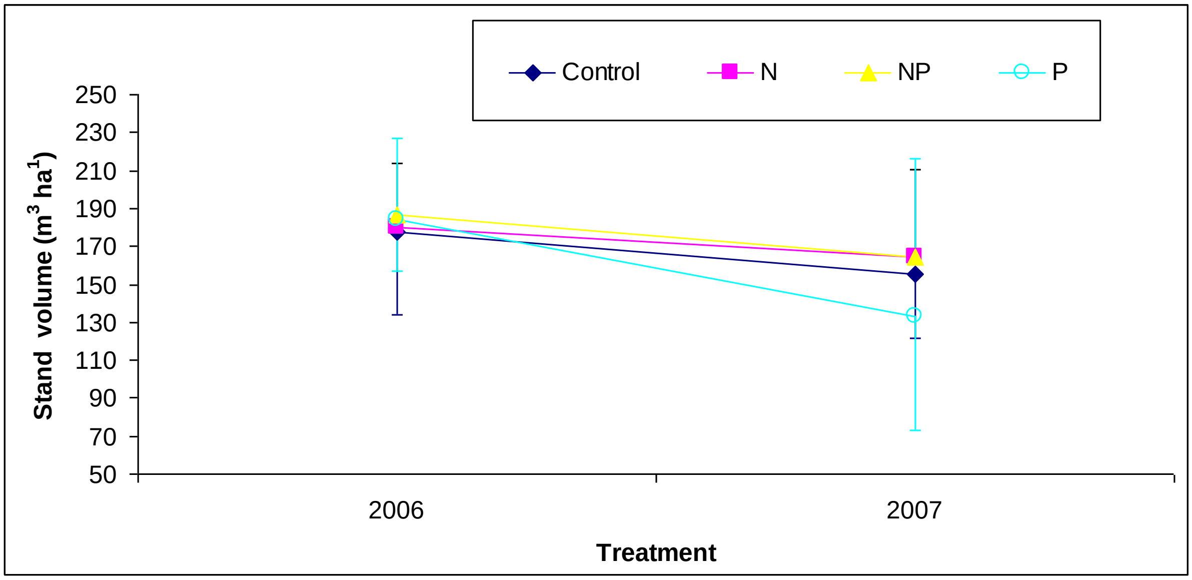

Figure 4.39 Stand volume (m^3 ha^{-1}) measured in February, 2006 before fertilizer application and in May 2007, 14 months after fertilizer was applied in different fertilizer treatments. Values are presented as means and the vertical bars indicate confidence intervals at the 5% level, n = 4

4.2.2 Soil properties

The details of the soil properties in years 2006 and 2007 across the treatments are shown in Table 4.10. The results of the analysis of variance for each of the elements in 2006 and 2007 showed that there were some significant treatment effects on the soil properties with the P treatment plots being generally higher, especially in 2006. The comparison of the soil properties between 2006 and 2007 showed that the following soil properties Mg^{2+}, K^+, Mn^{2+}, total P, available P, Al^{3+} and exchangeable acidity were significantly ($p<0.001$) higher in 2006 than 2007; concentrations of N and the pH (water) were higher in 2007, while Ca^{2+}, N, pH (KCl), percentage clay, silt and sand showed no differences in both years. The site is very rich in soil organic carbon with values that range from 8.9-9.9%, it is also an acidic soil with pHs' that ranging 4.2-4.8. The amount of available P recorded in this study showed that only a very small amount of P is available for plant use compared with the total amount of P that is present in the soil (Table 4.10), this may have been as a result of the soil having a high P fixation capacity.

Table 4.10: Soil properties sampled at 0-20 cm across the different fertilizer treatments in 2006 and 2007. Values are presented as means and standard errors, n = 4

Soil Properties	Treatment			
	Control	N	NP	P
	2006			
Ca^{2+} (mg kg^{-1})	15.9±4.1^{a}	16.4±0.3^{a}	14.9±6.5^{a}	18.2±1.7^{a}
Mg^{2+} (mg kg^{-1})	8.0±0.3^{a}	4.8±0.2^{b}	9.3±1.4^{a}	9.7±1.4^{a}
K^{+} (mg kg^{-1})	27.0±0.7^{a}	25.0±0.7^{a}	26.6±1.9^{a}	27.6±1.0^{a}
*ECEC (cmol$_c$ kg^{-1})	1.9±0.3^{ab}	1.7±0.2^{bc}	1.7±0.49^{bc}	2.2±0.39^{a}
Mn^{2+} (mg kg^{-1})	9.8±1.1^{a}	10.4±0.9^{a}	10.0±1.7^{a}	7.5±0.8^{a}
N (%)	0.4±0.0^{a}	0.4±0.0^{a}	0.4±0.0^{a}	0.4±0.0^{a}
Carbon (%)	9.5±0.5^{a}	9.3±0.8^{a}	8.9±0.3^{a}	9.9±0.4^{a}
Total P (mg kg^{-1})	221.1±5.9^{c}	251.8±31.5^{ab}	295.6±12.1^{a}	270.7±10.4^{ab}
Available P (mg kg^{-1})	6.8±0.7^{b}	5.9±0.9^{b}	14.4±0.5^{a}	8.5±1.3^{b}
Al^{3+} (mg kg^{-1})	4.3±0.3^{ab}	4.5±0.2^{ab}	4.7±0.3^{b}	5.6±0.7^{a}
Exchangeable acidity (cmol$_c$ kg^{-1})	1.7±0.2^{a}	1.4±0.2^{a}	1.4±0.2^{a}	1.9±0.3^{a}
pH (1 M KCl)	4.2±0.0^{b}	4.7±0.1^{a}	4.7±0.1^{a}	4.8±0.1^{a}
pH (distilled H_20)	4.7±0.1^{c}	4.1±0.0^{b}	4.2±0.1^{b}	4.5±0.0^{a}
$^{+}$Clay (%)	39.7±0.9^{ab}	42.3±0.9^{a}	40.1±1.2^{ab}	38.4±1.5^{b}
$^{+}$Silt (%)	34.1±2.3^{c}	39.8±0.9^{ab}	44.9±2.3^{a}	35.6±0.9^{bc}
$^{+}$Sand (%)	27.2±4.2^{a}	17.9±1.7^{bc}	15.0±1.1^{c}	26.0±2.3^{ab}
	2007			
Ca^{2+} (mg kg^{-1})	15.6±4.1^{a}	10.8±2.4^{a}	12.5±0.6^{a}	14.3±1.5^{a}
Mg^{2+} (mg kg^{-1})	6.6±0.7^{a}	6.8±1.0^{a}	2.2±0.6^{b}	4.8±0.5^{b}
K^{+} (mg kg^{-1})	24.1±0.5^{b}	20.8±1.3^{b}	17.7±0.7^{c}	25.2±0.6^{a}
*ECEC (cmol$_c$ kg^{-1})	2.6±0.13^{a}	1.7±0.12^{b}	1.7±0.21^{b}	1.0±0.1^{c}
Mn^{2+} (mg kg^{-1})	7.3±0.5^{b}	9.5±0.7^{a}	4.4±0.6^{c}	4.2±0.6^{c}
N (%)	0.5±0.0^{b}	0.5±0.0^{b}	0.5±0.0^{b}	0.6±0.0^{a}
Carbon (%)	9.4±0.4^{a}	8.9±0.6^{a}	8.4±0.6^{a}	9.6±0.9^{a}
Total P (mg kg^{-1})	172.7±4.3^{b}	175.9±6.0^{b}	157.9±0.0^{c}	214.8±4.3^{a}
Available P (mg kg^{-1})	4.1±0.3^{b}	4.7 ±0.2^{ab}	5.1±0.5^{a}	4.3±0.3^{ab}
Al^{3+} (mg kg^{-1})	4.6±0.1^{a}	4.7±0.1^{b}	2.6±0.2^{c}	2.6±0.1^{c}
Exchangeable acidity (cmol$_c$ kg^{-1})	2.3±0.1^{a}	1.5±0.1^{b}	0.7±0.1^{c}	0.8±0.1^{c}
pH (1 M KCl)	4.3±0.0^{b}	4.8±0.1^{a}	4.7±0.1^{a}	4.6±0.1^{a}
pH (distilled H_20)	4.1±0.0^{c}	4.3±0.1^{b}	4.5±0.1^{ab}	4.6±0.1^{a}
$^{+}$Clay (%)	37.3±1.5^{bc}	34.1±2.5^{c}	44.3±1.5^{a}	42.0±1.5^{ab}
$^{+}$Silt (%)	41.0±2.1^{ab}	45.3±1.8^{a}	37±0.6^{bc}	32.0±2.5^{c}
$^{+}$Sand (%)	21.7±0.9^{ab}	20.6±1.4^{ab}	18.3±1.8^{b}	26.0±1.7^{a}

Values with the same letter are not significantly ($p>0.05$) different for each element across the row for each year

*ECEC = Effective cation exchange capacity

$^{+}$ For the soil particle distribution values, n = 3 because of the limitation of soil mass.

4.2.3 Relationship between soil properties and tree growth parameters

Correlation analyses were carried out to evaluate the relationship between the tree growth parameters using their growth increment from February 2006 to May 20007 and soil properties using the mean of 2006 and 2007 measurements (although they were significantly different). The mean was taken because the soils were analyzed in both years (2006 and 2007), and the objective was to evaluate the relationship between the growth parameters using their growth increment between the years (2006 and 2007). There was an expectation that there would be a series of relationships, either negative or positive, between soil properties and tree growth parameters. Results showed that there were no strong relationships between soil properties and the tree growth parameters measured except a positive relationship ($r = 0.50$, $p=0.047$) between stand volume and Mn^{2+}, and a strong negative ($r = -0.71$, $p=0.002$) relationship between stand volume and pH in water (data not shown). It appears generally that there is little correlation between soil properties and other tree growth parameters measured. The lack of correlation between soil properties and tree growth was largely a result of no growth occurring over the study period.

4.2.4 Litter production

Annual litter fall production

The mean total litter production calculated by summing all the litter fractions across the four treatments over the sampling period, from May 2006 to May 2007 is 9.75 t ha^{-1} yr^{-1}. Needle litter fall accounted for 6.91 t ha^{-1} yr^{-1} (70.9 %), wood 2.01 t ha^{-1} yr^{-1} (20.6 %), and sporangia and cones contributed 0.83 t ha^{-1} yr^{-1} (8.5%) of the total litter fall. Results of the analysis of variance showed that needle litter fall under the P fertilizer treatment was significantly ($p=0.0018$) higher as well as wood litter fall ($p=0.0273$) than the NP and control treatments. The NP and N treatments had greater amounts of sporangia and cones as a proportion of the litter fall than in the control (Figure 4.40).

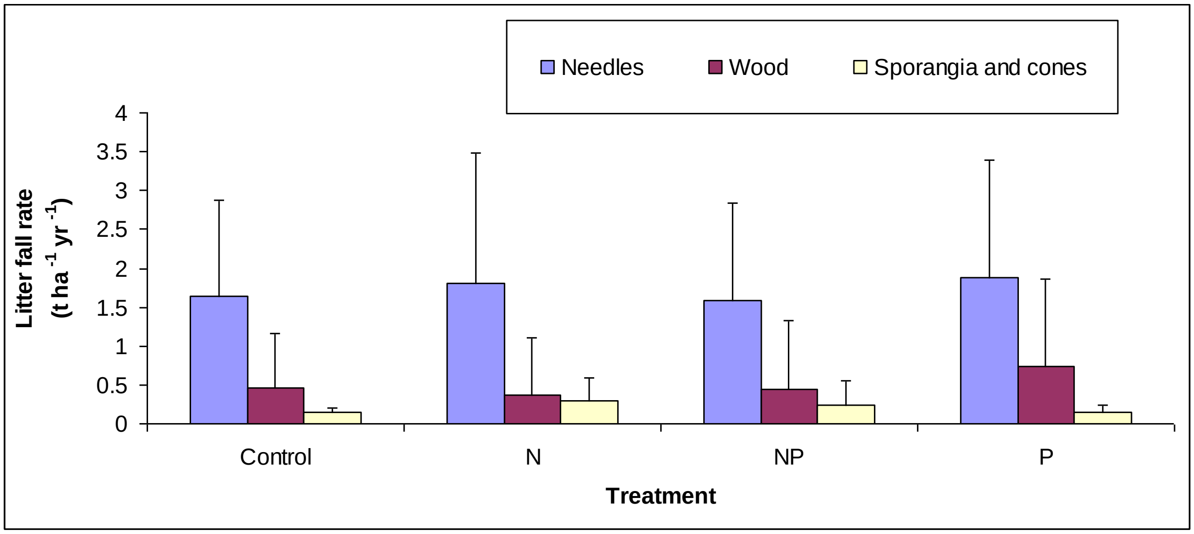

Figure 4.40 Litter fall in the different fertilizer treatments. Values are presented as means and the vertical bars indicate the confidence intervals at the 5% significant level, n = 48

Seasonal litter fall

There were bi-monthly ($p<0.0001$) differences in the needle, wood and and cones litter fall (Figure 4.41). The highest litter fall rate was recorded in July 2006, and the lowest occurred in November across the litter fractions. The strong wind that occurred in August 2006, after the July collection had little effect on September litter fall, this might be as a result of the fact that the site was regularly pruned and thinned (see Table 3.2 chapter 3). The amount of litter fall varied seasonally across the litter fractions, with a greater amount of litter falling in winter (May and July 2006) than in the summer period (September-March) (Figure 4.41).

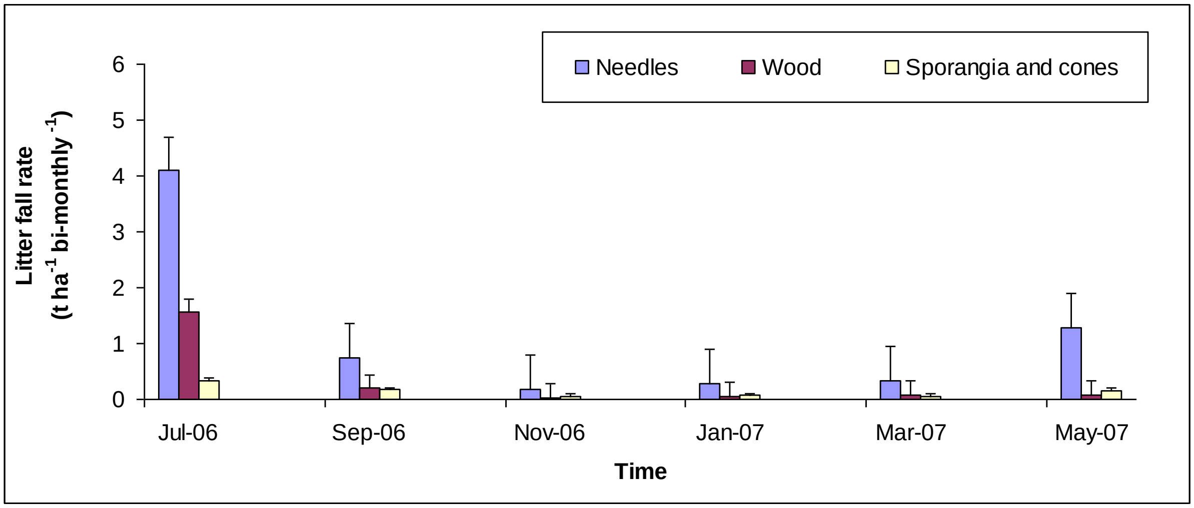

Figure 4.41 Bi-monthly litter fall (t ha^{-1} bi-monthly $^{-1}$) from July 2006 to May 2007 in *P. elliottii*. Values are presented as means and the vertical bars indicate the confidence intervals at the 5% significant level, n = 48

4.2.5 Forest floor litter accumulation and depth

Forest floor litter accumulation

The average amount of litter accumulated on the forest floor measured at the beginning of the study (July, 2006) across the treatments ranged from 14.1- 19.3 t ha^{-1} for needles, 4.4-8.6 t ha^{-1} for wood (small branches) and 0.48-1.82 t ha^{-1} for sporangia and cones. The needles were the greatest contributor to the total litter accumulated (Table 4.11). Results of the analysis of variance showed that there were significant treatment effects on the amount of needle litter ($p<0.001$) and wood litter ($p<0.05$) accumulated on the forest floor, while the amount of sporangia & cones litter accumulated was not significantly affected ($p=0.2703$). The amount of needle litter accumulated in the N and P treatments were higher than in the NP and the control treatments, while wood litter accumulation was higher in the P treatment when compared to other treatments.

Table 4.11: Forest floor litter accumulation (July 2006) under different fertilizer treatments

Treatment	Forest floor litter accumulation (t ha^{-1})			
	Needles	Wood	Sporangia and cones	Total accumulated
Control	14.12^{c}	4.40^{d}	0.48^{cd}	18.99^{c}
N	19.33^{a}	6.20^{b}	1.82^{a}	27.34^{a}
NP	14.19^{c}	5.59^{bc}	1.55a^{b}	21.33^{b}
P	18.39^{ab}	8.63^{a}	0.80^{bc}	27.82^{a}

Values with the same letter within each column are not significantly different at a probability $p<0.05$.

Litter depth

Results of the analysis of variance showed that the fertilizer treatments had significant ($p<0.0001$) effects on the forest litter depth. The lowest litter depth was measured in the NP treatment, while the litter depth in the control and P treatments were higher (Figure 4.42).

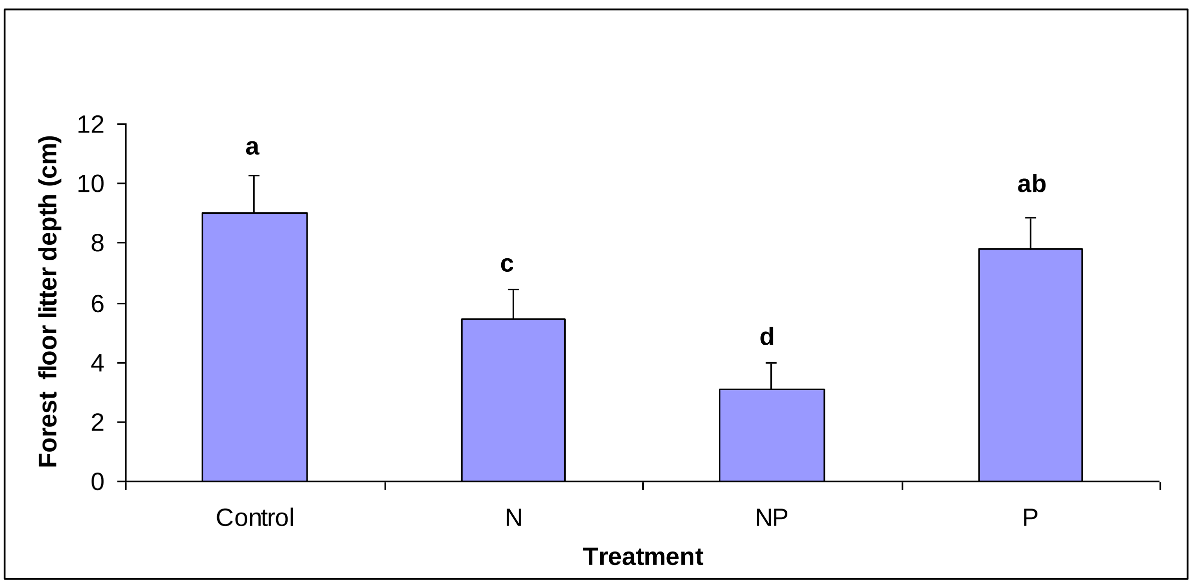

Figure 4.42 Forest floor litter depth measured in the different fertilizer treatments in *P. elliottii*. Values are presented as means and the vertical bars indicate the confidence intervals at the 5% significant level, n = 84; values with the same letter are not significantly different

4.2.6 Foliage, litter fall and forest floor litter nutrient concentrations

Results of the ANOVA showed that there were no significant ($p>0.05$) treatment effects on the foliar nutrient concentrations except for the P concentration ($p<0.005$), where NP (0.09%) and P (0.085%) treatments were higher than the control (0.073 %) (Data not shown). There were no correlations between foliar nutrient concentrations and tree growth except for weak positive correlations between foliar K^+ ($r = 0.49$, $p=0.04$) and tree height; foliar K^+ concentration and basal area increment ($r = 0.51$, $p=0.04$); foliar K^+ concentration and stand volume increment ($r = 0.46$, $p=0.07$) and carbon concentration and stand volume ($r = 0.48$, $p=0.07$).

The details of the nutrient concentrations and nutrient concentration ratios in the foliage, litter fall, forest floor; and litter fractions (needles and branch wood) across the treatments in *P. elliottii* are presented in Table 4.12. In Table 4.12 the data under the heading "litter fall" are the combined needle and wood data but do not include the sporangia and cones data due to the small number of samples in this fraction; the data under the headings "litter fractions" give the concentrations by litter fraction. There were generally no significant differences in the nutrient concentrations in each of the treatments (Table 4.12).

Results of the ANOVA showed the nutrient concentrations and nutrient concentration ratios differed significantly ($p<0.0001$) in the foliage, litter fall and forest floor litter. The concentrations of Mg^{2+}, K^+, P and N, and the nutrient concentration ratios of P:N and K:N were higher in the foliage for each of the treatments than in the litter fall. The concentrations of Ca^{2+}, C:N and Ca:N ratios were higher in the litter fall for each of the treatments than in the foliage and forest floor litter (Table 4.12), while there was no difference in concentration of carbon across the treatments in the foliage, litter fall and forest floor litter. Generally, nutrient concentrations are higher in the foliage (mean values in bold) (Table 4.12) than the litter fall and forest floor litter. The nutrient concentrations in the needle litter were significantly higher ($p<0.00001$) than the branch wood in both litter fall and forest floor litter, except for the concentration of C:N and K:N where the wood litter values were higher (Table 4.12).

Table 4.12: Nutrient concentrations in foliar, litter fall, forest floor litter across the treatments and in litter components in *Pinus elliottii*. Values are presented as the means ± standard deviations (n = 4). * P:N, K:N and Ca:N were calculated by multiplying by 100

Treatment and litter components	N nutrient concentrations (%)						Nutrient concentration ratios			
	Ca^{2+}	Mg^{2+}	K^{+}	P	N	C	C:N	*P:N	*K:N	*Ca:N
Foliage										
Control	0.40±0.17	0.10±0.02	0.32±0.05	0.07±0.00	1.09±0.04	50.13±0.39	45.99±1.47	6.42±0.19	29.36±4.52	36.70±16.11
N	0.32±0.13	0.10±0.02	0.35±0.03	0.08±0.01	1.14±0.12	49.75±0.66	43.64±4.16	7.02±0.45	30.70±4.05	28.07±14.16
NP	0.35±0.07	0.10±0.01	0.35±0.05	0.09±0.00	1.21±0.06	50.15±0.30	41.45±2.31	7.44±0.40	28.93±4.55	28.93±4.83
P	0.30±0.06	0.09±0.01	0.32±0.04	0.09±0.01	1.12±0.09	50.08±0.51	44.71±4.43	8.04±0.59	28.57±4.51	26.79±6.48
Mean	**0.34±0.11**	**0.10±0.02**	**0.33±0.04**	**0.08±0.01**	**1.14±0.09**	**50.03±0.46**	**43.89±4.23**	**7.02±0.58**	**28.95±4.14**	**29.82±10.79**
Litter fall										
Control	0.45±0.15	0.07±0.04	0.05±0.03	0.03±0.01	0.45±0.15	49.16±0.91	109.24±41.92	6.67±1.91	11.11±4.47	100.00±40.38
N	0.45±0.15	0.07±0.03	0.05±0.03	0.02±0.01	0.45±0.14	49.22±0.62	109.38±44.10	4.44±1.73	11.11±5.87	100.00±41.37
NP	0.47±0.16	0.07±0.03	0.06±0.04	0.03±0.01	0.48±0.18	49.06±0.78	104.38±47.29	6.38±2.37	12.77±5.30	100.00±39.69
P	0.46±0.17	0.08±0.06	0.06±0.04	0.03±0.01	0.45±0.20	49.19±0.58	109.31±115.87	6.67±11.34	13.33±11.59	102.22±57.74
Mean	**0.45±0.16**	**0.07±0.04**	**0.05±0.03**	**0.03±0.01**	**0.46±0.17**	**49.16±0.73**	**106.87±69.78**	**6.52±5.96**	**10.87±7.35**	**97.83±45.34**
Forest floor litter										
Control	0.21±0.12	0.05±0.02	0.03±0.01	0.02±0.01	0.48±0.14	50.08±0.92	104.33±29.04	4.71±0.97	6.25±1.53	43.75±24.77
N	0.20±0.10	0.05±0.02	0.03±0.01	0.03±0.01	0.54±0.15	49.75±1.06	92.13±24.34	5.56±0.62	5.56±1.07	37.04±10.64
NP	0.28±0.15	0.06±0.03	0.03±0.02	0.04±0.01	0.55±0.14	49.88±1.35	90.69±34.75	7.27±1.30	5.45±2.10	50.91±19.51
P	0.25±0.10	0.04±0.02	0.04±0.01	0.05±0.01	0.62±0.08	49.53±0.77	79.89±11.26	8.06±0.70	6.45±1.69	40.32±14.71
Mean	**0.23±0.12**	**0.05±0.02**	**0.03±0.01**	**0.03±0.01**	**0.55±0.14**	**49.81±1.02**	**90.56±27.33**	**5.45±1.57**	**5.45±1.56**	**41.82±17.63**
Litter fall										
Needles	0.53±0.01	0.10±0.00	0.06±0.00	0.03±0.00	0.53±0.02	49.30±0.06	93.02±2.66	5.66±0.50	11.32±0.50	100±0.50
Branch wood	0.38±0.02	0.05±0.00	0.05±0.01	0.02±0.00	0.38±0.02	49.01±0.09	128.97±9.05	5.26±0.49	13.16±0.53	100.00±1.00
Mean	**0.45±0.01**	**0.07±0.01**	**0.05±0.01**	**0.03±0.01**	**0.46±0.01**	**49.16±0.05**	**106.87±4.97**	**6.52±0.10**	**10.87±1.0**	**97.83±1.10**
Forest floor litter										
Needles	0.34±0.02	0.07±0.00	0.04±0.00	0.04±0.00	0.62±0.03	49.82±0.11	80.35±17.64	6.45±1.82	6.45±0.85	54.84±14.53
Branch wood	0.13±0.03	0.03±0.01	0.02±0.03	0.03±0.00	0.47±0.03	49.82±0.32	106.00±28.49	6.38±1.34	4.26±0.63	27.66±6.53
Mean	**0.23±0.03**	**0.05±0.01**	**0.03±0.02**	**0.03±0.01**	**0.55±0.03**	**49.81±0.32**	**90.56±27.32**	**5.45±01.58**	**5.45±1.56**	**41.82±17.63**

4.2.7 Decomposition rates

The mean needle litter decomposition rates calculated for *P. elliottii* at the end of the study across each treatment and over the months are presented in Table 4.13. Fertilization had significant effects on the decomposition rates ($p<0.0001$); where the NP and P treatments were higher than the control and the N treatments.

Table 4.13: Needle litter decomposition rates under different fertilizer treatments over the study period (months) July 2006-May 2007 in *Pinus elliottii*. Values are presented as means and confidence intervals at the 5% significance level, n = 3

Month	Decomposition rate (g day^{-1})				
	Treatment				
	Control	N	NP	P	**Mean**
May-July 2006	0.084±0.01	0.083±0.02	0.122±0.05	0.127±0.06	0.104±0.02^{a}
July-Sep 2006	0.045±0.00	0.045±0.01	0.072±0.01	0.065±0.01	0.057±0.01^{b}
Sep-Nov 2006	0.042±0.00	0.039±0.00	0.047±0.00	0.051±0.02	0.045±0.00^{c}
Nov-Jan 2007	0.030±0.00	0.031±0.00	0.043±0.00	0.045±0.00	0.038±0.00^{c}
Jan-Mar 2007	0.026±0.00	0.024±0.00	0.032±0.00	0.038±0.00	0.030±0.00^{d}
Mar-May 2007	0.025±0.00	0.027±0.00	0.032±0.00	0.030±0.00	0.029±0.00^{d}
Mean	0.042±0.02^{b}	0.042±0.02^{b}	0.058±0.03^{a}	0.059±0.03^{a}	0.050±0.01^{a}

Values with the same letter within the column (mean) indicate no significant difference for treatment, while values with same letter within the row (mean) indicate no significant difference for month at a probability $p<0.05$.

There were significant ($p<0.0001$) differences in the decomposition rate for the various months. The mean annual decomposition rate recorded in this study is 0.05 g day $^{-1}$. Post hoc tests showed that the highest decomposition rate of 0.10 g day^{-1} occurred in July 2006, followed by September 2006 (0.10 g day^{-1}), and the lowest rate of 0.03 g day^{-1} occurred in March and May 2007 (Table 4.13). There was a rapid decrease in the decomposition rate from May to July 2006 compared to the other months.

The percentage mass remaining in decomposing needle litter at the end of the incubation period also differed significantly ($p<0.0001$) across the treatments. The NP and P treatments were found to be lower than other treatments, though the control was greater than the fertilized plots (Figure 4.43). The percentage mass remaining also differed significantly across the months and post hoc tests showed that July, and September were higher than at the other months, with the lowest remaining mass occurring in May, 2007 (Figure 4.43).

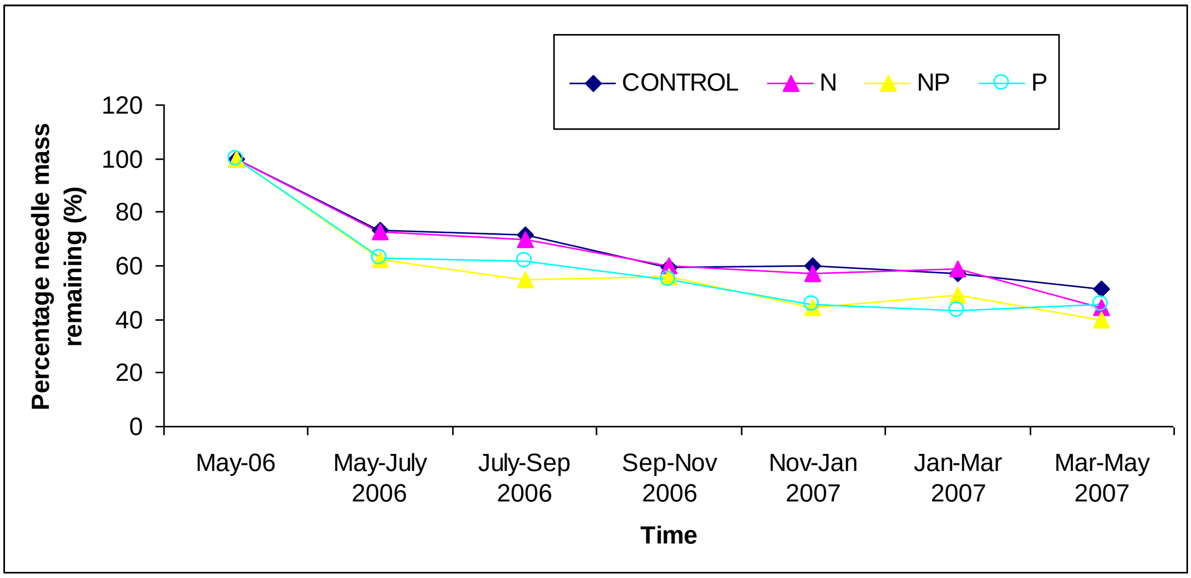

Figure 4.43 Percentage mass remaining in decomposing needle litter in different treatments and over the study period, July 2006 to May 2007

4.2.8 Nutrient concentrations in *Pinus elliottii* decomposing needle litter

The concentrations of nutrients and nutrient concentration ratios in *P. elliottii* needle litter at the beginning of the decomposition study are presented in Table 4.14. There was no effect of treatment on the nutrient concentrations, Ca and Mg were the only two elements where the treatments seemed to decrease the values relative to the control (Table 4.14). However, when all of the fertilizer treatment data are pooled and analyzed, the comparison between nutrient concentrations in the fertilized and control plots showed that only the Ca^{2+}concentration was significantly ($p=0.0210$) lower in two of the treatments.

Table 4.14: Nutrient concentrations and nutrient ratios in the initial needle litter at the beginning of the study in *Pinus elliottii* across the treatments. Values are presented as means and the confidence intervals at the 5% significant level, n = 3

Nutrient concentrations And ratios	**Treatment**			
	Control	N	NP	P
Ca^{2+} (%)	0.30±0.16[a]	0.15±0.04[b]	0.13±0.05[b]	0.28±0.05[a]
Mg^{2+} (%)	0.12±0.03[a]	0.12±0.03[a]	0.07±0.03 [b]	0.10±0.01[a]
K^{+} (%)	0.28±0.02[a]	0.34±0.01[ab]	0.31±0.02[ab]	0.25±0.13[a]
Mn^{2+} (%)	0.15±0.08[a]	0.11±0.03[ab]	0.08±0.03[c]	0.16±0.03[a]
P (%)	0.10±0.02[a]	0.09±0.02[a]	0.08±0.00[a]	0.10±0.04[a]
N (%)	1.06±0.00[a]	1.17±0.06[a]	1.10±0.11[a]	1.14±0.26[a]
C %	49.43±1.11[a]	48.63±0.38[ab]	49.53±0.70[a]	49.27±0.92[ab]
Nutrient concentrations ratios				
C/N	46.64±1.04	41.70±1.82	45.13±5.02	44.50±9.20
P:N	9.43±1.73	8.02±2.16	7.29±0.73	8.39±1.39
K:N	26.42±1.73	29.44±1.79	28.26±4.03	21.88±6.37
Ca:N	28.30±15.40	14.15±4.80	11.46±4.75	24.89±9.03

Values with the same letter across the treatment (row) are not significantly different ($p>0.001$).

The concentration of Ca^{2+} in the decomposing needle litter was lower at the beginning of the decomposition and this increased progressively from the beginning until the end of the study (Figure 4.44a). The concentration of K^{+} sharply decreased from July 2006 to November and then declined very slightly until the end of the study. The concentrations of Mg^{2+} and Mn^{2+} remained constant from the beginning till September and then became slightly variable towards the end of the study (Figure 4.44a). The concentration of C and P remained fairly constant from the beginning to the end of the study (Figure 4.44b). The concentration of N however, generally increased very slightly from the beginning to the end of the study. The ratios of C:N progressively decreased from 44.2 at the start of the incubation to 29.4 at the end of the study, and P:N decreased slightly from 8.3 at the start of the incubation to 7.3 at the end of the study (Figure 4.44b).

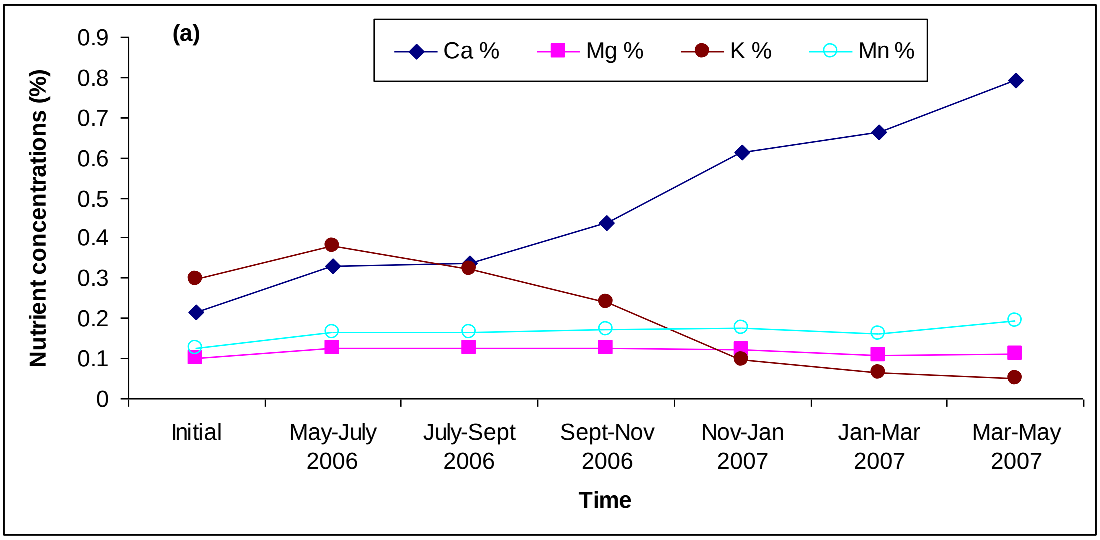

Figure 4.44a Changes in nutrient concentration in the decomposing needle litter over the study period, July 2006 to May 2007

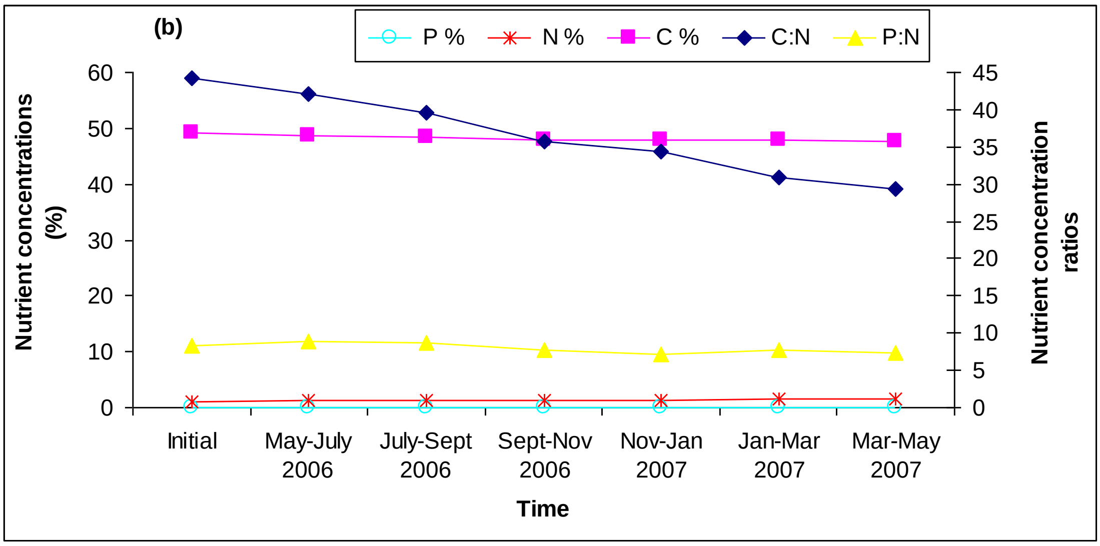

Figure 4.44b Changes in nutrient concentration and nutrient concentration ratios in the decomposing needle litter over the study period, July 2006 to May 2007

4.2.9 Soil ammonification, nitrification and N mineralization rates in *Pinus elliottii* site

Results of the ANOVA showed that there were no significant ($p<0.05$) treatment effects on the rates of ammonification ($p=0.04827$) and N mineralization ($p=0.6247$). However, there was significant ($p=0.0211$) treatment effects on nitrification rates, with the N fertilizer treatment being higher than the NP and control treatments (Figure 4.45).

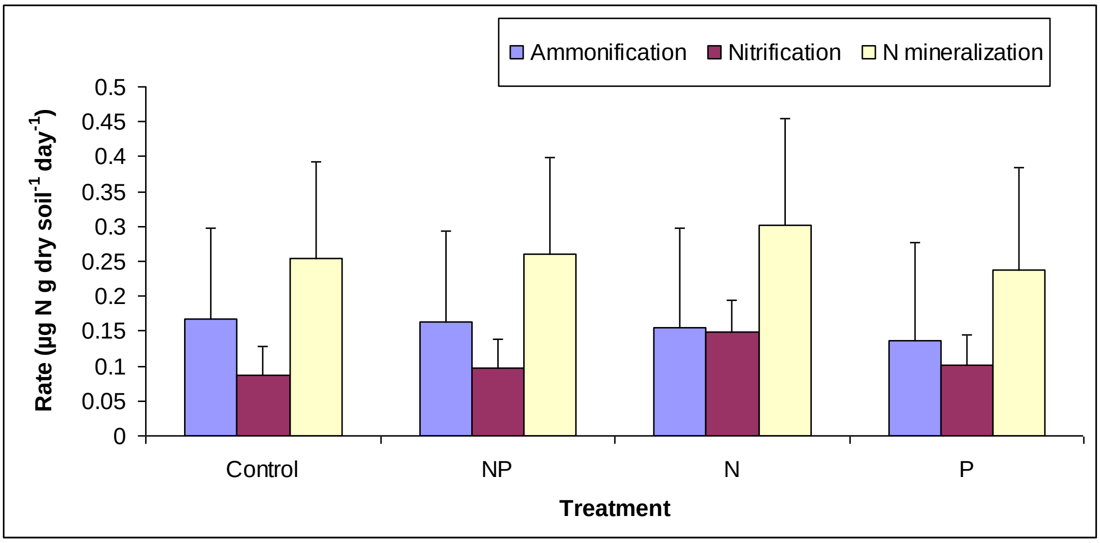

Figure 4.45 Ammonification, nitrification and N mineralization rates in the fertilizer treatment over the study period. Values are presented as means and vertical bars indicate confidence intervals at the 5% significant level, n = 160

The annual net rate (summing all positive values for all months across all treatments) of ammonification is 1.65±0.42 µg N g dry soil $^{-1}$yr $^{-1}$, nitrification is 1.22 ±0.09 µg N g dry soil^{-1} yr^{-1} and N mineralization is 2.69±0.05 µg N g dry soil^{-1} yr^{-1}. Ammonification, nitrification and N mineralization rates differed significantly ($p<0.0001$) for the different months (Figure 4.46). The ammonification rate recorded was highest in July 2006 while the nitrification and N mineralization rates were higher in September 2006 than in the other months. The lowest ammonification rates (immobilization) occurred in January 2007, while the lowest (immobilization) nitrification and N mineralization rates occurred in November, and in January (immobilization) 2007 respectively.

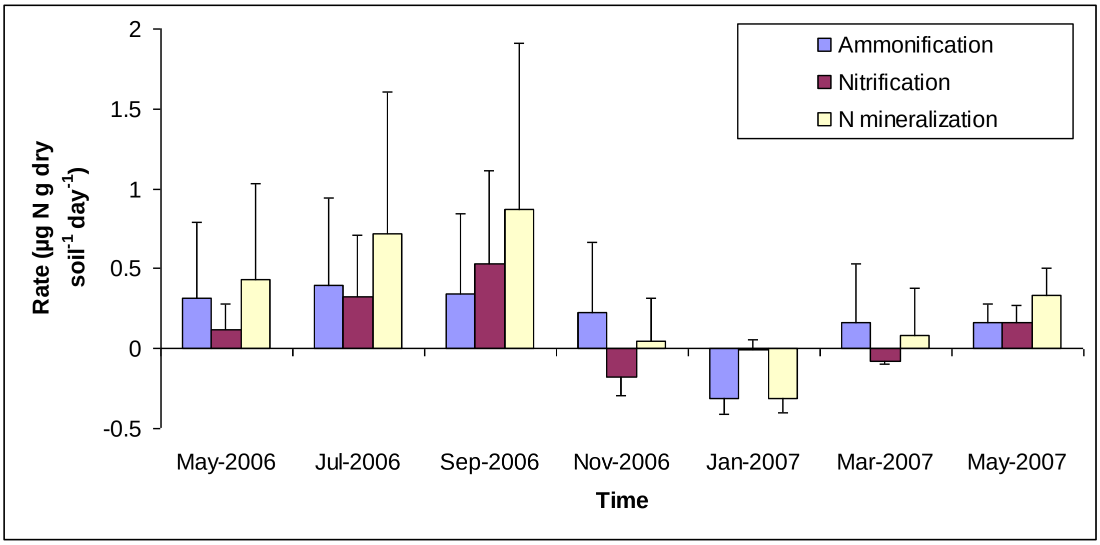

Figure 4.46 Ammonification, nitrification and N mineralization rates for different months, May 2006 to May 2007. Values are presented as means and vertical bars indicate confidence intervals at the 5% significant level, n = 160

There were seasonal variations in the rates of N mineralization, ammonification and nitrification. Higher (positive) rates were found in the winter months (May to July) and in September, the beginning of the summer period. The lower rates or negative values, showing different degrees of immobilization of N, occurred in the summer period from November 2006 to March 2007 across the three N transformation processes (Figure 4.46). This indicates that more N is available during the winter period than is being utilized possibly because of slow plant physiological activities and growth.

Correlation tests were used to evaluate the relationships between ammonification, nitrification and N mineralization rates and tree growth increments. Results showed a strong negative correlation between ammonification and tree height ($r = -0.66$, $p=0.006$), ammonification and basal area ($r = -0.51$, $p=0.042$) and ammonification and stand volume ($r = -0.56$, $p=0.024$) increment. Nitrogen mineralization rates showed a strong negative correlation with tree height ($r = -0.64$, $p=0.008$), basal area ($r = -0.55$, $p=0.028$) and stand volume ($r = -0.57$, $p=0.022$) increments. However, there was no relationship between nitrification rate and tree growth increment.

4.3 3-PG Model

The 3-PG growth model was used to evaluate and predict basal area, diameter at breast height (DBH) and stand volume in both *P. patula* and *P. elliottii* species, taking into consideration the climatic factors, rainfall and temperature, and nutrient availability across the study sites. This was to build on earlier studies on the use of 3-PG to predict tree growth since the model has been shown to be a useful tool for predicting forest productivity, with the aim of increasing the predictive knowledge of this system.

4.3.1 *Pinus patula*

The detailed results of the observed and predicted tree growth parameters measured at the Elandshoogte and Mooifontein sites are shown in Figure 4.47. At the Elandshoogte site, the observed tree growth parameters were compared to the predicted outputs. Results showed strong significant correlations between the predicted and observed quadratic mean DBH ($r = 0.99$, $p<0.0001$) and stand volume ($r = 0.82$, $p=0.024$), while there was no agreement between observed and predicted stand basal area ($m^2\ ha^{-1}$) ($r = 0.01$, $p>0.05$ (Figure 4.47a-c). Statistics of these comparisons showed that the proportions of the variance in the observed values accounted for by the predicted values (r) are all greater than 81%. Quadratic mean DBH was consistently over predicted whereas stand volume and basal area were well predicted between 11 and 15 years and then over predicted.

At the Mooifontein site, results showed strong significant correlations between the observed and predicted quadratic mean DBH ($r = 0.99$, $p<0.0001$), stand volume ($r = 0.95$, $p<0.001$) and stand basal area ($m^2\ ha^{-1}$) ($r = 0.88$, $p<0.01$) (Figure 4.47d-e). Statistics of these comparisons showed that the proportion of the variance in the observed values accounted for by the predicted values (r) are all greater than 88%, stand volume and basal area were generally slightly under predicted.

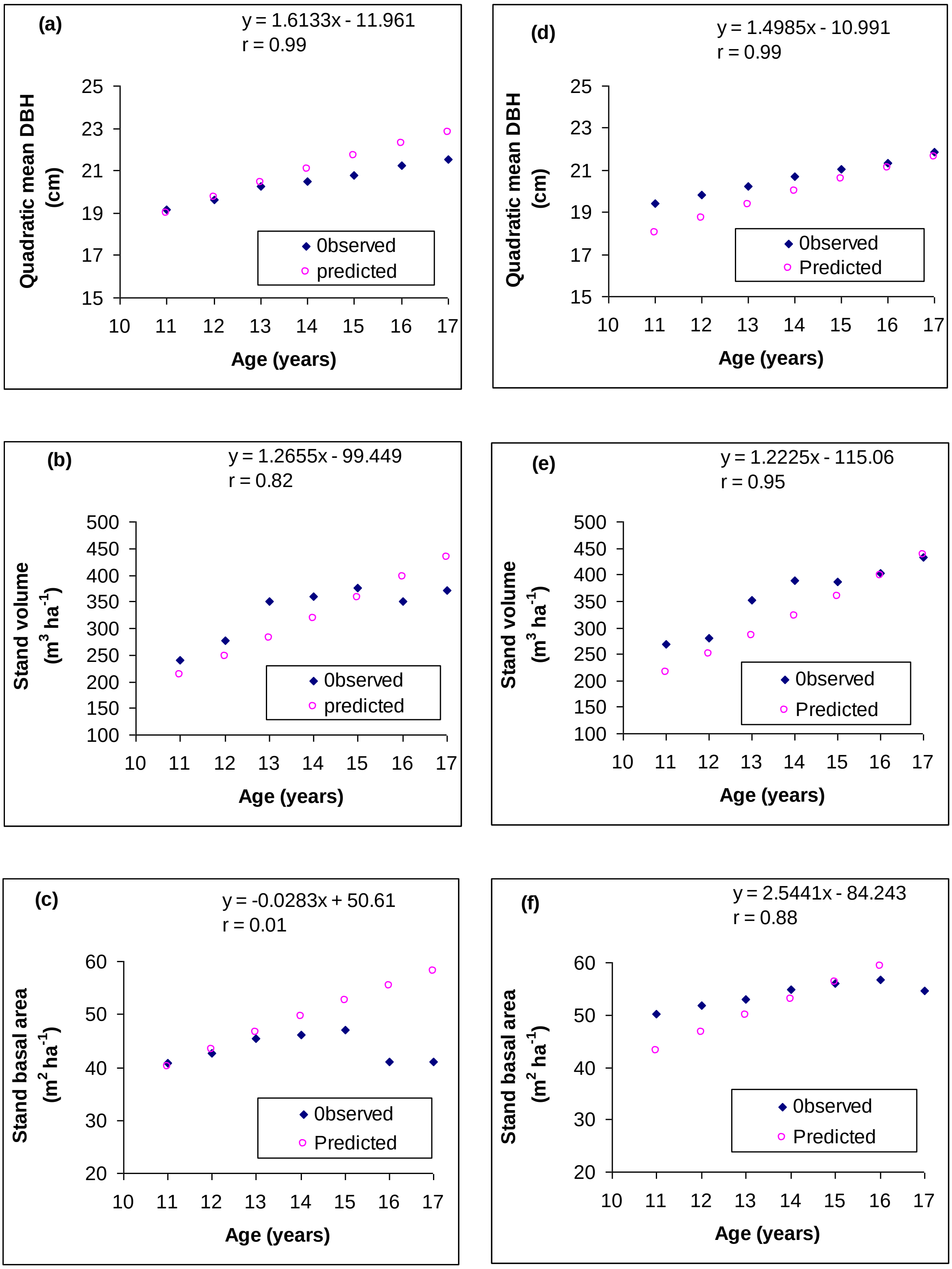

Figure 4.47 Comparison between the observed and predicted tree growth parameters measured at the Elandshoogte site (a-c) and the Mooifontein site (d-f) from 2001 at age 11 years to 2007 at age 17

At the Grootgeluk site, there were also strong significant correlations between the observed and predicted quadratic mean DBH (cm) ($r = 0.99$, $p<0.0001$), stand volume (m^3 ha^{-1}) ($r = 0.96$, $p<0.002$), and stand basal area (m^2 ha^{-1}) ($r = 0.80$, $p<0.03$) (Figure 4.48a-c). The statistical comparison between the observed and predicted parameters showed that the proportion of the variance in the observed values accounted for by the predicted values (r) are all greater than 80%, the parameters are generally slightly over predicted.

At the Mamre site, the calculated tree growth parameters were compared with the observed data (Figure 4.48d-e). Results showed strong significant correlations between the observed and predicted quadratic mean DBH ($r = 0.97$, $p<0.0001$), stand volume ($r = 0.98$, $p<0.001$), and basal area (m^2 ha^{-1}) ($r = 0.98$, $p<0.0001$). Statistics of these comparisons showed that the proportions of the variance in the observed values accounted for by the predicted values (r) are all greater than 88%. The difference between the observed and predicted values seems to be large in stand volume and basal area even though there were high correlation values.

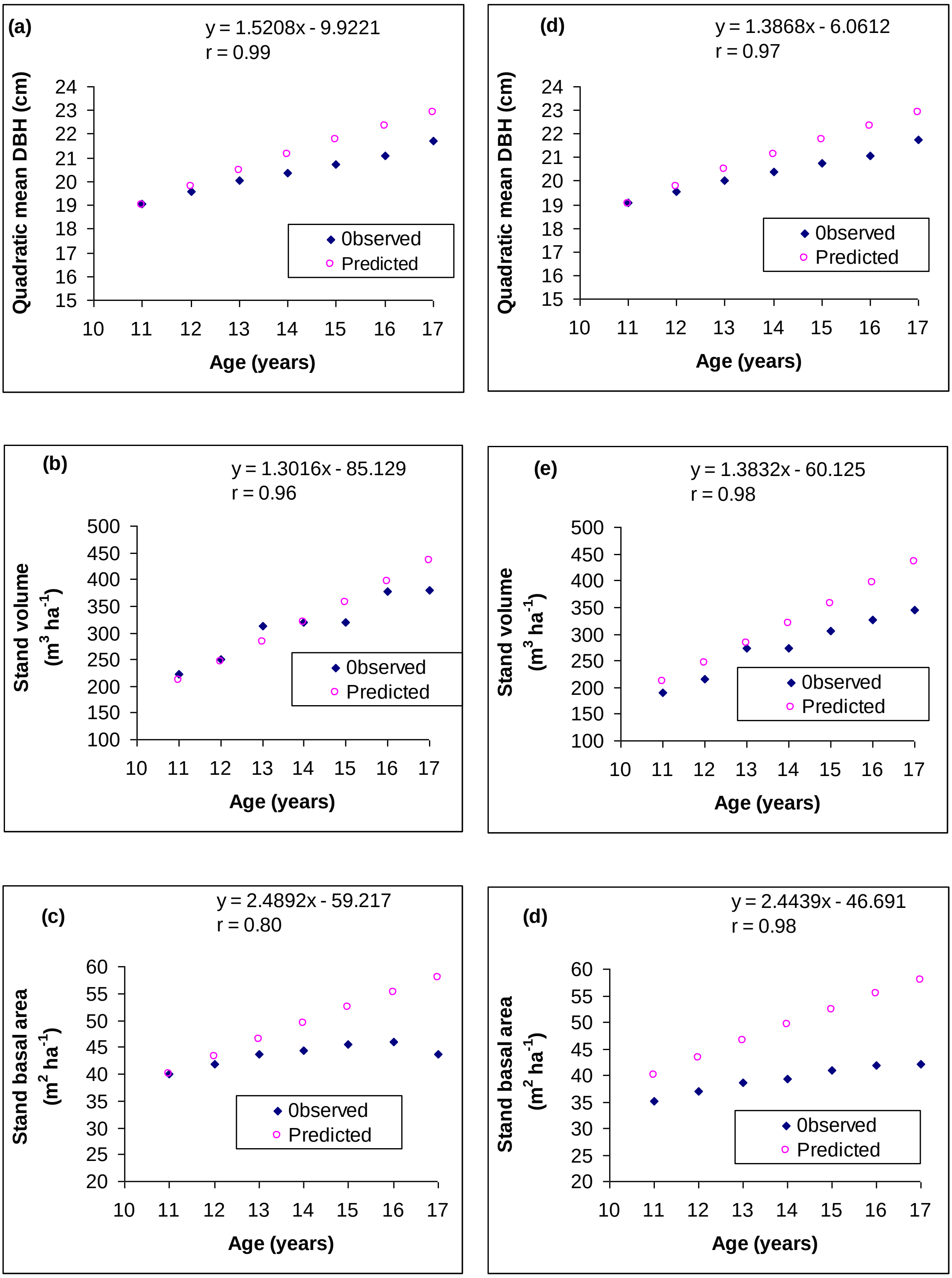

Figure 4.48 Comparison between the observed and predicted tree growth parameters measured at the Grootgeluk site (a-c) and the Mamre site (d-f) from 2001 at age 11 years to 2007 at age 17

Generally, there was a good agreement (high correlations) between the predicted quadratic mean DBH across the sites over the years with the r being over 99% in all the sites. Also stand volume showed correlation (r) that ranged from 95-98% in all the sites except at the Elandshoogte site where the stand volume was 82%. Stand basal area was less accurately predicted as shown in Figure 4.47 and 4.48. It is also very important to note that there were higher correlations between the observed and predicted values for the tree growth parameters when 2006 and 2007 data were excluded from the sites because of the effect of drought and wind damage that impacted tree growth in those years, especially at the Elandshoogte site. The recalculated correlation values, at Elandshoogte changed to r = 0.98 for quadratic mean DBH, r = 0.95 for stand volume and r = 0.97 for basal area. The other sites also showed better correlations, at the Mooifontein site the quadratic mean DBH became (r =0.99), stand volume (r = 0.94) and basal area (r = 0.99); at the Grootgeluk site, the quadratic mean DBH changed to (r = 0.99), stand volume (r = 0.91) and basal area (r = 0.99); whereas at the Mamre site, the quadratic mean DBH changed to (r = 0.96), stand volume (r = 0.99) and basal area (r = 0.99).

4.3.2 *Pinus elliottii*

At the *P. elliottii* site, correlation tests cannot be performed to evaluate the accuracy or the performance of the model between observed and predicted values (r) because tree growth parameters were only measured in 2006 and 2007. Therefore, model predictions of the tree growth parameters were assessed based on percentage bias calculated as the percentage of (Observed-Predicted)/Predicted) as described by Campion *et al*., (2005); and Esprey and Smith (2002). The 2017 (end of rotation) predicted tree growth parameters were compared with the empirical tree growth projection using a growth yield table (Kassier and Kotze, 2000). Negative values indicate that the model over predicted the tree growth parameters. The details are shown in Table 4.15

Table 4.15: Percentage bias of model predictions for tree growth measurements in 2006 and 2007; and comparison between the predicted in 2017 and the empirical tree yield projections

Tree growth Parameters	Year	Observed (O)	Predicted (P)	O-P	O-P x 100 / P
Quadratic mean DBH (cm)	2006	32.12	30.14	1.98	6.57
	2007	34.49	31.67	2.82	8.90
	2017	47.00	45.00	2.00	4.44
Stand basal area (m^2 ha^{-1})	2006	20.76	20.33	0.43	2.12
	2007	19.68	18.12	1.56	8.61
	2017	38.60	36.58	2.02	5.52
Stand tree volume (m^3 ha^{-1})	2006	182.14	168.76	13.38	7.93
	2007	154.44	157.36	-2.92	-1.86
	2017	530.00	429.94	100.06	23.27

There were generally good agreement between the observed and predicted tree growth parameters, quadratic mean DBH, stand basal area and stand volume across the years, 2006, 2007 and 2017 (Table 4.15). The mean biases expressed as a percentage of the predicted quadratic mean DBH were slightly under predicted in 2006 (6.58%) and in 2007 (5.75%); stand basal area was slightly under predicted in 2006 (2.12%) and in 2007 (8.62%); stand volume was under predicted (7.93%) in 2006 and slightly over predicted (-1.85%) in 2007 (Table 4.15). The predicted tree growth parameters in 2017 compared with an empirical tree yield projection of a saw timber stand at age 28 years, from a growth yield table in South Africa (Kassier and Kotze, 2000), showed that the mean biases expressed as a percentage of the predicted quadratic mean DBH and basal area were slightly over predicted by 4.44% and 5.52% respectively (in 2017), while stand volume was seriously under predicted by 23.27% (Table 4.15).

CHAPTER 5

DISCUSSION

This chapter is divided into five sections, which include investigating: the impacts of management practices (fertilizer treatments) on tree growth responses, biologically based processes and soil properties; the impacts of site on soil properties and the effects of climate; an integrated discussion on nutrient cycling and the positioning of the discussion into the growth modeling.

One of the purposes for plantation management is the sustainable and increased production of wood. Plantation productivity depends on many factors that include environmental factors such as the availability of essential resources particularly nutrients and water. The supply of nutrients varies from one site to another and may be influenced by management practices and climate. The knowledge of the transfer of the nutrients in and out, as well as within, the ecosystem, is crucial in understanding system function which directly impacts productivity.

The conceptual framework for this study, which includes two pine species, is based on the understanding of how the nutrients are being cycled between the different pools (soil, litter and tree) and the role played by the different fluxes (litter fall, litter decomposition and N mineralization). The rate and magnitude of nutrient transfer from different pools through different fluxes depends on many factors which include soil nutrient levels, the management practice, the type and age of the plantation. This study focused on the changes in pool sizes and fluxes as affected by management practice (fertilization) and climate, and how these influenced the tree growth response. The concept is shown graphically in Figure 5.1.

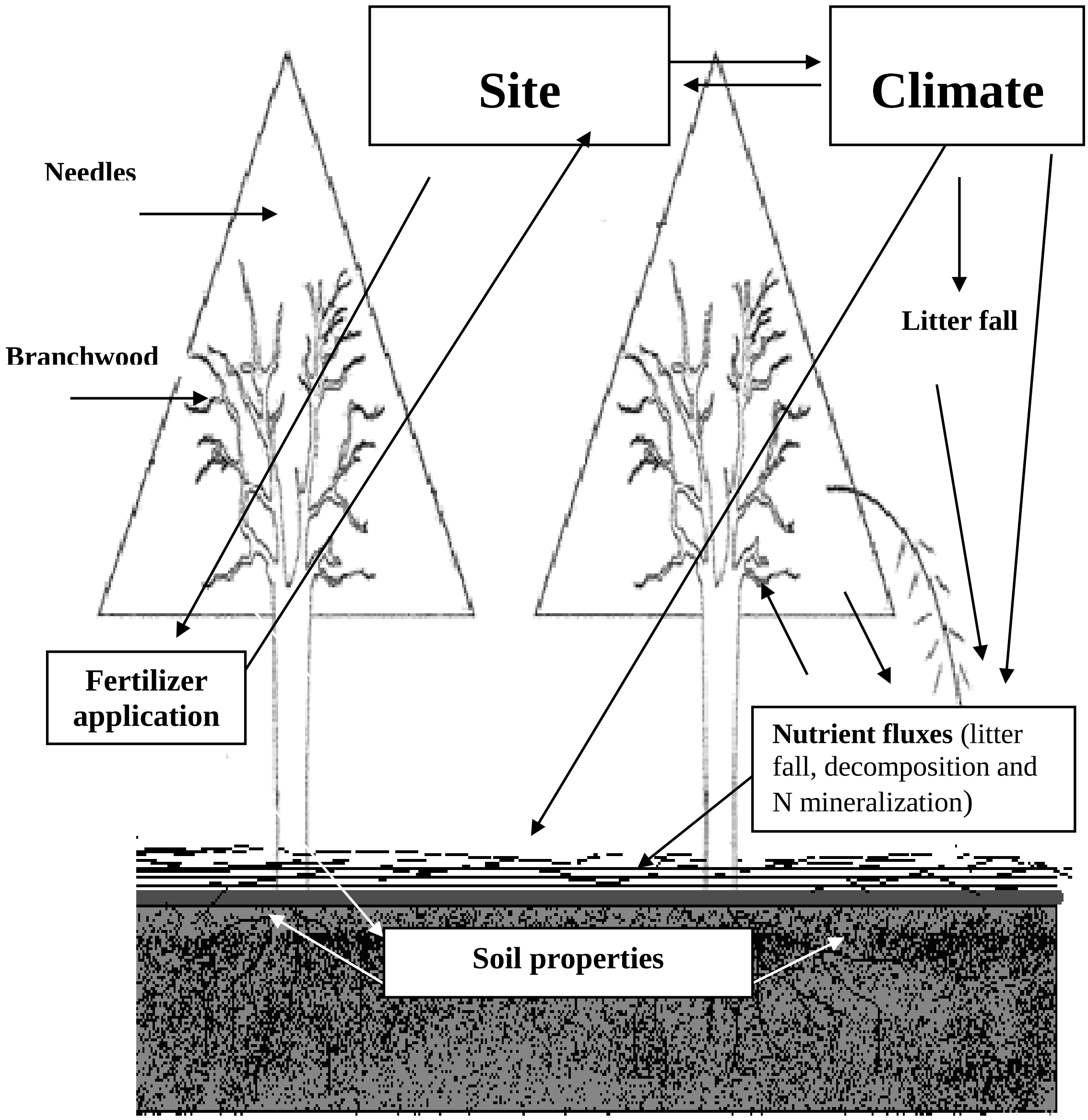

Figure 5.1 Different system drivers (climate and fertilization) on site and tree growth response.

Studies at Usutu, in Swaziland, have shown that due to forest floor accumulation, large amounts of nutrients, especially N were immobilized in the forest floor litter. It was also shown that the response to N fertilizer applied to *P. patula* between the ages of 10 and 12 years were closely related to forest floor mass. The application of 100 kg N ha^{-1} at age 12 years followed by a second application at age 14 years stands at high altitude, associated with large accumulations of forest floor, was recommended at Usutu as it was shown to have economic benefit (Crous, 2007). In order to test if the same response would be obtained in Mpumalanga, four trials were established on representative sites in 11-year-old *P. patula* compartments during January 2001. The results from these trials indicated that, in general, the initial N application at age 11 years increased basal area increment by only 0.7 m^2 ha^{-1} over a two year period. However, the four trials did not show a uniform pattern of response. After the second application at age 13 years no significant growth response as a result of N could be observed, although there was weak evidence that foliar N concentration was increased as a result of the N fertilizer (Crous, 2007).

Tree growth measurements, litter depth and foliar analyses were the only measurements taken at these four trials from 2001 till 2006 by Jacob Crous, a research scientist employed by Sappi. The lack of pattern of treatment effects and the inability to interpret the data led to the establishment of this PhD. The conceptual framework (Figure 5.1) which included the measurements of both pool sizes and fluxes was conceived to facilitate the interpretation of the data. It was hypothesized that by intensively measuring a wider range of biological processes that these would further elucidate tree growth response. This PhD study was hampered by the lack of soil data from the beginning of the trial as well as on-site climate data. It was also most unfortunate that the trials were severely impacted by drought and wind in 2006 and 2007.

The *P. elliottii* trial site was established in 2006 to address some of the short-comings of the *P. patula* trials. The *P. elliottii* trial had four fertilizer treatments and four replicates, as well as soil and climate data, in order to provide more evidence on the impacts of late rotation fertilization on tree growth. A fire devastated this site in 2007 bringing data collection to an end. In retrospect, both of these trial sites were inappropriately chosen in order to investigate fertilizer responses as both sites had a high site quality index which could infer a high inherent fertility status. The choosing of sites for research forestry trials is often not ideal and a compromise has to be reached between what is practical and what the research aims of the experiments are. Manipulating established trials, as in the case of the *P. patula* trials, relies on the gamble that the treatment effects will outweigh the site variability.

5.1 Treatment Effects

5.1.1 Tree growth

The general lack of treatment effects on tree growth (except for a temporary effect on the basal area of *P. patula*) at the *P. patula* and *P. elliottii* sites might indicate that the sites are not deficient in either N or P. Freimond and Allan (1995) and Ingerslev *et al*., (2001) have reported that the growth response after N fertilization is clearly lower in stands growing on soils with high nutrient status than on soils with low nutrient status. The studies of Albaugh *et al*., (2004); Ballard (1981) and Hynynen *et al*., (1998) confirmed that there will be tree growth responses following fertilization if the sites are nutrient limited. Unlike many other studies on plantation ecosystems (Binkley *et al*., 2000; O'Connell and Rance, 1999; Van Miegroet *et al*., 1990), where N and P were found to be the limiting nutrients, this study showed that there are generally enough nutrients to sustain growth.

The initial response to the treatments between 2001 and 2003 that resulted in an increase of 0.7 m^2 ha^{-1} at the *P. patula* sites was observed using basal area as the variable. This observation suggests that basal area is a better measurements to assess tree growth response following fertilization than tree height because of the error associated with tree height measurements. In this study, the forestry contractors, in 2004, were not sufficiently well briefed as to the importance of obtaining accurate data for tree heights. It was impossible to estimate to what extent the collected data were biased therefore interpolated data were used for all the other calculation requiring tree height in 2004. However, the treatment effects disappeared after the second fertilization application in 2003. There was evidence that the fertilizer had no effect on basal area increment for the first three years (2003-2005) after the second application, the statistical treatment differences that occurred in 2006 and 2007 were as a result of severe drought mortality and wind damage that was recorded in the control plots. Decreases in stem density could also have been counteracted by increases in DBH.

The increase in basal area response of 0.7 m^2 ha^{-1} was similar to the 0.4 to 0.5 m^2 ha^{-1} increase in basal area over 12 months after application of 100 kg N ha^{-1} to eight-year-old *P. patula* plantations, reported by Noble and Ramsden (1992), for two sites at Helvetia, in South Africa. The initial treatment effects on basal area agreed with the observations of Carlson and Soko (2000); Freimond and Allan (1995) and Morris (1994) that the response to a single application of N occurred mainly in the two years after application. In trials, in other parts of the world, the response to broadcast N fertilization in plantations has also been reported to be transitory with a peak of around 2 to 4 years after fertilization (Ballard, 1984; Gholz and Fisher, 1984; Hynynen *et al*., 1998). The short duration of the response to added fertilizer has been attributed to the fact that the typical rates applied (200 kg N ha^{-1}) do not substantially increase the N levels for a long period of time (Allen, 1987). Based on these findings it would have been unlikely for treatment effects, in this study, to be still evident in 2006 and 2007. It must also be remembered that photosynthetic rates decline with tree age and it is possible that the trees were unable to effective use of the additional nutrients supplied as fertilizers. It is impossible to substantiate the reasons behind the lack of response due to the difficulties associated with the small number of replicates in the study and the wind and drought damage experienced in 2006 and 2007.

5.5.1 Litter fall, litter accumulation, litter depth and decomposition

Wienand and Stock (1995) reported a significant increase in the annual litter fall rates and litter accumulation following P fertilization in a *P. elliottii* stand in South Africa. These data lead one to assume that if a site is P limited the litter fall rate will increase with fertilization, this did not occur in the *P. patula* and *P. elliottii* trails again providing evidence that the sites were not nutrient limited, except perhaps for available phosphorus. The measurements were taken far too late to the time of fertilizer application were applied and this may have limited the detection of treatment effects. Vitousek (1984) showed that the rate of litter fall was positively correlated to a low soil P status in a forest system in Hawaii.

The rate of litter production recorded in this study was higher than those recorded elsewhere in southern Africa (Dames *et al*., 1998; Wienand and Stock, 1995; Versveld, 1981), which may be due to an unusual windstorm that occurred in 2006 during data collection. Litter fall data from this study are higher than the results from a number of other studies as shown in Table 5.1. It is however interesting to note the fairly tight range in numbers considering the number of factors that can influence litter fall.

Table 5.1: Litter fall (t ha^{-1} yr^{-1}) and forest floor accumulation (t ha^{-1}) from pine plantation studies. Values are presented either as means or ranges

Species	Country	Age of Plantation	Quantity	Reference
Litter production (t ha^{-1} yr^{-1})				
P. patula	South Africa	19	6.7*	Present study
P. elliottii	South Africa	19	9.8*	Present study
P. patula	South Africa	15-20	4.4-4.8	Dames *et al*., 1998
P. radiata	South Africa	37	3.7	Versveld, 1981
P. elliottii	South Africa	19	1.0	Wienand and Stock, 1995
P. patula	India	17-25	4.7-11.4	Singh, 1982
P. kesiya	India	15-22	8.1-8.9	Das and Ramakrishnan, 1985
P. radiata	New Zealand	28	6.6	Will, 1959
P. caribaea	Nigeria	7-10	5.9	Egunjobi and Onweluzo,1979
P. patula	Tanzania	19	6.2	Lundgren, 1978
P. elliottii	U.S.A	15	4.9	Gholz *et al*., 1985
Forest floor litter accumulation (t ha^{-1})				
P. patula	South Africa	19	46.3-94.8	Present study
P. elliottii	South Africa	19	18.9-27.8	Present study
P. patula	South Africa	15-20	31.4-52.2	Dames *et al*., 1998
P. patula	South Africa	Mature	102.0	Von Christen,1964
P. patula	South Africa	Mature	320.0	Schutz, 1982
P. patula	South Africa	44	217.0	Schutz, *et al*., 1983
P. radiata	South Africa	37	7.0	Versveld, 1981
P. patula	Swaziland	11-15	50.6-155.6	Morris, 1995
P. patula	India	2-34	21.0-70.0	Singh, 1982
P. patula	Tanzania	10-30	25.0-35.0	Lundgren, 1978
P. elliottii	U.S.A	34	41.0	Gholz and Fisher,1982
p. caribaea	Nigeria	10	4.0	Egunjobi and Onweluzo,1979
P. elliottii	Australia	14-19	13.0-20.0	Maggs, 1988
P. radiata	Australia	30-40	16.0-28.0	Florence and Lamb,1974
P. radiata	Australia	12	17.0	Forrest and Ovington, 1970
P. radiata	Australia	12	23.0	Williams, 1976

*Values for all the *Pinus patula* and *Pinus elliottii* sites, since generally there was no significant differences between the control and fertilized plots.

Water limitations and cool temperatures in the winter season (July-Sept) led to decreased physiological activity and greater litter fall. In addition, the heavy windstorm that occurred after the July collection might have also contributed to the peak fall in September. Similar findings of peak litter production in September have been recorded by Dames *et al*., (1998); Morris (1995) and Wienand and Stock (1995); but these peak values coincided with rainfall.

The lack of treatment effect on the forest litter mass is in agreement with the findings of Carlson and Soko (2000), where no significant differences in the dry litter mass was detected following the applications of (N, P, K) fertilizers. The high amount of forest litter accumulated on the *P. patula* sites falls within the range of values reported for other southern African plantations (Dames, *et al*., 1998; Morris, 1995; Von Christen, 1964), but were lower than the values reported by Schutz (1982); Schutz *et al*., (1983) (Table 5.1). The values recorded at the *P. elliottii site* were lower than the *P. patula* sites, but within the values reported by other workers (Forrest and Ovington, 1970; Maggs, 1988) (Table 5.1). Several factors, including climatic factors, stand age, thinning and pruning and the net effect of litter fall versus decomposition have been reported to influence litter accumulation.

The litter depth recorded in *P. patula* (8.2-21.4 cm) was higher than the *P. elliottii* values (2.3-23.9 cm). The values for the *P. patula* site were greater than the range (3.9-12.1 cm) reported by Dames *et al*., (1998) but falls within the 3.0-35.0 cm values reported by Schutz (1990), while the *P. elliottii* site was lower than the reported values. Litter depth and accumulation are not simply correlated, one could assume that with increased depth one would get an increase in mass, however, this is determined by the degree of compaction of the litter. Schutz (1990) attributed the higher litter depth to disturbances causes by the removal of logs from thinning operations and the impact of bush pigs when searching for food. Dames *et al*., (1998) attributed the reason to silvicultural practices and local climatic conditions such as occasional heavy storms and strong winds.

The lack of treatment effects on decomposition rate when the fertilized and unfertilized plots are compared might indicate that the sites are not deficient in nutrients. Many studies have been conducted on the influence of N on the rate of decomposition, with the majority showing that increased decomposition rates occur in the presence of N or high quality litter (Berg *et al*., 1987; Conn and Day 1996; Downs *et al*., 1996; Miller *et al*., 1989; O'Connell 1994; Prescott *et al*., 1992, 2000; Sanchez, 2004). Other studies, however have reported decreased rates of decomposition in fertilized plots (Ågren *et al*., 2001; Hobbie, 2008; Titus and Malcolm, 1987) compared with unfertilized plots, thereby leading to increased litter accumulation (Magill and Aber, 1998).

The decomposition rate was calculated in this study and not the decomposition constant "k". In this section, the decomposition rate was calculated on a per area basis in order to make the value comparable with other studies. The rate was 0.05 g cm^{-2} day^{-1} for *P. patula* and *P. elliottii* and was calculated as a function of mass loss over time (difference between the final and initial mass over the period of incubation). Most other studies have calculated "k". Different decomposition rates have been reported for pines by many workers in South Africa; Versfeld and Donald (1991) reported a decomposition constant of 0.30 for *P. radiata* in Southwestern Cape; Wienand and Stock (1995) reported values of 0.19-0.35 for *P. elliottii* in Southern Cape of South Africa. Gholz *et al*., (1985a) in Southeastern U.S.A. reported a value of 0.15 for *P. elliottii* plantations. The litter decomposition in this study is fairly low and it is therefore expected that the higher litter fall rate and lower decomposition rate will lead to more litter being accumulated on the forest floor, especially at the *P. patula* sites.

Litter accumulation can simply be viewed as the net effect of litter fall and decomposition, however this would imply that the system is in steady state and it is well known that natural systems tend away from steady state conditions. The average annual litter fall for 2006-2007 is 6.69 t ha^{-1} yr^{-1} at the *P. patula* sites (Figure 5.2) and 9.75 t ha^{-1} yr^{-1} at the *P. elliottii* site (Figure 5.3), the expected litter accumulation from planting till 2007 is 120.4 t ha^{-1} for *P. patula* and 175.5 t ha^{-1} for *P. elliottii.* These estimates were obtained by assuming that the measured average annual litter fall was constant over the 18 years since plantation establishment. These data indicate that this system was not at steady state.

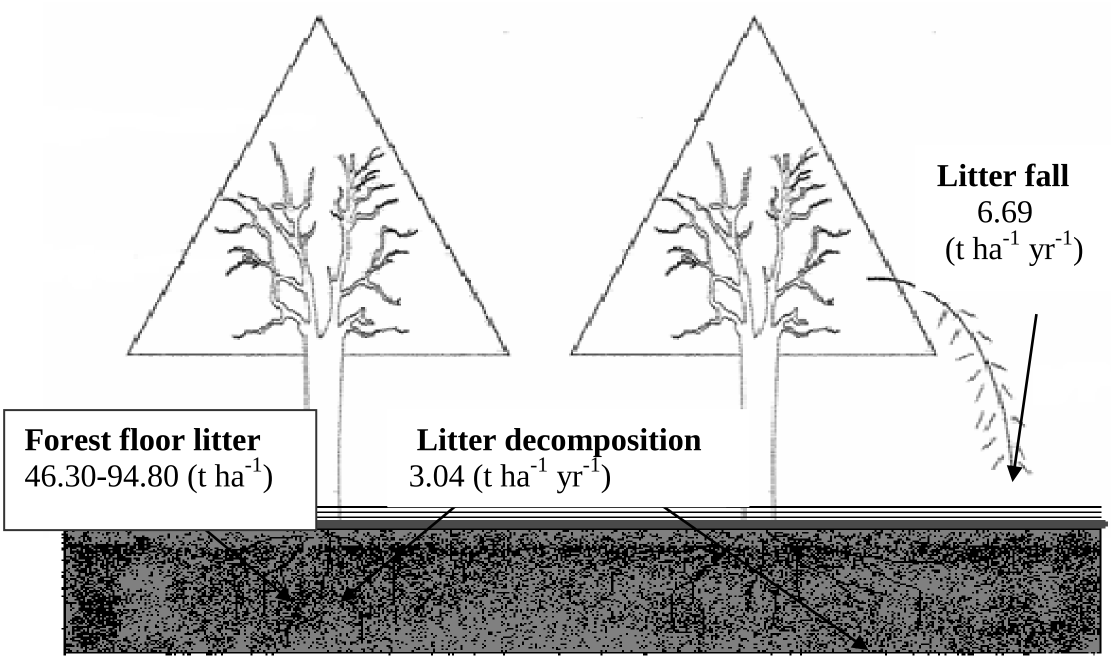

Figure 5.2 Forest floor litter pool (t ha^{-1}) and fluxes (t ha^{-1} yr^{-1}) in the *Pinus patula* sites

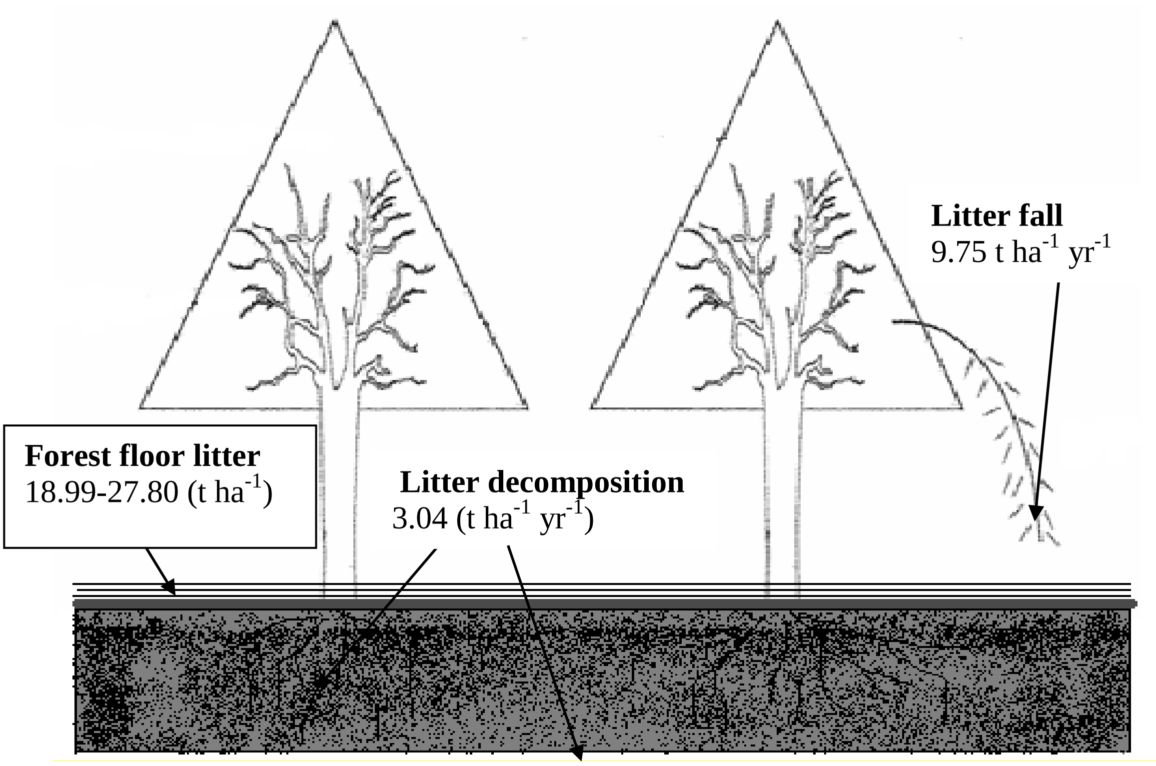

Figure 5.3 Forest floor litter pool (t ha^{-1}) and fluxes (t ha^{-1} yr^{-1}) in the *Pinus elliottii* site

The measured amount of forest floor litter in 2006 ranged from 46.3-94.8 t ha^{-1} (Figure 5.2) across the *P. patula* sites and 18.9-27.8 t ha^{-1} in *P. elliottii* site (Figure 5.3). The rate of decomposition for both the *P. patula* and *P. elliottii* plantations is 0.05 g^{-1} cm^{-2} day^{-1} and when scaled up becomes 3.0 t ha^{-1} yr^{-1}. Making the same assumptions as above the amount decomposed over the 18 years would be 54.8 t ha^{-1} yr^{-1} for both sites. If the decomposed mass is subtracted from the litter fall mass for the two sites, then there should be approximately 65.6 t ha^{-1} yr^{-1} remaining in the *P. patula* site and about 120.7 t ha^{-1} yr^{-1} remaining in the *P. elliottii* sites. The value for *P. patula* falls midrange between the measured values but the value for *P. elliottii* is about 5 times higher than measured.

It is acknowledged that these estimates are very simplistic and probably incorrect but they were undertaken to get a ball-park estimate of the net accumulation over time. Litter fall and decomposition rates were assumed to be constant over time which is not true as younger trees in open canopies do not have as great a litter fall as closed canopy plantations, in addition decomposition rates vary with environmental factors and litter quality. An additional factor that must be considered in this study are the management practices which were very variable across the two species and may account for the large discrepancies in the *P. elliottii* estimates. Pruning was done once, in 1993 at the *P. patula* sites (see Table 3.1 chapter 3) while, it was done continuously from 1995 to 2000 at the *P. elliottii* site (see Table 3.2 chapter 3). In addition, the trees were thinned at age 8, 12 and 17 at the *P. elliottii* while there was no thinning at the *P. patula* sites. The thinning might have reduced the competition for both water and nutrients under *P. elliottii*, resulting in the retention of more needles, due to lower stress, unlike *P. patula* that would shed the needles to alleviate the stress. In addition, strong winds might have contributed to increased litter fall at the *P. patula* site than at the *P. elliottii* site, thereby increasing the amount of forest floor litter.

Dames *et al*., (1998) attributed the higher litter accumulation to stand age and increasing altitude, where temperatures are cooler and are not favourable to litter decomposition; Morris (1995) attributed the high accumulation of forest floor litter at the Usutu plantation, Swaziland to differences in rates of decomposition rather than the amount of litter fall; while Wienand and Stock (1995) have suggested that the higher litter accumulation recorded in their study might be due to low decomposition rates and slow recycling processes in the system; while litter accumulation has been reported to have adverse effect on site fertility and tree growth. Most of the essential nutrients that the trees needs for growth are immobilized in the forest floor litter and this influences long-term productivity, this is supported by the published literature as well as the data collected in this study (Morris, 1995; Wienand and Stock, 1995).

5.1.3 Foliar nutrient concentrations and tree growth

The general lack of treatment effects on the foliar nutrient concentrations is in contrast with the findings of Gaud (1980) and Smaill *et al*., (2008) where fertilization has been reported to increase the N content of the live needles (foliage). However, the foliar nutrient concentrations recorded in this study are comparable with results from other studies (Table 5.2). Foliar nutrient concentrations and nutrient concentration ratios have been variously used to determine if a site is deficient or not and to explain tree growth response. The optimal nutrient target ratio approach was used by Crous *et al*., (2008) and Linder (1995), Beaufils, 1973 and Campion and Scholes, 2007 made use of the DRIS method to determine tree growth response.

The foliar N concentration in *P. patula* (1.36-1.50%) and *P. elliottii* (1.09-1.21%) was lower than the optimum concentration of 1.8% reported by Linder, 1995. The foliar N value was similar with the range of optimum values reported by Morrison (1974) (1.00-1.35%) and by Allen (1999) (1.20-1.55%) and other comparisons are shown in Table 5.2. The foliar P level is similar to the range reported in other studies (Table 5.2). A critical foliar P concentration of 0.09% for *P. elliottii* and 0.10% for *P. taeda* were reported from other parts of the world (Ballard, 1980; Ballard and Pritchett, 1975b; Wells *et al*., 1986). The foliar K^+ levels in this study can be compared to values from other studies (Table 5.2). The foliar Ca^{2+} concentration was however higher than the values reported for other studies (Table 5.2). Morris (1986) and Schutz (1990) have reported that Ca^{2+} might be limiting late in the rotation in southern African but the results from this study showed that Ca^{2+} is not limiting in both the *P. patula* and *P. elliottii* sites. The foliar Mg^{2+} level recorded in this study also falls within the range reported.

Table 5.2: Foliar nutrient concentrations from a number of studies in *P. patula* stands in southern Africa. Values are presented either as means or ranges and standard deviations are in brackets

Nutrient concentrations (%)					
N	P	K^+	Ca^{2+}	Mg^{2+}	Reference
1.4 (0.15)	0.12 (0.02)	0.69 (0.10)	0.40 (0.15)	0.16 (0.04)	***P. patula*** **This study**
1.14 (0.09)	0.08 (0.01)	0.33 (0.04)	0.34 (0.11)	0.10 (0.02)	***P. elliottii*** **This study**
1.24-1.79 (0.17-0.33)	0.13-0.17 (0.03-0.03)	0.50-0.76 (0.17-0.22)	0.17-0.25 (0.06-0.48)	0.10-0.11 (0.02-0.02)	**Louw and Scholes, 2003**
1.65 (0.14)	0.15 (0.03)	0.52 (0.14)	0.21 (0.06)	0.12 (0.02)	**Carlson and Soko, 2001**
1.67 (0.37)	0.15 (0.02)	0.84 (0.17)	0.21 (0.19)	1.06 (0.09)	**Dames *et al.*, 1998**
1.29-1.77	0.11-0.16	0.67-1.02	0.06-0.61	0.08-0.27	**Morris, 1986**
2.15 (0.16)	0.18 (0.02)	0.87 (0.17)	0.26 (0.11)	0.17 (0.43)	**Schutz, 1990**
1.37	0.10	0.71	0.30	0.21	**Germishuizen, 1979**

Foliar nutrient concentrations have been reported to depend on the soil nutrient availability, plantation age, silvicultural practices and climatic factors (Lambert and turner, 1988, Linder, 1995). The differences in nutrient concentrations between the studies can be related to the soil nutrient levels and age of the plantations which varied from 18-38 years old.

The P:N ratio expressed as a percentage reported in *P. patula* (7.2-9.6) and *P. elliottii* (7.0-8.1) were slightly lower than the value of 10 reported by Linder (1995) and 9.1 by Carlson and Soko (2001). However, the Ca:N ratios of 17.3-41.7 in *P. patula* and 26.8-36.7 in *P. elliottii* were greater than 2.5 and 12.8 which were the target optimum ratios reported by Linder (1995) and Carlson and Soko (2001) respectively. Likewise, the K:N ratio was also higher than the reported values by Linder (1995) and Carlson and Soko (2001).

Generally, it is clear that the results of foliar nutrient concentrations from this study showed that nutrients are not limiting including N and P across the sites. The higher concentrations of Ca^{2+} and other elemental interaction (ratios of Ca:N, and K:N) also showed that the sites are not nutrient deficient. This provides further supporting evidence for the absence of tree growth responses following late rotation applications of N and P in this study. It has however been pointed out that foliar nutrient concentrations must be interpreted with caution (Louw and Scholes, 2003) and should be coupled with information on soil nutrient status. Foliar concentrations are influenced by soil nutrient availability, stand age, sampling position in the crown and season. Structural and non-structural carbohydrate concentrations usually confound the interpretation of foliar analyses and that is why it is strongly recommended that needles are sampled and analysed when their metabolic activity is at its lowest. The data presented in this study were collected in winter in an attempt to reduce any error (Lambert, 1984; Linder, 1995; Payn and Clough, 1987).

5.2 Site Effects

5.2.1 Soil properties

The lack of treatment effects on the soil properties at the *P. patula* sites might indicate that the sites are not nutrient deficient especially for the added nutrients (N). The values of soil properties obtained in this study are comparable to the values obtained in previous studies in *P. patula* plantations in the summer rainfall region of southern Africa (Morris, 1995; Schutz, 1990) (Table 5.3). The levels are however, higher for Ca^{2+} and Mg^{2+} than what was reported by Louw and Scholes (2006) in *P. patula* plantations on shale derived soils in the same region. The amount of nutrients recorded in the *P. elliottii* site was lower, for the cations, when compared with the *P. patula* site and the other studies, but were comparable to the levels reported by Louw and Scholes (2006) with the exception of organic C that was higher.

Table 5.3: Concentration of soil nutrients recorded from this and other studies in the summer rainfall region of southern Africa

Exchangeable cations ($mg\ kg^{-1}$)			**Other soil nutrients**				
Ca^{2+}	**Mg^{2+}**	**K^{+}**	**N (%)**	**C (%)**	**Total P ($mg\ kg^{-1}$)**	**Available P ($mg\ kg^{-1}$)**	**References**
15.9-947.7	3.8-301.5	31.9-80.2	0.2-0.4	3.4-9.3	126.0-515.6	2.4-8.7	*P. patula* Present study
12.5-18.2	2.2-9.3	20.8-27.6	0.4-0.6	8.4-9.9	157.9-295.6	4.1-13.4	*P. elliottii* Present study
1.0-770.0	1.0-256.0	9.0-251.0	ND	0.6-9.5	ND	1.0-26.0	Schutz, 1990
20.0-451.2	10.0-332.4	7.2-180.0	ND	2.2-9.6	ND	0.2-9.4	Morris, 1995
4.0-68.0	8.0-23.0	31.0-62.0	0.2-0.7	1.5-6.3	625.0-750.0	1.0-3.0	Louw and Scholes, 2006

Soil nutrient levels at the *P. patula* sites were never measured from the beginning or at any point of the trial, until 2006. This made it difficult to determine the impact of the fertilizer treatments after the fertilizer applications over the study period. It is clear from these results that the treatments had no effects on the amount of nutrients available in the soil, however, nutrients are generally higher at the *P. patula* sites, especially at the Elandshoogte site compared to other *P. patula* sites. The *P. elliottii* site is also not deficient in nutrients especially N and P. The amount of available P present across the sites was low compared with the total P present though it was still enough to sustain tree growth as there were no P deficiency symptoms present on the foliage nor was there any response to added phosphorus at the *P. elliottii* site. This might be an indication that the sites are not N and P limited.

The tallest trees were measured at the Elandshoogte site as were the greatest soil base concentrations (Ca^{2+}, Mg^{2+} and K^{+}). Even though all of the *P. patula* sites are on shale, the Elandshoogte site has a greater proportion of Andesite than the other sites. This could result in there being a high base concentration, low exchangeability acidity, low Al^{3+} and high pH at Elandshoogte. Singer and Munns (1987) have pointed out that, as soil becomes more acidic, the minerals (Al^{3+} and Mn^{2+}) become more soluble, releasing these minerals into solution and increasing their concentrations, displacing other exchangeable cations that occupy a large fraction of the exchangeable capacity. This explanation would be applicable for all the sites other than Elandshoogte. This was also supported by Abreu *et al*., (2003) and Thomas and Hargrove (1984) where it was reported that effective cation exchange capacity decreases with a decrease in soil pH. This might have accounted for lower cations, cation exchange capacity and P availability, in other sites, especially Mamre and Mooifontein, due to the higher exchangeable acidity and lower pH.

There are significant site differences in this study which play a major role in determining the type and magnitude of tree growth response, and it is in line with the results of Carlson *et al*., (2000); Louw (1997) and Morris (2003), where site was a major factor that determined the occurrence or absence of tree growth response. The results from Carlson *et al*., (2000) attributed the tree growth response obtained in her study to parent material among other factors. They stated that trials based on granitic parent materials at high altitude tended to respond to P and K compared to other sites**.** Louw (1997) also pointed out that different sites showed different tree growth response in his study on fertilization in South Africa, while Morris' (2003) study on *P. patula* on gabbros and granite-derived soils in Usutu, showed that site in addition to stand age played a vital role in determining tree growth. He reported that significant responses to fertilizer were associated with gabbro-derived soil. Results from these studies have clearly demonstrated that site, in addition to other factors played a major part in determining the growth response following fertilizer applications to established *Pinus* stands.

The lack of a strong or no relationship between soil properties (organic carbon, N, Mn^{2+}, $Al^{3+}$and exchangeable acidity as hypothesized in this study) and tree growth parameters suggests that there is no attributable cause and effect relationship between soil properties and tree growth. This is however in contrast to widely reported findings that N and possibly P are usually the limiting nutrients in many natural and plantation forests (Binkley *et al*., 2000; O'Connell and Rance, 1999; Van Miegroet *et al*., 1990).

5.3 Climate

In addition to nutrient levels across the sites being a factor influencing the type and magnitude of the tree growth responses recorded in this study, climatic factors, rainfall and temperature may have contributed to the absence of tree growth response and the different tree growth patterns obtained across the sites. Several studies in South Africa and the rest of the world have reported that climate, rainfall and temperature play a major role in influencing tree growth responses to fertilization (Campion *et al.*, 2005; Carlson and Soko, 2000; Louw, 1997; Pereira *et al.*, 1994; Sands and Mulligan, 1990; Sheriff, 1996; Turner *et al*., 1996). Water availability and its interaction with nutrients have been reported to have overriding influences on the magnitude of stand response to silvicultural practices. There is also evidence of interactions between tree density and water availability (Graciano *et al*., 2005; Landsberg and Waring, 1997; Nambiar *et al*., 1984; Sheriff, 1996).

The average annual rainfall amounts recorded at the *P. patula* sites, Elandshoogte and Mamre sites (873.5 mm) (Figure 5.4a) and at the Mooifontein and Grootgeluk sites (928.8 mm) (Figure 5.4b) were lower than the long-term annual rainfall of 1174 mm on the same land types reported by Pallet (1991). The annual rainfall, at the Elandshoogte and Mamre sites, over the years (between 2001-2007) was generally below the annual average of 873.5 mm for that period for those two sites (Figure 5.4a). A similar pattern was observed at the Mooifontein and Grootgeluk sites, where the average annual rainfall was 928.8 mm (Figure 5.4b) from 2001-2007. There were however ascendances in 2001, 2006 and 2007. The temperatures (maximum and minimum) were significantly ($p<0.0001$) higher in 2005 than in the other years (Figure 5.5). The below average rainfall in 2002, 2003 and 2005 at all of the sites and the dissimilar rainfall distribution in 2001 and 2007 across the sites, in addition to the high temperatures in 2005 may have led to the lack of pattern in tree growth response. Fertilizers were applied in 2001 and 2003, during a period of below average rainfall, the average rainfall received in 2004 may have resulted in increased nutrient uptake but these effects were probably lost by the below average rainfall in 2005. Studies have shown that fertilization is most beneficial when trees are not water stressed. Sands and Mulligan (1990) reported that soil water availability determines not only whether a response to nutrient additions occurs, but also the magnitude of the observed response. Studies have shown that mid-rotation fertilization is most likely to be effective following thinning (Cole *et al*., 1990; Donald, 1987; Sands and Mulligan, 1990; Yang, 1998) since soil moisture is likely to be more limiting than nutrients in unthinned trials like in *P. patula* in this study.

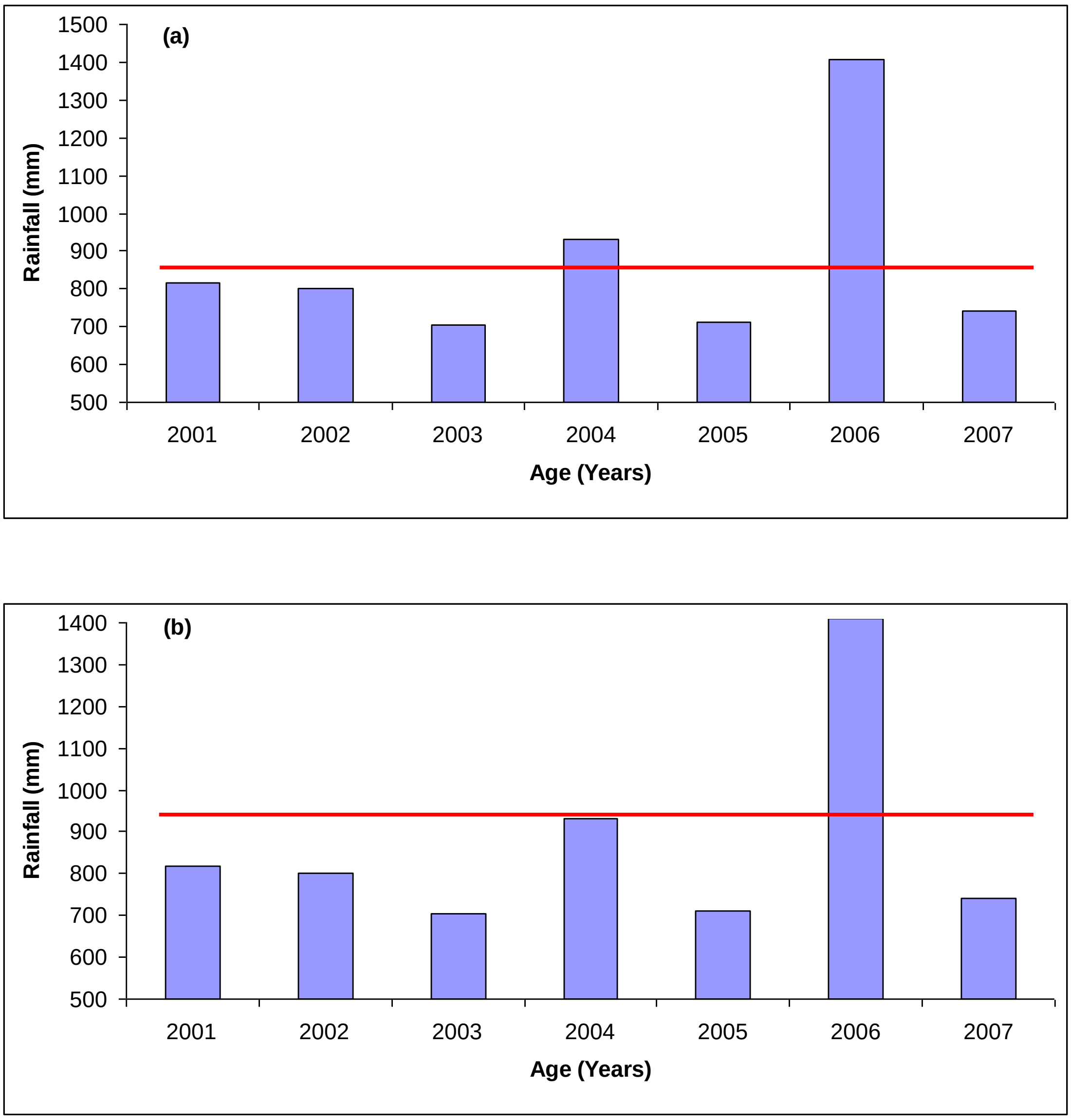

Figure 5.4 Annual rainfall distribution for *Pinus patula* sites (a) Elandshoogte and Mamre sites and (b) Mooifontein and Grootgeluk sites for the seven-year (2001-2007). The bold horizontal bar indicates the annual average rainfall for the study period

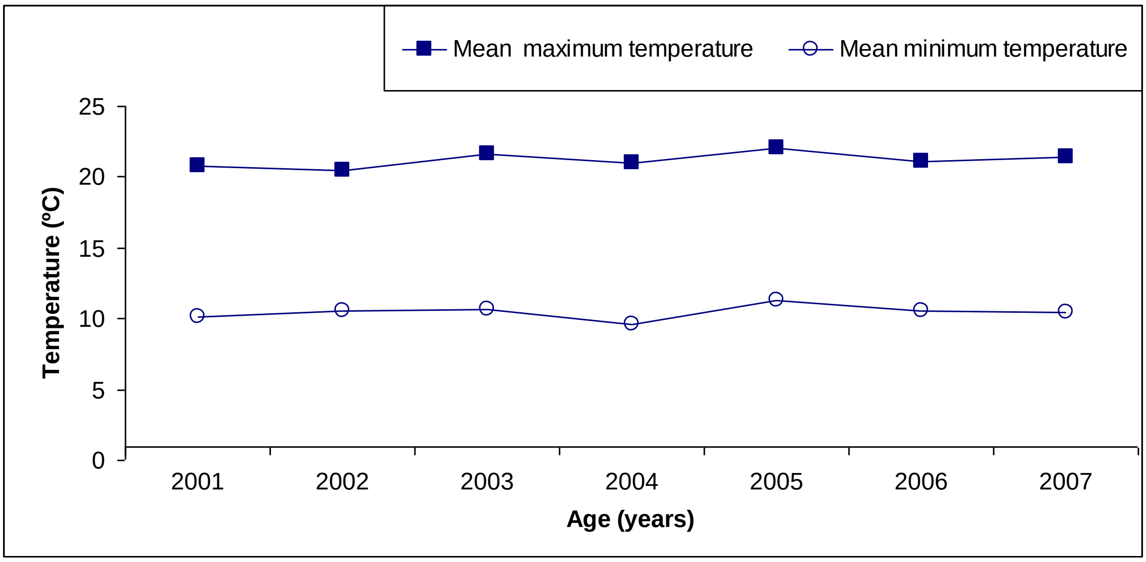

Figure 5.5 Mean annual temperatures (maximum and minimum) for *Pinus patula* sites for the seven-year (2001-2007)

Climate, the amount and distribution of rainfall, has also been shown to influence the rate of litter fall, litter accumulation, and N mineralization across the sites. Generally it is clear from the above explanations that nutrient status and nutrient supply differed across the sites and the years, these together with the climatic factors interacted to influence the response and the pattern of tree growth obtained. Climate, site and the nutrient levels are the major drivers influencing the tree growth in the *P. patula* plantations whilst at the *P. elliottii* site, climate and nutrient levels are the drivers of the system.

Allen (1987) and Jokela *et al.*, (1988) have pointed out that stands may still not respond or respond poorly to high doses of fertilization even when the levels of nutrient availability are high if the level of water availability is not sufficient. They pointed out that nutrient uptake e.g. Ca^{2+} and Mg^{2+} are relatively insensitive to water deficits, but uptake rates of N, K^{+}, and especially P may be reduced. Morris (1993) found that N applications made in mid-summer (January) at the peak of the growing season, the period with the highest soil moisture resulted in the best response, as opposed to applications made in April, July and October. The lack of treatment effects on the tree growth parameters obtained in the study even when the fertilizer was applied during the wet period (January) for *P. patula* and (February) for *P. elliottii* might indicate that N and P might not be the limiting nutrients.

5.4 Nutrient Cycling and Plant Growth

5.4.1 Needle and litter nutrient pools

Pinus patula

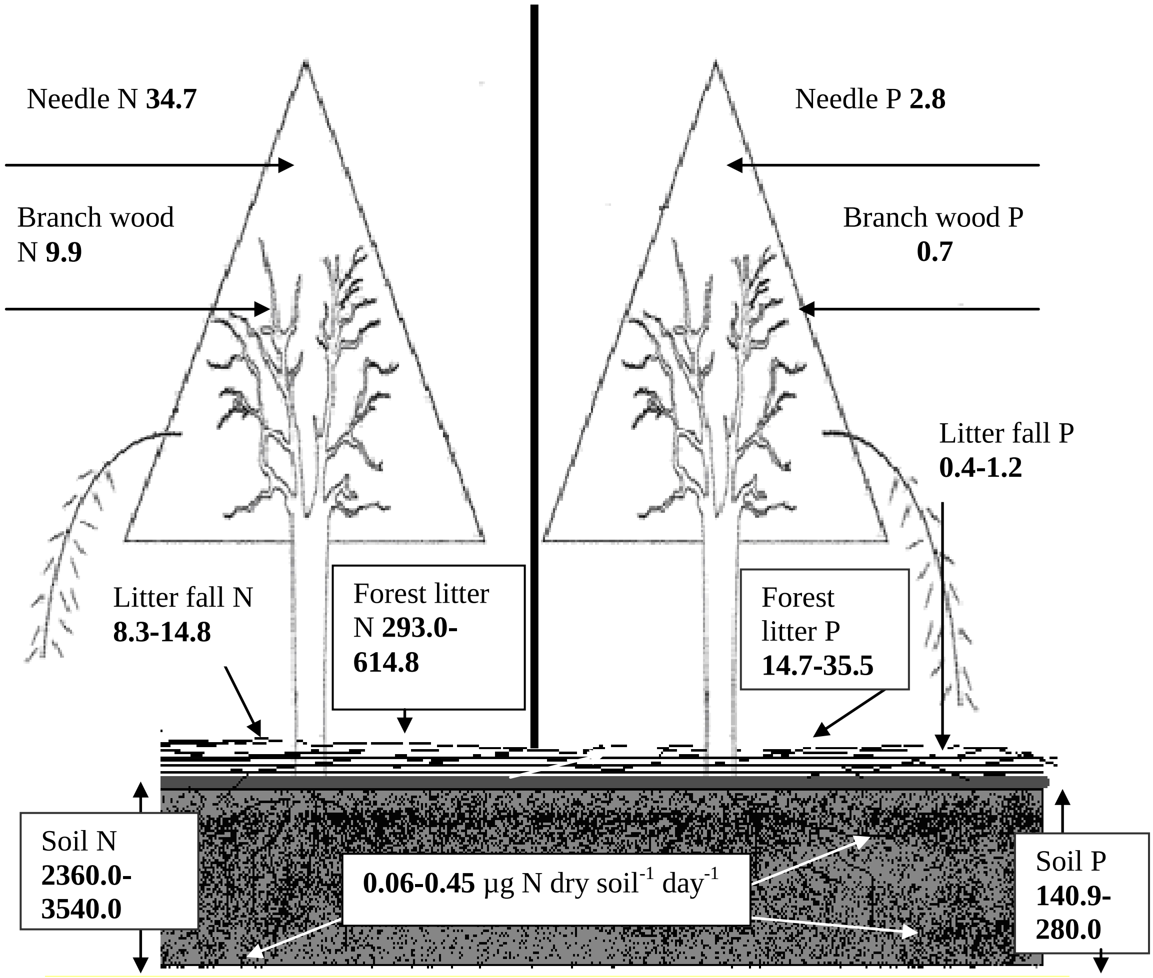

Figure 5.6 Mean of the N and P pools (kg ha^{-1}) and fluxes (kg ha^{-1} yr^{-1}) in the *Pinus patula* sites

Nitrogen and P pools and fluxes are shown in Figure 5.6. The N pool in the litter layer is approximately 8-18 times greater than the N pool in the needles and 30-62 times greater than the N pool in the branchwood. The needles contained 78% and the branchwood 22% (Figure 5.6) of the N in the tree canopy. The percentage of N returned to the forest floor through litter fall is 19-33%, with 67-81% of the N being re-translocated prior to litter fall. The amount of N stored in the soil pool is the greatest of all the pools (Figure 5.6). These data clearly show that the N in the litter pool is an critical factor in understanding nutrient availability in this system. The amount of N returned through N mineralization is 0.06-0.45 µg N dry soil^{-1} day^{-1}. It is difficult to calculate this on an annual basis as bulk density measurements were not taken and assumptions that would be needed to scale this value up to an annual estimate would be tenuous. Similar studies, from international sources, give annual soil N mineralization estimates of 6-100 kg N ha^{-1} yr^{-1} (Perez *et al*, 1998). It can be seen that the fertilizer applied in this study was approximately equal or double the annual soil N mineralization estimates. It must however be remembered that the fertilizer additions occurred only once in the 18 years.

Based on the assumption that the amount of nutrients equivalent to one year's litter fall is mineralized in each year from the forest floor (Dames *et al*., 1998; Helmisaari, 1995), it means that 8.3-14.8 kg N ha^{-1} will be available assuming that 100% loss of N from litter decomposition occurs. However, this assumption would not hold in this situation as there is a significant accumulation of N in the forest floor litter. Results from the decomposition study showed that about 42% of the litter was decomposed in *P. patula* in one year, therefore 3.5-6.2 kg N ha^{-1} is made available in one year (calculated by multiplying 8.3-14.8 kg N ha^{-1} by 42%) and 62.8-111.9 kg N ha^{-1} in 18 years assuming that all N mineralized from the litter will be taken up.

Therefore the amount of N that is made available to the trees on an annual basis must be the sum of that from soil mineralization, the major share, together with N mineralized from the litter (as well as any N from fertilization and aerial deposition). There were no studies carried out on the efficiency of N uptake from the two mineralized pools and it is suggested that the N made available from the litter would have been immediately taken up due to the proliferation of ectomycorrhizae in the litter. It is suggested that nutrient uptake from the litter is a more tightly coupled process than N taken up from the soil mineralization processes.

The P pool in the litter layer is approximately 5-10 times greater than the P pool in the needles and 21-40 times greater than the P pool in the branchwood. The needles contained 80% and the branchwood 20% (Figure 5.6) of the P in the tree canopy. The percentage P returned to the forest floor through litter fall is 11-34%, with 66-89% being re-translocated prior to litter fall. The amount of P stored in the soil pool is greater than any of the other pools. Based on the same assumptions as discussed above, 0.4-1.2 kg P ha^{-1} could be mineralized, assuming that 100% loss of P from litter decomposition occurs. Results from the decomposition study showed that about 42% of the litter was decomposed in *P. patula* in one year, therefore 0.2-0.5 kg P ha^{-1} is made available in one year (calculated by multiplying 0.4-1.2 kg P ha^{-1} by 42%) giving 3.1-9.1 kg P ha^{-1} in 18 years assuming that all litter P mineralized will be taken up. It is again suggested that P uptake from the litter mineralization processes will be rapid facilitated by the extensive presence of ectomycorrhizae.

Pinus elliottii

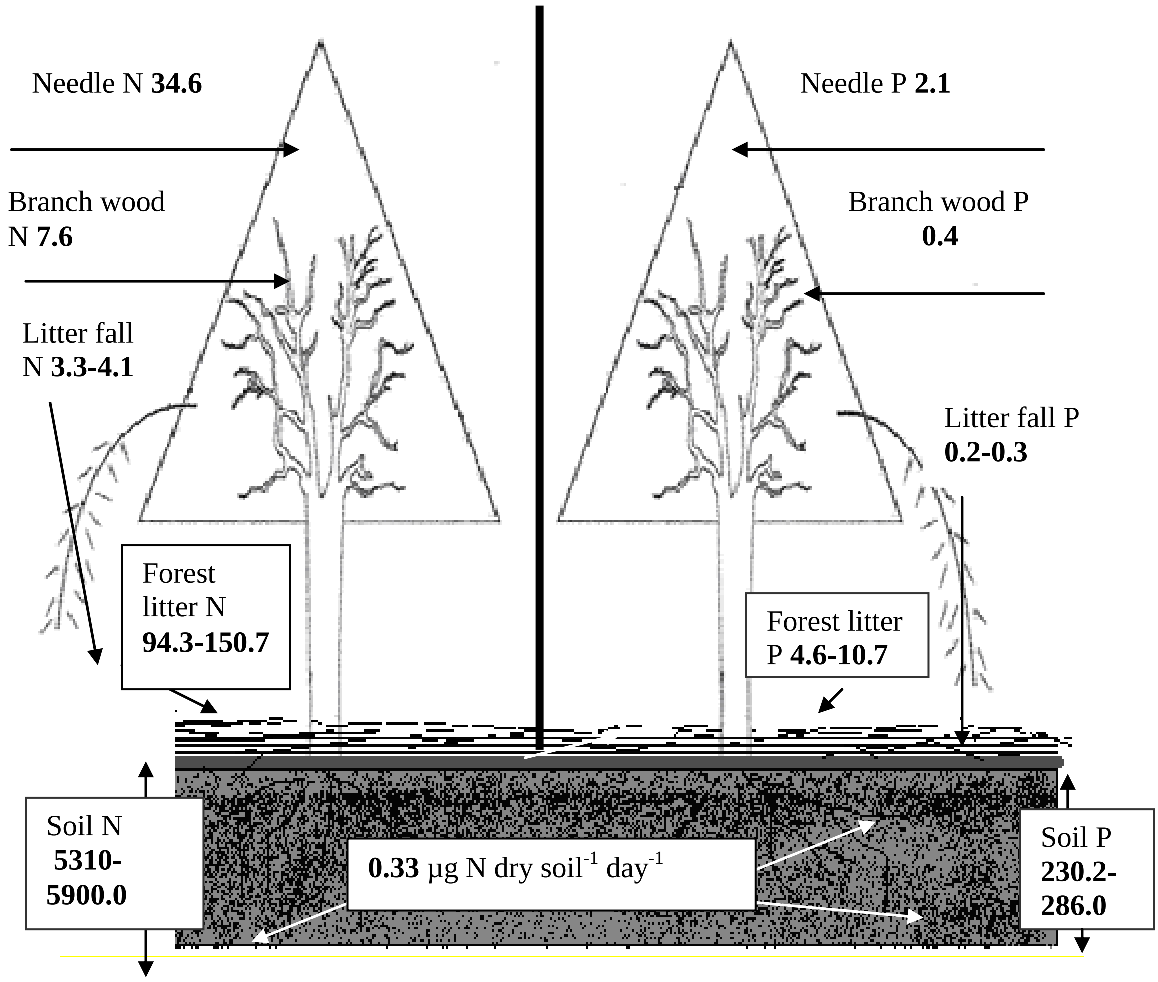

Figure 5.7 Mean of the N and P pools (kg ha^{-1}) and fluxes (kg ha^{-1} yr^{-1}) in the *Pinus elliottii* sites

Nitrogen and P pools and fluxes are shown in the Figure 5.7. The discussion relating to P. *patula* also applies to *P. elliottii*. The major differences are that, for N and P, the rate of litter fall and forest floor accumulation of litter are much greater in *P. patula* than they are in *P. elliottii*. On the other hand, the soil N pool is greater in *P. elliottii* making it even more unlikely for there to be a fertilizer response at the *P. elliottii* site.

The litter nutrient concentrations reported in this study compared with concentrations measured in other *Pinus* plantations in southern Africa (Table 5.4).

Table 5.4: Nutrient concentrations of needles and branch wood in the litter fall and needles in the forest floor litter from this study and other *Pinus* plantations in southern Africa. Values are presented either as means or means and standard deviations

Litter fraction and forest litter pool	**Nutrient concentrations (%)**				
	N	P	K^+	Ca^{2+}	Mg^{2+}
Present study (*P. patula*)					
Needles in litter fall	0.88±0.21	0.07±0.02	0.25±0.08	0.48±0.14	0.16±0.03
Branch wood in litter fall	0.54±0.15	0.04±0.01	0.09±0.04	0.44±0.19	0.06±0.02
Needles in forest floor litter	1.05±0.14	0.06±0.01	0.10±0.03	0.27±0.18	0.19±0.05
Present study (*P. elliottii*)					
Needles in litter fall	0.55±0.15	0.03±0.01	0.06±0.04	0.53±0.12	0.10±0.02
Branch wood in litter fall	0.41±0.15	0.02±0.01	0.05±0.03	0.40±0.17	0.05±0.05
Needles in forest floor litter	0.47±0.11	0.03±0.01	0.02±0.01	0.13±0.03	0.03±0.01
Dames *et al*., (2002)					
Needles in litter fall	1.67±0.37	0.15±0.02	0.84±0.17	0.21±0.19	1.06±0.09
Branch wood	0.05±0.03	0.02±0.01	0.28±0.07	0.05±0.03	0.34±0.08
Litter 0i-1	1.12±0.53	0.07±0.01	0.70±0.30	ND	0.62±0.14
Morris, 1992c					
Needles in litter fall	1.55±0.18	0.13±0.02	0.83±0.11	0.30±0.15	0.18±0.03
Branch wood	0.28±0.05	0.04±0.01	0.25±0.09	0.14±0.05	0.07±0.03
Litter 0i-1	1.36±0.19	0.07±0.01	0.11±0.03	0.32±0.08	0.15±0.02
Schutz (1990)					
Needles in litter fall	2.15	0.18	0.87	0.26	0.17
Litter	1.28±0.16	0.16±0.01	0.10±0.05	0.28±0.21	0.08±0.05

ND = Not determined
0i-l = newly fallen litter lying loosely on the forest floor.

The lower nutrient concentrations in the litter compared with the green needles in this study, except for Ca^{2+}, which is structurally bound mostly in cell walls, indicated that re-translocation of nutrients had occurred from senescing tissues prior to needle abscission (Jonasson, 1989; Turner and Lambert, 1986 and Wienand & Stock, 1995). The results from *P. patula* across the sites (see Table 4.7 chapter 4) showed that 58% of P was re-translocated, whereas 62% was re-translocated in *P. elliottii* (see Table 4.12 chapter 4). These percentages were calculated by comparing the concentrations in the green needles (foliage) with the concentrations in the needles in the litter fall. Other nutrients were also re-translocated with varying percentages, except for Ca^{2+}. These data indicate a conservation of nutrients at the sites. The same redistribution pattern was recorded both in the control and fertilized plots thereby showing that treatments had no effect on the amount of nutrients available across the sites. Higher concentrations of Ca^{2+} were measured in the litter fall compared with the foliage which shows the concentrating effect of the re-translocation of the other nutrients (Vitousek, 1982, 1984; Cuevas and Medina, 1988) (Table 5.4). The re-translocated nutrients become available to meet the demands of plant metabolic activity.

Nitrogen, was the nutrient having the highest concentration, in the litter, followed by Ca^{2+}, K^{+}, Mg^{2+}, and P in that order (Table 5.4). Re-translocation of substantial quantities of nutrients, except Ca^{2+} in the needles took place prior to needle fall. The C:N ratios recorded in both *P. patula* and *P. elliottii* forest floor litter are above 35 and this does not favour N mineralization. Morris and Campbell, 1991 and Jansson and Persson, 1982 have reported that a C:N ratio below 25 favours N mineralization. The added nitrogen in the fertilizer may have altered the immediate mineralization rate but no changes could be observed by the time the mineralization studies were conducted for this PhD. It is evident that the litter layer plays a very important role, in this and many other studies, in the cycling of nutrients considering the amount of the nutrients that are available in the litter pool.

5.4.2 Rates of soil nitrogen transformation: Ammonification, nitrification and N mineralization

The amount of nutrient turnover through N mineralization was not significantly affected by treatment and did not influence tree growth of the two species. The general lack of treatment effects on the rates of ammonification, nitrification and N mineralization in the two species is in agreement with the findings of Chappell *et al*., (1999); Prescott *et al*., (1993); Strader and Binkley (1989) and White *et al*., (1988), who have all reported that fertilization has no effect on N mineralization rates. However, Carlyle (1995b); Fenn *et al*., (2005); Hart and Stack (1997); McNulty and Aber (1993) and Polglase *et al*., (1992) have reported that N additions in the form of fertilizer do affects N mineralization rates. These discrepancies can be partially explained by sampling of different soil horizons, methods of analyses used, and specific location of the studies e.g. forest floor litter versus mineral soil. In addition, some of the studies were determined in the field (*in situ*) while others were undertaken in the laboratory.

The results of N mineralization rates from this study was used to test the N mineralization model described by Louw and Scholes (2002) to predict tree growth response following N fertilizer application. The model equation is shown below:

[0.830 – 0.0107* Monthly net N mineralization rate] (R^2 = 0.80; p< 0.0001)

They reported that tree growth on sites experiencing a positive value in N mineralization rate, will not react significantly to N fertilization, while sites experiencing N immobilization are likely to produce a significant response. The N mineralization results from this study were converted to monthly data estimates assuming linearity. The resulting R^2 ranged from 0.69-0.81 in *P. patula* species and 0.72 in *P. elliottii* species, indicating no N limitation at the sites and therefore no benefit would be gained from fertilization. The soil C:N ratios of (16-25) in *P. patula* and (17-25) in *P. elliottii* favour N mineralization rate over immobilization (Jannson and Persson, 1982).

There was no correlation between the N mineralization rates across the *P. patula* sites and the tree growth responses, this may be explained as discussed earlier that N availability occurs from both the mineral soil and the forest floor litter. The variation in N mineralization rates across the sites were in agreement with the findings of Carlyle *et al*., (1990) and Louw and Scholes (2002), and may be caused by a large number of factors including parent material, season and climatic differences.. Dames *et al*., (2002) working on soils from the same region reported a higher N mineralization rate of (4.66 µg N dry soil^{-1} day^{-1}). The higher values can be attributed to the method of analyses used, where Dames used an anaerobic laboratory incubation technique to estimate the N mineralization potential of the soils. Studies have shown that N mineralization rates determined in the laboratory are higher than those ones carried out in the field (*in situ*) due to disturbance at sampling and the assay is usually carried out under optimum conditions (Anderson and Ingram,, 1993).

The results of higher N mineralization values in the summer months recorded at the *P. patula* sites were similar to the findings of Gurlevik *et al*., (2004) in a 14-year old *P. taeda* plantation in North Carolina, U.S.A. and these were attributed to increased temperature and higher soil moisture content. Positive relationships between temperature and net N mineralization rates under laboratory conditions have also been reported by Goncalves and Carlyle (1994) and Sierra (1997). Generally, temperature has been reported to influence microbial and enzymatic activities, while movement of substrate is controlled by moisture (Zak *et al*., 1999; Power, 1990). Therefore, increased temperatures and moisture contents usually result in more rapid N mineralization. However, this was contrary to the findings of Allen (1999) who found no relationships between soil temperature and monthly field net N mineralization rate in mid-rotation *P. taeda* stands in the U.S.A. In this study, higher N mineralization rates were recorded in the winter months at the *P. elliottii* site. There is no apparent explanation for this observation and can probably be best explained by simple variability. The variability of all the soil transformation processes was very high, this is a common phenomenon due to microsites of carbon availability and water availability in soils.

The significantly higher nitrification rate compared with ammonification, and the positive correlation ($r = 0.47$, $p=0.001$) between NO_3^- and tree height when compared with the negative correlation ($r = -0.34$, $p=0.02$) with ammonification rate might indicate that NO_3^- is the dominant form of the inorganic N in *P. patula* sites. This is in contrast with the findings of Louw and Scholes (2002) in the same region, where NH_4^+ was reported as the dominant N ion. The results from *P. elliottii* site, however, showed a negative correlation between tree height ($r = -0.53$, $p=0.035$), tree volume ($r = -0.71$, $p=0.002$) and ammonification rate and no relationships with NO_3^-. This might indicate that NH_4^+ is more related to tree growth, and may be the dominant and main source of N ion in the *P. elliottii* site. The predominance of the form of inorganic N ion is important when trying to understand the potential of the sites for leaching and denitrification. However, at both of the sites these processes would be negligible due to water limitations.

5.5 Modelling Tree Growth

The 3-PG growth model was found to be useful and the correlation was good for predicting diameter at breast height (DBH), basal area and stand volume in both *P. patula* and *P. elliottii* species, when climatic factors, rainfall and temperature, and nutrient availability across the study sites were integrated. The deviations in the observed versus predicted data can be discussed based on the effects of the wind and the assumptions used to estimate the climatic data up to the end of the rotation age in the *P. elliottii* species. The tree growth parameters were generally well predicted across the sites except at the Elandshoogte site where the basal area was poorly predicted. The poor prediction at the Elandshoogte site might be attributed to the severe drought and wind damage that impacted the 2006 and 2007 tree measurements. This explanation was supported when the model was re-run excluding the data for 2006 and 2007. These re-runs gave a very strong correlation ($r = 0.97$, $p=0.0001$) especially for basal area at the Elandshoogte site and equally for other parameters across the sites.

The general deviations between the observed and predicted values in this study, especially stand volume and basal area can be explained based on the fact that stand volume may have been over estimated. In addition, the soil water module of the model is based on a number of assumptions that may not allow for rigorous estimates of water availability. Landsberg and Waring (1997) reported that the soil water balance component in 3-PG is a simple, single layer model obtained as the difference between monthly precipitation and monthly evapotranspiration., This difference was calculated using the Penman-Monteith equation provided in the soil water module of the model. The assumption of this calculation is that rainfall is uniformly distributed over the month, which is obviously not the case, and this is compounded by drought at the *P. patula* sites and the estimated monthly rainfall numbers from 2007-2017 (which were based on monthly averages of rainfall at the *P. elliottii* site over the last 10 years). Soil water availability may have been either over or under estimated in the model and these values may have contributed to the deviations observed in the stand volume predictions. Systematic deviations were observed in the output and further sensitivity analyses would need to be conducted to investigate the reasons for these deviations

The deviations between the observed and predicted stand volume and basal area could also be related to an over estimation of the allocation of net primary production (NPP) and/or an over estimation of NPP allocation to stem wood, which may be attributed to errors in the calculation of soil water or vapour pressure deficit or from the assigned fertility rating (FR) values. In the 3-PG model, adjustments to FR influence above-ground biomass production by altering the canopy quantum efficiency and carbohydrate allocation to roots. Landsberg *et al*., (2000), Louw and Scholes (2006), Makela *et al*., (2000) have all reported that the fertility rating in the model is relatively crude and subjective. An, under or over estimation of (FR) might have allocated more or less to below ground components and this could result in carbohydrates not being accurately allocated for stem growth (Binkley, 1986). Esprey *et al*., (2004) has reported that the stand volume is highly sensitive to the ratio of net gross primary production, maximum canopy efficiency, maximum canopy conductance and basic wood density, and a moderate sensitivity to the maximum and minimum fractions of biomass allocated to roots.

CHAPTER 6

CONCLUSIONS

This section considers the findings of the thesis in the context of the hypotheses posed.

Hypothesis I

Late rotation fertilization of *P. patula* and *P. elliottii,* with inorganic fertilizers, will result in increased tree height, basal area and stand volume, across the sites, if other environmental growth conditions are favourable.

Results from the study showed that late rotation fertilization generally had no significant effect on the tree height, basal area and stand volume at any of the sites. It is evident from this study that the unfavourable climatic factors, especially the low and variable distribution of the rainfall contributed partly to the lack of treatment effects and the pattern of tree growth response recorded across the sites. The inherently high fertility status of the sites can also be used to explain the lack of treatment effects. The timing of the fertilization and the sampling for the PhD study may have contributed to the lack of detection of the fertilizer response at the *P. patula* sites, especially for the soil properties and the other process based measurement. The hypothesis is rejected.

Hypothesis II

The growth response in tree height, basal area and stand volume in *P. patula* as well as in *P. elliottii* with late rotation fertilization is positively correlated with soil exchangeable bases (Ca^{2+}, $Mg^{2+}$and K^{+}) and negatively correlated with exchangeable acidity and pH across the sites.

Late rotation fertilization does not have any effect on the soil exchangeable bases (Ca^{2+}, Mg^{2+} and K^{+}) at the *P. patula* sites, however, there were site differences. At the *P. elliottii* site, the soil exchangeable base concentrations were higher in the treatment where nitrogen and phosphorus fertilizer were combined. The fertilizer treatments, however, did not affect tree growth pattern across the two sites. The hypothesis is accepted for only the Elandshoogte site because it was only at this site that the tallest trees as well as the highest exchangeable base concentrations, high pH values and lowest acidity were recorded. At the other sites there was no positive or negative correlation between the tree growth parameters measured and the levels of exchangeable bases and acids. Hypothesis II is accepted only with respect to the relationship between exchangeable bases and tree growth at the Elandshoogte site. There was no pattern whatsoever at the *P. elliottii* site. Hypothesis two is rejected for all other sites.

Hypothesis III

Late rotation fertilization of *P. patula* and *P. elliottii* will lead to short term enhanced soil N mineralization rates due to decreased C:N ratios in the litter and soil.

The late rotation fertilizer applications did not affect the soil N mineralization rate across the two species and had no effect on the tree growth response. However, it should be noted that soil exchangeable bases (Ca^{2+}, Mg^{2+} and K^{+}) were highest and exchangeable acidity was lowest at one of the *P. patula* sites (Elandshoogte) where the lowest N mineralization rate of 0.06 µg N g dry soil^{-1} day^{-1} was recorded. The soil C:N ratio (16-25) across the two species is favourable for N mineralization availability, while the C:N ratio of above 35 recorded in the litter is not. Therefore the hypothesis is accepted for Elandshoogte but rejected for all the other sites.

Hypothesis IV

The concentration of N, P, P:N ratios and cations (Ca^{2+}, Mg^{2+} and K^{+}) in the foliage of *P. patula* and *P. elliottii* with late rotation fertilization is positively correlated with tree height, basal area and stand volume in *P. patula,* as well as in *P. elliottii* across the sites.

The concentration of N, P and N:P ratios and cations (Ca^{2+}, Mg^{2+} and K^{+}) in the foliage of *P. patula* and *P. elliottii* with late rotation fertilization were found not be positively correlated with the tree height, basal area and stand volume across the sites. The levels of foliar N and P and their ratios were similar to published optimum concentrations and showed no response to the addition of nutrients. . Therefore, the hypothesis is rejected, however, the levels of N, P and P:N ratios could possibly be used an indicators for whether the trees will respond positively to fertilizer application.

6.1.5 Hypothesis V

Tree height, basal area and stand volume are positively correlated with the rate of litter fall, accumulation, decomposition and nutrient concentrations in *P. patula* and *P. elliottii* litter across the sites following late rotation fertilization.

The tree height was highest at the Elandshoogte site which had the lowest litter fall, litter accumulation and litter nitrogen concentration, while Mooifontein was the site with the highest basal area, stand volume, litter fall, litter accumulation and the highest litter N concentration for the *P. patula* sites. There was no pattern at the *P. elliottii* site. Therefore hypothesis five can be accepted for Mooifontein but rejected for all the other sites.

6.1.6 Hypothesis VI

The predictive capacity of the growth of *P. patula* and *P. elliottii* with late rotation fertilization using the climatic factors and other input parameters across the sites was improved using the 3-PG model.

The 3-PG model was found to be a useful tool for the prediction of tree growth in both species across the sites. The tree growth parameters were well predicted with high correlations for basal area, stand volume and quadratic mean DBH, across all the *P. patula* sites except for basal area. Basal areas were poorly predicted at the Elandshoogte site. At the *P. elliottii* site, the tree growth parameters were well predicted for 2006, whereas, in 2007 there were deviations because of wind damage. The hypothesis is accepted.

6.2 Concluding remarks and recommendations

Forest productivity is controlled by a number of drivers including genetic, management and environmental factors. Nutrient availability has been the key focus of this study. The availability of these nutrients may be affected by the addition of fertilizer and also by a number of management practices to conserve and increase the nutrient levels and ultimately increase productivity. This study used a combination of laboratory and modeling studies to improve the mechanistic understanding of tree growth. It is very interesting to note that the same pattern of tree growth response were obtained across the two species thereby showing that the species plays no major role in determining the pattern of tree growth response. Other factors, including variable climate conditions, high inherent soil fertility, high foliar nutrient concentrations and ratios and high nutrient concentrations in the litter pool, all influenced the pattern of tree growth.

It is therefore, very clear from this study, that tree growth response and pattern across the sites is not influenced by fertilization but by the amount of nutrients locked up in the nutrient pools especially the forest floor litter. There is likely to be a better and more uniform tree growth response to fertilizer applications at other sites showing nutrient limitation and higher and less variable rainfall. It is recommended, that due to the important role that forest litter plays in nutrient availability, that the litter is managed more intensively to enhance decomposition.

The study provided some interesting pointers for further research, these include positioning late rotation fertilizer trials on soils that are nutrient limited, especially with respect to N, P and exchangeable bases and in areas with reliable and higher rainfall. A systems based approach to measuring pools and fluxes should be adopted and not just an emphasis on measuring the components of yield. Soil sampling should be conducted prior to the establishment of the trial and on going monitoring of key processes in all soil and plant pools and fluxes should be done.

CHAPTER 7

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