ABOVE-GROUND ALLOMETRY, BIOMASS AND NUTRIENT CONTENT OF *ACACIA MEARNSII* ACROSS FOUR AGES AND THREE SITES IN THE KWAZULU-NATAL MIDLANDS

STEVEN B. DOVEY

January 2005

ABOVE-GROUND ALLOMETRY, BIOMASS AND NUTRIENT CONTENT OF *ACACIA MEARNSII* ACROSS FOUR AGES AND THREE SITES IN THE KWAZULU-NATAL MIDLANDS

by

STEVEN B. DOVEY

Submitted in fulfilment of the academic requirements for the degree of

Master of Science

in the
School of Life and Environmental Sciences
University of KwaZulu-Natal
Durban

January 2005

ABSTRACT

Acacia mearnsii (black wattle) is one of the few tree crops of which both timber and bark are utilised, with branches sometimes being collected for fuel wood. There is a great potential for nutrient loss from plantations with intense harvesting practices. Allometric relationships were developed to estimate above-ground biomass across four ages and three site qualities of *A. mearnsii* stands. The three sites were based on high, medium and low site quality classes of productivity. Differences in biomass and the distribution of biomass between the stem, bark, live branches, dead branches and foliage components are described in relation to site and age. Relationships between biomass and light interception and plant area index are investigated and show some merit. Nutrient concentrations were used with the above-ground biomass data to estimate quantities of nutrients held in the various biomass components in each of the stands. Nutrient distributions in the above-ground biomass (AGB) were examined and compared to other studies. Foliar phosphorus (P) and potassium (K) concentrations were shown to be sub optimal, agreeing with results and recommendations of South African fertilisation studies. Some concentration differences were observed between site and age classes for certain nutrients, although these differences may have been due to seasonal effects. Biomass and nutrient quantities were adjusted to yield a wood production of 100 t ha^{-1} and compared with adjusted calculations for similar studies on other plantation crops. Total nutrients contained in the AGB of the adjusted calculations were 540.8 kg ha^{-1} nitrogen (N), 20.4 kg ha^{-1} P, 200.6 kg ha^{-1} K, 241 kg ha^{-1} calcium (Ca), 55.7 kg ha^{-1} magnesium (Mg), with a half to two thirds of the nutrients held in the stem and bark alone. Nutrients losses vary with harvesting intensity as bark and branches may be harvested with the stem wood. Levels of nutrient removal with harvesting intensity are discussed with reference to estimated losses and gains from natural processes and management practices. An incomplete nutrient budget calculation indicated that P, K, Ca and Mg might potentially be removed in quantities greater than replaced by natural processes under stem and bark harvesting. The budget calculations lack processes such as leaching and N-fixation. It is highly probable that these processes, once quantified, may yield more negative budget results, especially for the base cations K, Ca and Mg.

Keywords: above-ground biomass, *Acacia mearnsii*, allometry, biomass, black wattle, LAI, leaf area index, nutrient budget, nutrient concentrations, PAI, plant area index, sustainability

DEDICATION

To my wife and children for giving...

Every way of a man is right in his own eyes, but the LORD weighs the hearts.

Proverbs 21:2

PREFACE

DECLARATION

The experimental work described in this dissertation was carried out (under the supervision of Professor Norman Pammenter) of the School of Life and Environmental Sciences, University of KwaZulu-Natal, with the assistance of Institute for Commercial Forestry Research (ICFR) from January 2003 to December 2004.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

Steven B. Dovey

Pietermaritzburg.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

LIST OF ABBREVIATIONS

(3PG) Physiological Principles in Predicting Growth

(AGB) Above-Ground Biomass

(ANOVA) Analysis Of Variance

(BA) Basal Area

(Bk) Branch bark fraction

(dbh) Diameter at breast height

(GPP) Gross primary production

(h) Tree height

(iPAR) intercepted Plant Available Radiation

(k) Light extinction coefficient

(LAI) Leaf Area Index

(MAI) mean annual increment

(MAP) Mean Annual Precipitation

(MAT) Mean Annual Temperature

(NDVI) Normalized Difference Vegetation Index

(NPP) Net primary production

(PAI) Plant Area Index

(PAR) Plant Available Radiation

(PCA) Plant Canopy Analyser

(SAWGU) South African Wattle Growers Union

(SeeleMtH) Seele and Mountain Home

(SI) Site Index

(SLA) Specific Leaf Area

(V) Individual tree utilisable volume

(Vol) Volume of all utilisable timber per hectare

(VPD) Vapour Pressure Deficit

(Ws) Sum of stem, branch and bark mass

(WUE) Water use efficiency

(WUE$_r$) Rainfall water use efficiency as stem mass production per unit rainfall (t ha^{-1} m^{-1})

CHAPTER 1: GENERAL INTRODUCTION

1.1 General introduction

Acacia mearnsii (black wattle) (Sherry, 1971) is harvested for both its timber and bark with branches sometimes being collected for fuel wood. Estimating the quantities of these products and the nutrients held in them is of great value. Allometric relationships are used to predict these complex tree attributes from easily measured attributes such as diameter at breast height or tree height (Medhurst *et al.*, 1999). Allometry and biomass information have many uses other than predicting forest resources, such as the parameterisation of process based growth models and forest water use models. Biomass information in conjunction with remote measurements (satellite or solar radiation) may also be used to generate and test alternate methods of biomass estimation. Nutrient removal can be estimated as the product of nutrient concentration and the estimated biomass of the harvested stand components.

Nutrient removal during harvesting or utilisation of harvesting residue is an important consideration in a sustainable forest management regime. Various levels of harvesting intensities (stem-only, stem and bark, branch harvesting) can be used to assess the impact of different harvesting regimes in relation to potential nutrient supply on nutrient pool sizes of a particular site (Ranger *et al.*, 1995; Moller, 2000). The nutrient pools include the forest biomass, the forest floor (litter and harvest residues) and the soil pool. The most appropriate way to calculate the approximate nutrient loss from a system is to draw up an input-output budget. In most intensively managed agricultural / forestry systems, a net loss of nutrients takes place, which is strongly affected by the management regime. Exceptions occur where symbiotic nitrogen-fixation or atmospheric deposition contributes large quantities of nutrient inputs. If a net loss occurs, the loss needs to be quantified and augmented by fertilisation, nitrogen-fixation or addition of residues to ensure sustained productivity. Forestry management regimes need to consider the effect of current practices on future growth and productivity, the environment and economical viability, and to replace nutrient losses appropriately.

Allometric relationships predicting biomass and associated nutrient contents are considered important tools in estimating the supply of forest products to consumers and the effects of harvesting practices on nutritional sustainability. Limited allometry, biomass, nutrition and sustainability work in black wattle has resulted in little understanding of these issues in South African black wattle forestry. Allometric equations generated over a broad plantation age and site range will help understand changes in these relationships and tree attributes as affected by

site factors. Remote measurements need to be tested to ascertain their predictive ability in relation to plantation biomass or any stand attribute at a larger scale.

1.2   The Structure of the Thesis

The first chapter of this thesis introduces the reasons for undertaking this study by looking at allometry, biomass and nutritional aspects of *A. mearnsii*. This helps in understanding why it is necessary to quantify the allometry and biomass of *A. mearnsii* at a stand-level. It also explains why it is necessary to assess nutrient contents and develop estimates of nutrient losses through various harvesting practices. Chapter two describes the methodology used in this study, the sampling, lab analysis and data analysis, including a description of the study areas. Chapter three presents and discusses results of the allometry and biomass determinations with alternative light-based estimates of stand attributes. Chapter four presents and discusses nutrient concentrations and distributions found in this study, where harvesting practices and nutrient removal, with a simple nutrient budgeting, are used to assist in the interpretation of the results. Chapter five deals with conclusions and recommendations from this study.

1.3   Literature Review

1.3.1   Introduction

Literature on allometry, biomass and nutritional sustainability of plantation-grown *A. mearnsii* is reviewed, particularly considering the effects of site quality, soil fertility, soil water availability, rotation age and stand density. Methods for developing allometric relationships and estimating plantation biomass are described in this review. Growth and physical characteristics of *A. mearnsii* are reviewed with reference to past research. Methods for estimation of plantation biomass and nutrient contents are outlined in this chapter. The effects of site quality and management in terms of fertility, soil water availability, rotation age and stand density are discussed. Nutritional sustainability, the loss of nutrient capital or soil fertility with various harvesting intensities is described with reference to losses and gains from natural processes and management practices. Past studies are referred to with some results presented from limited black wattle work showing the distribution of biomass and nutrients between various tree components. This chapter ends with the aims and objectives of this study, with some key questions that are relevant to the study.

1.3.2   A brief review of *Acacia mearnsii*

A. mearnsii is a leguminous tree native to Australia, initially used as structural timber for fences or houses. *A. mearnsii* is also referred to as *A. mollissima auct.* (*non* Willd) and *A. decurrens* var. *mollis Lindl*. It grows in many areas of Australia ranging from the warmer southern Queensland, to the cooler Tasmania up to elevations of 1100 m. The species was introduced into Africa in the early 20th century and is now widely distributed both naturally and in plantations. This tree is an efficient nitrogen-fixer and good source of green manure, yielding up to 200 kg ha^{-1} yr^{-1} of fixed nitrogen (Sherry, 1971), and may be used to restore and regenerate soils low in nitrogen and organic carbon. Black wattle can tolerate steep slopes with shallow soils and grows well on poor acidic soils. It can also be used effectively in preventing soil erosion on susceptible sites (Dunlop and MacLennan, 2002).

Growth in South Africa

In South African commercial plantations, black wattle is grown as a drought-resistant hardwood on sites with a mean annual precipitation (MAP) of 750 to 850 mm and a mean annual temperature range (MAT) of 16°C to 20°C (Sherry, 1971; Smith *et al.*, 2002). This crop is commercially grown along the eastern escarpment between altitudes of 400 m and 1200 m in the cool mist belt region of South Africa, stretching from south eastern Mpumulanga through northern KwaZulu-Natal, and the KwaZulu-Natal midlands into southern KwaZulu-Natal (Herbert, 1993).

Establishment

Black wattle can be established using seedling transplants, direct seeding or vegetative propagation. Plantations are commercially established at 2400 trees per hectare and thinned over two successive operations to 2000 then 1500 trees when the trees are 4 m and 7 m tall, respectively (Smith and Dunlop, 2002). Trees grow rapidly, generally reaching a height of 20 m and have blackish coloured bark and feathery foliage. Height growth has been reported to reach over 10 m in three years at 2000 ma.s.l. in Kenya with a mean annual temperature range of 13 °C to 17 °C (Schönau, 1972). This tree crop is moderately frost-tolerant and exhibits vigorous growth at high elevations (above 1000 ma.s.l.) in India and East Africa.

Uses of black wattle

Originally grown as a source of tannin, black wattle is now also used for pulpwood for the production of paper, fuel wood, rayon or hardboard, poles, props, green manure and windbreaks. In South Africa the area under wattle is 132 000 ha producing approximately 1.6

million tonnes of timber, 2.0 million tonnes of fibre and 186 000 tonnes of wet (50% moisture content) bark per annum. A fraction of the timber is used in the manufacture of charcoal, and most is used for pulp production (Dunlop and MacLennan, 2002; Edwards, 2000). The wood has a calorific value (dry) of 19259 kJ kg^{-1} and ash content of about 1.5%. The timber has a high density in relation to other tree crops (approximately 600 kg m^{-3}) and yields a high-quality charcoal (Sherry, 1971; Duke, 1981; Dunlop and Hagedorn, 1998). A Zimbabwean study found that *A. mearnsii* produced 323 kg of pulp per cubic m of wood compared with 224 kg per cubic m for *Eucalyptus grandis* (Muneri, 1997). The ability to produce a higher pulp yield may result in this species being grown more extensively in the future.

South African black wattle research

South African research efforts have been at the forefront of black wattle research for many years, and have been undertaken with comprehensive empirical understanding, but often not exploring the physiological processes underlying the observed responses. Past studies focussed on issues such as tree improvement, fertilisation, vegetation management, silviculture, disease and pests, tannin extraction, timber qualities and soil hydrological impacts. The tree improvement work has concentrated on bark and tannin yields, but now focuses on fibre quantity and quality with a limited understanding of other tree processes such as tree dry mass partitioning and site sustainability (Dunlop and MacLennan, 2002). Little allometry and biomass distribution work has been done on black wattle and even less is known with regards to nutrient contents of the various biomass components.

1.3.3 Allometry and biomass

Relationships between stem, bark, branch and leaf components can be described with allometric relationships. As allometric relationships are empirical, describing the relative growth of a plant part in relation to the growth of another plant part (Medhurst *et al.*, 1999), a single attribute of a tree component may be used to predict biomass or attributes of other tree components. Such relationships may be compared spatially, temporally and between different species, from which simple or complex relationships for predicting the allocation or partitioning of growth resources between the plant parts may be developed. Allocation is defined by Bartelink (1998) as the dynamic apportionment of assimilates among plant parts. Some authors use the terms allocation and partitioning interchangeably. Distribution describes a static tree or stand state in terms of the dry biomass of tree components and the relative mass relationships between them. Biomass accumulation and allocation patterns in stands are affected by species, stocking, rotation length and variations in thinning operations (Van Laar, 1982). Site location, soil water, nutrient

availability and silvicultural practices may also have an effect on carbon allocation (Naidu *et al.*, 1998). The distribution of biomass between the tree components changes with age as the storage and structural organs become larger. Leaf biomass, relative to total biomass, for example, decreases with age, contributing the largest proportion of the total biomass in a young stand, and the lowest contribution in older stands (Cromer *et al.*, 1985).

1.3.4   Forest resources

The increased pressure on forest resources over the past few decades has resulted in an increased use of plantation forestry to meet demands for renewable energy (charcoal), pulpwood fibre, sawlogs, mining timber and poles. Merchandisable bole wood (debarked wood within a specified size range), branches, bark, and sometimes the leaves, are used commercially or by communities living in and around the plantations. Obtaining estimates of the mass or dimensional attributes of these tree components at the stand level is essential in estimating the quantity of resources in forest plantations, and adding to the understanding of plantation growth. The rate and volume of carbon dioxide absorption and storage in forest products is very important in estimating the extent to which trees are countering the global greenhouse effect (Thompson and Matthews, 1989).

Over the past few decades the focus on biomass estimation in forest stands, and variables controlling the allocation, partitioning and distribution of carbon to various tree and forest components has increased (van Laar, 1982; Snowdon, 1985; Parresol, 1999; Moller, 2000;). Biomass predictions, estimates of plantation yield and residue loads are essential in assisting management decisions with respect to site productivity estimations and the effect of harvesting practices on the sustainability of a site. The prediction of plantation residue loads after harvesting is a useful output of biomass estimations, as it can be added to estimates of plantation fuel loads in order to determine the risk of fire after harvesting (Catchpole and Wheeler, 1992), or to model fire behaviour under controlled burning conditions. The ability of a plantation to support the firewood fuel needs of the surrounding local population may be estimated if the quantity of branches and non-utilisable trees remaining on a site after harvest is known (Allen *et al.*, 1988; Chavangi *et al.*, 1992).

1.3.5   Leaf area index and light interception

Forest biomass growth may be linearly related to intercepted plant available radiation (PAR), and light interception by forest canopies is largely dependent on leaf area index (LAI), defined

as the single-sided leaf area per unit ground area (Pierce and Running, 1988; Gower and Norman, 1991; Deblonde *et al.*, 1994). Linder (1985) shows how above-ground biomass (AGB) production is related to intercepted PAR (iPAR) by demonstrating how an increase in leaf area results in an increase in light interception and a subsequent increase in growth. Leaf area is directly related to net primary production (NPP) and an increase in LAI can therefore be directly translated into increased yield (Cromer *et al.*, 1993). Leaf area index, an important component of forest growth process-based models, is used to calculate net primary production, rainfall interception, transpiration and ecosystem processes such as CO_2 flux and dry deposition (Chason *et al.*, 1991; McMurtrie *et al.*, 1994; Battaglia *et al.*, 1998). Leaf area index may be used as an integrated measure of site, soil and climatic factors, allowing for the detection of spatial and temporal changes in forest ecosystems as attributed to soil fertility, water balance and long-term stress (Battaglia *et al.*, 1998; Waring and Running, 1998; Nackaerts *et al.*, 2000). Leaf area index alone may also be used to assess differences between experimental treatments, the impact of site disturbance, drought effects and disease and pest defoliation (Cherry *et al.*, 1998; Waring *et al.*, 1998).

Biomass sampling may also be used for the purpose of testing, i.e. "ground-truthing" and calibrating indirect or remotely sensed measures of plantation structure. The measurement of plant area index using an optical gap-fraction based instrument, such as the LICOR LAI-2000, may be calibrated with data collected from such a study (Cherry *et al.*, 1998). Remote sensing via satellite imagery or low flying aircraft can be used to gather data that may be correlated with some measure of forest biomass or LAI. A relationship between the remotely gathered spatial imagery and the biomass of a forest stand component may be used to make further spatial predictions of other biomass components.

1.3.6 Process-based growth models

Models may be developed from empirically-derived allometric relationships to predict physiological processes and ultimately tree growth. These models may be used to estimate timber growth, above-ground primary production, tree architecture, carbon cycling and total standing biomass (Bond-Lamberty *et al.*, 2002). The models, for example, simulate biological processes that determine the growth of a forest as affected by climatic and edaphic factors. They are primarily used to predict the effects of environmental and management effects on forest growth (Cromer *et al.*, 1995). Levels of efficiency in terms of growth output per unit of water, nutrients, light and management costs may be estimated and compared across sites. Studying the effects of site quality, rotation age, stocking and silvicultural practices may be useful in

developing an understanding of the influence these factors have on growth and biomass distribution.

Parameters required for these process-based models may be estimated with the data and information from simple biomass studies. A process based model such as 3-PG (Physiological Principles in Predicting Growth), can be parameterised using empirical relationships from biomass estimation studies and long-term measurements in forest plantations (Landsberg and Waring, 1997). This model calculates gross primary production (GPP) from absorbed utilisable iPAR and canopy quantum efficiency (Landsberg and Waring, 1997). Dimensionless modifiers, reflecting the environmental constraints determining stomatal closure and stand age, are used to reduce absorbed PAR. Net primary production is estimated from a constant ratio of NPP to GPP and is allocated as carbon to various plant parts by using allometric ratios. Rainfall interception, transpiration, water use and many other forest growth parameters are also calculated by the model (McMurtrie *et al.*, 1994; Battaglia *et al.*, 1998;). A simple validation of the 3-PG model was done for *A. mearnsii* in South Africa for three sites (Dicks, 2001). Predictions by the model in this study were adequate, although needed improvement by the inclusion of more sites and age groups, as many of the parameters were either set intuitively or to a default value.

1.3.7 Nutrients held in the biomass

Estimations of yield of all the utilisable components and the impact on their removal of nutrients from the areas where they are grown, is very important in managing issues around site sustainability. In order to assess the nutrients removed from a site, the total AGB has to be estimated with the nutrient concentrations for each tree component. The mass of timber, bark and branches may be predicted using allometric relationships, and their nutrient contents summed for each harvested tree product. Once the nutrient removals have been estimated, the impact on the site can be assessed in terms of the supply potential of the site, in addition to considering any additional inputs such as atmospheric deposition and N-fixation, where necessary. The supply potential involves the fluxes of available nutrients within and between various nutrient pools and the additions and losses of nutrients to the forest system. The cycling, release and immobilisation of nutrients between and within these pools are termed the nutrient fluxes. The magnitude of these fluxes results in temporally divided pools of nutrients that constitute availability (or lack thereof) to the trees over the short to long term. Nutrient removals by harvesting must be considered in relation to forest system losses and gains of nutrients by other processes. Simple nutrient budgets or balances may be constructed that

compare the inputs and removals from the forest system over a rotation period. A negative budget will imply a net loss of nutrients from the system and give an indication of the risk of nutrient depletion and growth decline if expressed in relation to the system supply potential (du Toit and Scholes, 2002). The system supply potential involves the rate at which nutrients become available to the trees through natural processes, such as weathering and atmospheric deposition. However, a nutrient will become limiting only if the forest system becomes incapable of supplying the nutrient demand. The supply potential of a forest system depends on the sizes of the nutrient pools, the availability of the nutrients in the pools, and the rate at which the nutrients become available. The magnitude of the depletion and a knowledge of the quantity of nutrients stored in the soil can be used to ultimately indicate risk of nutrient depletion and growth decline (du Toit and Scholes, 2002).

1.3.8   Estimating the plantation biomass and nutrients

In order to estimate stand biomass and associated nutrient concentrations or contents, an adequate sampling procedure needs to be selected. The basic steps of the entire procedure are the selection of a sample area and sample trees, the destructive harvesting and weighing of the sample tree masses and the individual components thereof, formulation of relationships between tree components, and the scaling up from the single tree level to the stand level. Sampling involves the destructive and orderly removal of individually selected trees for measuring purposes. The procedure for selecting sample trees and the number of trees selected is dependent on the final objectives, financial costs involved in the exercise, as well as available time. Depending on the proposed outcome of the sampling exercise, various components may be measured, weighed, dried, reweighed and analysed. The wet mass of the tree components that are too large to oven dry are converted to dry mass by recording the in-field wet mass of the component, and then taking a sub-sample which is oven dried to determine the wet : dry mass ratio. This ratio is used to convert the in-field wet mass to a dry mass. Nutrient analyses may also be conducted on sub-samples of the tree components to determine nutrient concentrations (Newbould, 1967).

The sample area

Harvesting an entire sample area of a stand will produce the most accurate estimates of the population, provided that the area is representative of the population and the conversions from wet mass to dry mass are done correctly (Hitchcock and McDonnell, 1995). As this is often not practical, being costly and time consuming, smaller sample sets have to be taken, involving the selection of single sample trees.

Sample tree selection

The trees that are sampled need to be selected to represent the entire stand. Sample tree selection often begins with the measurement of tree diameter at breast height (dbh) and tree heights (h) over a set sampling area. Data collected from this sampling area are used to convert the individual sample tree attributes to an attribute value per unit area. A distribution of the dbh, height or a function such as dbh^2 x h is then generated from these data. The distribution may be split into size classes with sample trees selected from each size class.

Trees may be selected randomly from each class or at the centre point of each class. Choosing the number of sample trees is a compromise between the cost of sampling, time taken for sampling and data processing, and obtaining lowest possible sampling error. A stratified selection may be used in some cases where more trees are taken from the classes representing the largest portion of trees and less from the classes with the lowest number of trees from the sample population. The number of trees assigned to each class is dependent on the range of the distribution and the type of distribution found. Large trees may necessitate the use of sub-sampling, involving taking representative samples from the sample trees (Newbould, 1967).

Scaling up to the stand level

Converting fresh mass to dry mass, individual tree sampling units to the stand attribute and total biomass to utilisable biomass is the next step in achieving the set objectives. Allometric relationships used for these conversions usually need to be developed for each sampling event as they may not be applicable between different ages or sites. Once allometric relationships have been established, estimations of the biomasses of the plantation components can be done. Scaling up entails applying derived allometric equations to all trees in a sample stand to produce stand level attributes (Cromer and Williams, 1982). Six methods have been listed by Art and Marks (1971) to convert sample tree attributes with field data to a whole stand attribute. The technique used is dependent on the proposed outcome, although regression methods are the most widely used. Regression techniques that describe the allometric relationships between the simple dimensional measures of the sample trees and their weight or areas may be generated. In order to obtain good statistically sound relationships, it may be necessary to transform the dependent and independent variables (Snowdon, 1992).

A ratio method is an alternative method where the ratios between various tree components are used to predict the mass of a component on other trees, i.e. the ratio between basal area (BA)

and stem mass of a sample tree is used with the BA of other trees to predict their stem mass (Art and Marks, 1971). Total BA of the stand is multiplied by these ratios to achieve stand level mass values of the biomass component (Cromer and Williams, 1982). In each case, final results of the biomass estimation are expressed per unit area, e.g. dry mass in tons per hectare. The ratio method may be used to convert nutrient concentrations in sample trees to whole stand nutrient contents.

1.3.9 Allometry and biomass of plantations

Age, site and silvicultural effects

Total biomass generally increases with improved silviculture, site quality and stand age. The general distribution of tree component masses in plantations can be summarised as 55-65% bole, 15-25% crown (leaves and branches) and 17-23% roots with moisture contents of around 50% of the fresh mass (Hitchcock and McDonnell, 1995). Site quality, stocking and silvicultural treatment have been attributed to differences in the distribution of biomass between the stem, branches and leaves. As stocking increases, final total biomass increases up to a maximum level. In *Pinus radiata* (Birk, 1992) decreased stocking has been found to increase the proportion of biomass in branches, while improved site quality and silviculture increased the proportion of foliage biomass. A similar decrease in branch biomass at higher planting densities was found in a *P. radiata* study (Madgwick *et al.*, 1977). This study showed an increase in branch weight with age and an increase in foliage biomass with stocking. Bradstock (1981) and Judd *et al.* (1996) found that foliage mass increased to a maximum with age and then declined. Bark and branches increased in mass with increased age with branch mass stabilising at a maximum level.

Fertility effects

When comparing high and low fertility sites in British Columbia, Compton and Cole (1991) found that the more fertile sites resulted in a greater nutrient accumulation in the trees only as a result of a higher biomass, i.e. there was no significant change in concentration. These authors also showed a resultant growth reduction in the subsequent rotation. They pointed out how poor sites with a low nutrient storage capacity are in greater danger of being depleted as a similar quantity of nutrients were removed from the soil per unit biomass as with fertile sites. High risk of nutrient depletion on these poor sites was mostly due to nutrients being tied up in the biomass and therefore unavailable for plant growth requirements.

Growth manipulation through management practices

Nitrogen fertiliser treatments in eucalypts and pines have been shown to increase the crown allocation, with an increase in leaf mass related to an increase in production (Schönau and Boden, 1982; Negi and Sharma, 1985; Misra *et al.*, 1998). Fertiliser application in pines was found to produce less below-ground biomass and more AGB (Misra *et al.*, 1998; Xu *et al.*, 2002). Application of fertiliser has also been shown to increase the total AGB in Australian experiments, especially with respect to leaf area. Seedling experiments have shown similar results with the application of fertiliser resulting in an increase in relative leaf mass and a decrease in relative root mass, thereby increasing the photosynthetic capacity of the plant (Cromer *et al.*, 1993).

Management practices that increase production will often also result in greater nutrient depletion (Ranger and Turpault, 1999; Santana *et al.*, 2000). Birk (1993) demonstrated that the addition of fertiliser increases nutrient export, as a result of both increased biomass production and higher nutrient concentrations. This author shows how nutrients accumulate in relation to biomass accumulation independent of site fertility. Experiments on a few *Eucalyptus* species in India by Hunter (2001) demonstrate how nutrient content increased with increased dry weight, but nutrient concentrations decrease with added fertiliser and irrigation. Although Cromer *et al.* (1993) found no significant improvement in growth with irrigation, Hunter (2001) showed that an irrigation growth response can result in greater nutrient export due to a greater biomass production. This author goes on to show that irrigation also increases total dry weight with more above-ground allocation of dry mass to stems and canopy branch portions, relative to below-ground components.

These studies show that a manipulation of site resources can result in a change in total biomass and a switch in biomass and nutrient allocation patterns in the tree crop. An increase in plant available resources may result in a biomass increase, with greater allocation to canopy and structural components and less to below-ground components. An increase in harvestable biomass will also result in an increase in the mass of nutrients removed from a site.

1.3.10 Nutrient concentrations and distributions in plantations

Concentrations of nutrients

Predicting tree and stand biomass in conjunction with nutrient concentrations is important in deriving estimates of the nutrients held in the living tree biomass pools. Knowing the quantities of nutrient held in the utilisable plantation products is essential in creating estimates of the

quantities of the various nutrients being removed through harvesting practices. A large amount of work has been done on the biomass and nutrient distributions of many commercial tree species (Hitchcock and McDonnell, 1995). The total mass of nutrients contained in the biomass can be calculated by multiplying the concentrations of the nutrients by the total biomass. Concentrations of particular nutrients in the various plant components are dependent on the component and nutrient in question; each component must therefore be analysed separately.

Concentrations differ in different tree tissues, being generally lowest in the stem wood and highest in the bark and foliage. The general order of concentrations from lowest to highest is usually stem, branches, bark then leaves, with some exceptions for those that accumulate in various plant organs (Tandon *et al.,* 1988). Foliar nutrient concentrations also vary with leaf age and position in the canopy, with the extent of this variation being element specific (Grove *et al.,* 1996). *Eucalyptus* N, P, K and Mg are highest in the leaves, while Ca is the highest in the bark (Laclau *et al.,* 2000, Judd *et al.,* 1996). A *Eucalyptus* clone study in the Congo (Laclau *et al.,* 2000) showed P, Ca and Mg concentrations to be higher in the live branches than in the stem. A South African *E. grandis* study by du Toit (2003) showed N, P, and K to increase in concentration from the stem to the branches, bark and foliage respectively. Calcium and Mg followed the same trend, except that the bark concentrations were higher than the foliar concentrations.

Nutrient concentration may also differ with site quality, season and stand age (Binkley, 1986). Jorgenson *et al.* (1975) showed that maximum nutrient accumulation coincided with canopy closure in *Pinus taeda*. The nutrient concentration also decreased with age in the stems and branches of *Pinus radiata,* except for Mn and Ca (Switzer and Nelson, 1972). In a Congo *Eucalyptus* clone study, a change in concentration of all elements, especially K in the stem wood, occurred with age. All nutrient concentrations tended to decrease in the leaves, except for N. A general increase in P and a decrease in K and Mg were found in the rest of the tree, with N and Ca remaining relatively stable with age (Laclau *et al.,* 2000).

Nutrient distribution

The proportions of each nutrient held in each tree component with respect to the total mass held in the AGB varies between species, with soil supply, and with tree size or age (Jorgenson *et al.,* 1975; Grove *et al.,* 1996). This is due to an increase in relative masses of tree components with age. Initially more nutrients are held in the foliage than in any other tree component. As a stand grows, the proportion of stem and bark increases, resulting in a greater proportion of nutrients

being held in these components. In mature trees, the foliage comprises the smallest portion of the AGB (2% - 10%), but contains a large relative portion of both N and P (20% - 45%), although these values are species dependent (Grove *et al.,* 1996). The bark, stem and branches are major stores of nutrients, while the foliage is a sink and a major source of nutrients for new growth. A *E. grandis* study by du Toit (2003) revealed decreasing amounts of N and P in the stem, foliage, branches and bark respectively. Potassium followed the same pattern, but more was held in the branches than in the foliage. Half of the P and a third of the N and K are held in the stem wood alone. Calcium and Mg had the greatest fractions in the branches, followed by the bark, stem and foliage respectively. These fractional quantities of nutrients held in the various biomass components need to be considered in assessing the removal of nutrients through various harvesting intensities.

1.3.11 Sustainability in forestry management

Sustainable forest management is the economically viable management of forests without having a present or future negative impact on the ecological or social environment (Higman *et al.,* 2000). In the South African context, five sustainability issues are outlined by Olbrich *et al.* (1997), these being water, site fertility, labour, environmental and national and international market forces. True sustainability encompasses a balance between all of these factors together with a detailed understanding and quantification of each factor and how they interact (Nambiar, 1996).

The ecological sustainability of a plantation is related to the maintenance of the site's capacity to supply all of the necessary resources for photosynthesis and growth. Incoming photosynthetically active radiation, atmospheric carbon dioxide, soil water and nutrients are the resources that the trees draw on. Soil water availability to some extent and soil fertility are the only resources that can be manipulated by site management operations (du Toit and Scholes, 2002). The nutrients held in individual tree components and entire plantations have been used to an increasing extent for predicting of the impact of forestry on ecological and economic sustainability (Madgwick *et al.,* 1977; Santana *et al.,* 2000). High nutrient losses in short rotation, fast-growing plantations raise much concern about long-term site productivity and sustainability.

Soil fertility

Many South African forest soils are low in fertility and occur on ancient weathering surfaces in relatively high rainfall areas, especially the sandstone, quartzite and acid crystalline rock-

derived soils, with P and K as the key limiting nutrients (Olbrich *et al.,* 1997). Soil fertility as defined by Ranger and Turpault (1999), is the sum of physical, chemical and biological soil factors characterising the capacity for biomass production. Fertility can be separated into two temporal components; the short-term and the medium-to long-term. The short-term, characterised by soil analysis, is related to the present pools of nutrients available to the plants. Medium-to long-term fertility is represented by fluxes of elements that are held in the soil and slowly made available to plants, as well as additions to the soil through atmospheric deposition and mineral weathering (Ranger and Turpault, 1999). Plantation soils lose nutrients through the export of wood and bark from a site, burning of residues, soil erosion and leaching (Spangenberg *et al.,* 1996; du Toit and Scholes, 2002). These losses are often not compensated for by the inputs to the system pools. Maintaining soil fertility can, in theory, be done by using fertilisers, but may not be desirable due to economic constraints or by the risk of the negative environmental impacts of fertiliser addition (Nambiar, 1996).

Increasing demand for tree products is resulting in an increase in the plantation areas and a shortening of rotation lengths, with a consequent loss of soil fertility. Shortening a rotation can increase the rate of nutrient export and result in increased nutrient depletion rates, as the proportion of nutrient rich sapwood is higher in younger trees than in older trees (Richards and Charley, 1983). Renewable energy production demands have often forced the use of whole tree harvesting with the non-stem tree portions used for fuel wood. Stem-only harvesting has been shown in numerous cases, to be the most effective method of site conservation, having the lowest potential nutrient removal. Harvesting studies looking at varying intensities and different rotational ages show potentially more rapid nutrient depletion with shorter rotation lengths and increased harvesting intensity (Moller, 2000; Ranger *et al.,* 1995). On sites where whole tree harvesting is the only option, it has been recommended to leave the trees to dry out, allowing the nutrient-rich leaves and twigs to fall to the ground before tree removal (Moller, 2000).

Removal of more biomass from plantations, especially by whole tree harvesting, may result in substantial system nutrient and soil carbon losses from the system as shown by Parrotta (1999) in *Eucalyptus* plantations. Losses to soil carbon pools are especially important, as this is difficult to replace (Noble *et al.,* 1991). The soil carbon pool is the principle source and sink of plant nutrients and holds the major portions of soil nutrients, especially N (Fisher and Binkley, 2000). The best ways to reduce these losses include altering the rate of removal, changing the components that are removed and by selecting low nutrient removing species (Kumar *et al.,*

1998; Moller, 2000). Optimising silvicultural practices specific to various site class ranges will ensure optimal wood production and environmental protection (Ranger and Turpault, 1999).

Understanding the potential long-term impacts of nutrient loss as a result of various management practices or harvesting intensities, in conjunction with site factors, may help managers to select the most ecologically and economically sound management practices, while understanding the potential long-term impacts (Santana *et al.,* 2000). Creating a budget-type balance of nutrients entering and leaving a site, is essential in determining the impact of commercial operations on the nutritional sustainability of the site. The subsequent development of nutrient budgets to examine and predict the changes in biomass and hence nutrient content across sites, rotation ages and stand densities is highly desirable for the comparison of nutrient removal between different commercial operations.

1.3.12 Nutrient budgeting

Nutrient budgeting involves the quantification of nutrients entering and leaving the forest nutrient cycle by drawing up a comparative input-output budget (Moller, 2000). The nutrient budget attempts to quantify the nutrient cycle and encompasses the inputs, movement within the cycle and outputs from the cycle, with inputs usually nearly balancing outputs in a natural ecosystem. The rates at which nutrients enter and exit systems are commonly presented on a per year basis in order to compare systems of different ages and different management practices.

Additions of nutrients to the system

Nutrients are added to the system by atmospheric deposition, mineral weathering, nitrogen fixation, and anthropogenic inputs. Lateral fluxes are of lesser importance and include processes such as movement of fauna, colluvial movement and lateral drainage. Nitrogen enters the system via wet and dry atmospheric deposition and by soil microbial N fixation in the forms of NO_3, NO_2, and NH_3. Although geological weathering is not an important short-term source of minerals, many nutrients such as K, Ca, Mg and especially P, become available to the trees through mineral weathering (Jorgenson *et al.,* 1975) whereas addition of N by this process is often negligible. Deposition is also an important source of P, Ca, Mg, and K (Binkley, 1986; Morris, 1992; Ranger and Turpault, 1999).

Fertilisation, an important N and P source, is an anthropogenic input, although Binkley (1986), shows, on average, only 20% of added nutrients to be taken up by the trees. Much of the fertiliser will become immobilized by adsorption through geochemical processes and microbes,

and only become available in the long-term. Immobilisation of nutrients in the organic soil layer may also result in the unavailability of these nutrients for a time (Olbrich *et al.*, 1997). The cost of fertilisers and the risk of polluting rivers and ground water are important considerations if this method of nutrient replacement is to be used. The supply and rate at which nutrients become available is important for the ability of the soil to supply nutrients for tree growth. For example, small nutrient pools may not be a limitation to growth rate of the current tree crop, provided that sufficient quantities of nutrients become available to supply tree demands.

Losses of nutrients from the system

Losses occur through leaching of nutrients out of the rooting zone, soil erosion, burning of harvesting residues or wildfires, and biomass harvesting (Binkley, 1986; Ranger and Turpault, 1999; du Toit and Scholes, 2002). Losses also occur naturally, varying from site to site, as a result of overland flow, subsurface flow and groundwater movement (Olbrich *et al.*, 1997).

Fire and biomass removal are the two most important ways by which nutrients can be lost, with the latter often being the largest removal mechanism (Binkley, 1986). Black wattle sites may be prone to high levels of losses due to the intensity at which they are harvested and as a result of burning being used for residue management. This burning may result in large nutrient losses through exports in smoke, volatilisation and oxidation. Oxidation is the major loss mechanism, while lesser quantities of N and S may volatilise (Fisher and Binkley, 2000). Smoke contains large amounts of ash, which contains all nutrients (Binkley, 1986). Loss of ash by water and wind erosion can also add to the nutrients lost. However, Beard (1961) points out that a decline in the growth of subsequent rotations of *A. mearnsii* after burning could be detected only if ash is lost through erosion. Losses are lower with low intensity fires; N losses rise quickly with temperature increases above 200°C (Binkley, 1986). Temporally immobile nutrient stores in the organic matter may also be lost through fire either by volatilisation or subsequent leaching (Olbrich *et al.*, 1997). Black wattle growers have moved away from burning of residues (Norris *et al.*, 1995), and the retention of plantation residue has resulted in silvicultural operations being more difficult, especially with the preparation of planting position, planting and fire risk management (Little *et al.*, 1996).

Leaching losses in the rotational period are dependent on soil water movement and soil water balance (Ranger and Turpault, 1999). These losses are most important for N, K, Ca, and Mg. Processes that increase water percolation or the quantity of mobile anions in the soil may lead to increased base cation losses through leaching. Nitrate ions may increase in soil through

increased mineralization or N fixation, followed by nitrification in both cases (Fisher and Binkley, 2000). Nitrogen fixation by black wattle may also accelerate soil acidification and base cation leaching if the trees do not take up the N. Atmospheric deposition will supply NO_3^- and SO_4^{-2}, which could increase leaching losses (du Toit, 2002b). Losses are accelerated in the interim period between harvesting and re-establishment by the increase in decomposition, leaching and soil erosion rates (Binkley, 1986). A decrease in water uptake increases soil temperatures with greater water movement through the soil. This adds to the losses, which can last up to five years after re-establishment (Worrell and Hampson, 1997). These losses need to be considered when estimating the losses associated with harvesting.

Studies of whole tree harvesting effects on site soil nutrient capital show variable results; Mroz *et al.* (1985) found losses in soil N, Ca, Mg and K, while P was unaffected. The loss of N in the upper soil layers may have been the result of soil disturbance through harvesting. Greater nutrient loss has been reported from higher quality sites through the extraction of a larger biomass (Birk, 1993). The impact of harvesting removals may be more severe for sites that are climatically more favourable than for poor sites, especially for sites with a low nutrient capital. A reduction in productivity as a result of biomass and hence nutrient removal is dependent on the site in question, the frequency of biomass removal and the quantity of biomass removed (Ranger *et al.*, 1995; Moller, 2000). Sites with low proportions of soil nutrients relative to the biomass such as shallow sandy soils may be more rapidly depleted (Compton and Cole, 1991).

Analyses balancing nutrient inputs and outputs in southern African plantations in general have shown mixed results. Morris (1992) found that the export of nutrients in *P. patula* logs should be balanced by all nutrient inputs into the system, while Scholes *et al.* (1995) concluded that there was a high potential for nutrient depletion, particularly of magnesium. Each forest ecosystem must be considered individually in drawing up a nutrient budget, as each site has a unique set of species, site factors and harvesting practices. In most cases where nutrient budgets have been completed, N, P and K have been found to have the greatest risk of depletion (Norton and Young, 1976; du Toit and Scholes, 2002).

1.3.13 Past biomass and nutrient studies on *A. mearnsii*

Although a vast amount of work has been done on allometry and biomass for many species, including a few commercial tropical plantation species, only a limited number of studies provide nutritional information (Santana *et al.*, 2000). Allometric relationships from studies on species and sites cannot be used on *A. mearnsii* in South Africa, as these relationships may not

be transferable between species, sites or growing conditions (Waring and Schlesinger, 1985). Complete studies of biomass production and allometry of many Australian acacia species are also limited. However, work has been done on *A. mearnsii* provenances in Brazil (Pereira *et al.*, 1997; Caldeira *et al.*, 1999; Caldeira *et al.*, 2000a; Caldeira *et al.*, 2000b; Pereira *et al.*, 2000; Caldeira *et al.*, 2001;), India (Tandon *et al.*, 1988) and South Africa (Dicks, 2001; Williams, 1927). The studies in Brazil describe dry masses of the various tree components, bole, bark, dead and live branches, and foliage. These studies together with those in India include information on the nutrient content of the total AGB and individual tree components. However, the work in India does not include dead branches, and foliage was sampled together with small twigs.

South African biomass and leaf area estimation studies were carried out for firewood fuel estimation (Garbutt *et al.*, 1978), pest and disease assessment (Veldtman *et al.*, 1995) and 3-PG model parameterisation (Dicks, 2001). Dicks (2001) performed a preliminary estimation of 3-PG parameters using a small sample data set covering three sites. Veldtman *et al.* (1995) attempted to estimate leaf areas using non-destructive techniques, and Garbutt (1978) used a biomass study to estimate the firewood fuel yields of a wattle plantation. Another biomass estimation study in South Africa used 10.5-year-old trees on poor and "average" quality sites, with foliage including small twigs (Schönau, 1978). One important factor that was excluded in most of these studies was LAI, only attempted by Veldtman *et al.* (1995), with limited success.

Although little has been published on the analysis of nutrient concentrations and contents, the earliest works found on South African black wattle were completed in 1927 and 1937 (Williams, 1927; Steyn, 1937). Williams (1927) analysed concentrations of iron (Fe), Ca, Mg, K and P in each of the various plant components and calculated the potential removal of these elements by bark and wood harvesting. His work focussed on the bark yield and quality for an eight-year-old stand, with nutrient analyses to estimate potential rates of soil nutrient exhaustion. The work by Steyn (1937) lists only the foliar concentrations of nutrients in wattle leaves. Advances in laboratory techniques and the effect of recent breeding studies on *A. mearnsii* may have reduced the validity of this past work. A comprehensive study in South Africa on allometry and biomass estimation with nutrient distributions sites has not yet been done.

Findings from past studies

Table 1 and Table 2 details results obtained from international and local biomass sampling exercises showing biomass of individual tree components and total aboveground nutritional content. Total harvesting removals (Table 3) were estimated for each nutrient using nutrient content (Table 2), for total AGB removal (Table 1). No further calculations were performed by these authors to estimate the quantities of nutrients removed by various harvesting practices, although all the necessary data are available. Logarithmic conversions and linear regression techniques were used to generate allometric equations, predicting each of the tree component masses. The correlation coefficients and significance levels were high in each study, although no other statistical data was shown for the derived relationships. The proportion of wood mass to total biomass is greater in older trees and on sites that are more productive, while the proportion of leaves and branches decreases in both cases. The stem wood contributed the most to total biomass with contributions decreasing in the following order; branches, leaves with twigs, and bark respectively.

Foliar element concentrations in the younger wattle trees were higher than those in the branches and bark, except for Ca, where bark concentrations in four-year-old trees exceeded those in the foliage (Tandon *et al.,* 1988). Pereira *et al.* (2000) and Tandon *et al.* (1988) demonstrated that older wattle trees have the highest concentrations of elements in the leaves, except for Ca and Mg, which are highest in the bark. The lowest concentrations of nutrients were found in the wood, although stem wood is the largest contributor to total AGB. Wood and bark combined contain the greatest proportion of the above-ground nutrient mass, comprising a total of 75% (Pereira *et al.,* 2000; Tandon *et al.,* 1989).

Nutrients contained in the AGB (Table 2) have high levels of variability between ages and locations, hence making it difficult to compare the resultant data, although the masses of nutrients held in the biomass seems to be strongly related to the mass of the biomass.

Table 1: Biomass of above-ground components of *A. mearnsii* (t ha^{-1}) at different ages and locations.

Location	Brazil (Prov 1)	Brazil (Prov 2)	Brazil (Prov 3)	India	India	SA	Brazil	India	SA Poor	SA Average
Age (years)	2.4	2.4	2.4	4.0	7.0	8.0	9.0	10.0	10.5	10.5
Total	19.4	36.1	41.1	20.5	27.1	217.1	158.5	151.4	109.9	148.2
Leaves	4.3	7.2	7.5	3.0	4.1	11.6	4.2	17.9	5.3	7.0
Live branches	3.8	7.0	8.0	5.0	7.0	24.6	11.3	33.7	16.7	20.0
Dead branches	0.1	1.0	0.5	-	-		4.0	-	5.2	6.8
Bark	2.4	4.3	4.8	2.1	2.6	19.8	14.0	14.1	11.4	15.3
Wood	8.7	16.6	20.3	10.3	12.6	161.2	125	85.7	71.3	99.1
Reference	Caldeira *et al.* (2000a)	Caldeira *et al.* (2001)	Caldeira *et al.* (2000b)	Tandon *et al.*,(1988)	Tandon *et al.*,(1988)	Williams (1927)	Pereira *et al.*,(1997)	Tandon *et al.*,(1988)	Schönau (1978)	Schönau (1978)

Prov. = provenance; SA = South Africa

Table 2: Nutrient contents of the above-ground biomass of *A. mearnsii* (kg ha⁻¹) at different ages and locations.

Location	Brazil (Prov 1)	Brazil (Prov 2)	Brazil (Prov 3)	India	India	South Africa	Brazil	India
Age (years)	2.4	2.4	2.4	4.0	7.0	8.0	9.0	10.0
Nitrogen	182.1	-	334.4	515.0	464.0	-	1509.3	912.0
Phosphorus	8.2	297.9	23.7	19.0	11.0	26.0	15.6	26.0
Potassium	104.4	191.7	259.7	420.0	388.0	354.0	200.9	496.0
Calcium	66.7	101.1	107.7	85.0	140.0	457.0	348.9	247.0
Magnesium	16.1	28.9	35.1	62.0	33.0	120.0	128.4	72.0
Sulphur	10.0	18.3	21.4	-	-	-	-	-
Reference	Caldeira *et al.* (2000a)	Caldeira *et al.* (2001)	Caldeira *et al.* (2000a)	Tandon *et al.* (1988)	Tandon *et al.* (1988)	Williams (1927)	Pereira *et al* (2000)	Tandon *et al.* (1988)

The potential removal of N, P, K, Ca, and Mg may be calculated as a sum of the nutrients contained in the harvested parts (Table 3). Pereira *et al.* (2000) and Tandon *et al.* (1988) showed large differences in potential nutrient removals, which may be attributed to higher nutrient concentrations found by the former author. Very large differences are evident between values displayed in Table 3, especially with N and Ca in the wood. These differences (underlined in Table 3) may indicate that a very large range is possible from such studies as a result of different ages, site growing conditions or silvicultural practices. They may also be due to analytical or calculation errors.

Table 3: Nutrient removals for wood, bark and branches (kg ha^{-1}) in *A. mearnsii* stands.

Component	N	P	K	Ca	Mg
9-year-old stand in Brazil (Pereira *et al.*, 2000)					
Wood	1088.7	2.5	26.3	117.5	55.0
Bark	160.8	3.4	52.3	133.8	25.3
Branch	111.7	5.1	83.6	49.6	26.0
7-year-old stand in India(Tandon *et al.*, 1988)					
Wood	171.3	6.0	60.0	17.1	25.7
Bark	106.0	0.6	91.8	251.2	12.7
Branch	107.7	2.7	148.1	37.0	10.1
8-year-old stand in South Africa (Williams, 1927)					
Wood	-	9.0	154.0	208.0	69.0
Bark	-	4.0	56.0	135.0	14.0
Branch	-	9.0	47.0	53.0	16.0

Large amounts of nutrients are removed with harvesting; extraction of stem wood, bark and branches can result in losses of over 80% of the nutrients held in the AGB. Large amounts of nutrients may potentially be removed from a black wattle site if whole tree harvesting is practiced or if firewood collection (branch harvesting) is undertaken. With current South African fertiliser recommendations of 19 - 36 kg P ha^{-1} and 0 - 29 kg K ha^{-1} as a general application at planting (du Toit, 2002a), it is clear that fertilisation alone cannot replace harvesting losses. Although P addition by fertilisation is close to the maximum lost through harvesting, P fixation and limited P uptake may result in a net loss of P from the system. Demonstrating a high nutrient depletion rate may be misleading as other natural system inputs may be amending these losses to soil nutrient stores, although a proper assessment cannot be done for the sites in Table 3 without knowing the supply potential of each site. The pressures exerted on the plantation forest ecosystems and hence the sustainability of forestry practices may be better understood through measuring the system nutrient supply capacity in conjunction with the inputs to and outputs from the forest system. If the removal of nutrients is significantly greater than a site's supplying capacity and inputs by processes such as weathering and atmospheric deposition, then the site will eventually become depleted over time.

1.3.14 Conclusion

Allometric relationships are useful in estimating unknown plantation biomass components from known components such as height or diameter. However, some of these relationships may change slightly between sites and with management practices. Knowledge of how resource manipulation changes the ratios of biomass between tree components may also be useful, and can be used in manipulating growth to optimise the quantity of utilisable tree product. Using models or alternative remote measurements to predict growth on multiple sites may allow for a more comprehensive understanding of management effects on plantation growth. Black wattle is an intensively harvested tree crop, and the potential removal of nutrients by harvesting alone, may be enough to rapidly deplete sites with a low nutrient supply and replacement potential.

A lack of information with regards to the biomass and nutrients of black wattle in South Africa has created a need for studies to assess the distribution of biomass between tree components in conjunction with nutrient analyses. The establishment of equations to predict tree biomass and nutrient content will be of great value in assessing current silvicultural and management practices in terms of the impact on the land they occupy. Estimating yields of various plantation tree components with allometric ratios will prove useful in quantifying production of utilisable tree components. Nutrient budgets will be a useful and important step in creating indicators of sustainability in terms of identifying areas that are sensitive to high-level nutrient export. Further studies need to be done on a broad set of sites in the black wattle growing areas of South Africa to assess the impacts of current harvesting and management practices on sustainable black wattle farming.

1.4   Aim and Objectives

The aim of this study was to develop allometric equations from direct field-based measurements (destructive sampling) to estimate above-ground biomass and nutrients masses of stand attributes for *A. mearnsii*. The specific objectives of this study are:

A. Allometry and biomass
- Developing allometric equations for *A. mearnsii;*
- Determine whether age and site (growth rate) have an effect on these allometric equations;
- Develop estimates of above-ground biomass and individual biomass of stand components for *A. mearnsii;*

- Determine biomass, stand attributes and leaf area index from indirect field-based light measurements (through the use of LAI-2000 optical instrument) or estimated PAR.

- **Key questions:**
    i. Can individual components such as leaf area, bark mass, and branch mass be estimated from simple allometric measures?
    ii. Are any the relationships affected by age or relative growth rates? Can any of the components be estimated independently of age or site?
    iii. Do the contributions of each stand component to ABG (biomass distribution) change with age or site?
    iv. Can any stand attribute be accurately quantified with alternative measures (light interception, solar radiation)?

B. Nutritional factors

- Determine the macro- and micro-nutrient concentrations and pools held by each plant component and nutrient pools of the total above-ground biomass;
- Evaluate the relationship between these pools and concentrations with respect to individual tree components;
- Compare nutrient pools and capital across ages and sites;
- Develop estimates of nutrient removals by various harvesting techniques and show these in relationship to known additions and losses in a forest system.

- **Key questions:**
    i. Can changes in nutrient concentrations and contents be attributed to site or age differences?
    ii. Are nutrient pool sizes influenced by concentration differences between sites or by biomass differences?
    iii. How are the nutrients distributed between the stand components?
    iv. Do nutrient losses from the plantation systems (especially through harvesting) exceed estimates of additions from natural or anthropogenic sources and can this be used to indicate the level of nutritional sustainability?

CHAPTER 2: MATERIALS AND METHODS

The next two sections deal with the methods used in the selection and description of the study sites. Methods employed in selecting the sampling sites, compartments and trees to be destructively harvested are described. Sampling of these trees and the determination of masses, densities and area are presented, and sub-sampling and data analysis methods are also described.

2.1   Sampling Methods

2.1.1   Site Selection

Using GIS (ESRI, 2000), the spatial distribution of black wattle stands in the KwaZulu-Natal midlands was considered. These sites were classified in terms of mean annual precipitation (MAP) and mean annual temperature (MAT). Three black wattle plantations were selected to cover a range of high, medium and low rainfalls, with MAP being assumed as an indicator of levels of potential productivity. Climatic data used in the selection of these sites was obtained from grid estimates of MAP and MAT (Schulze *et al.*, 1997) available when the sites were being considered. Grid value estimates shown in Table 4 were taken from an updated grid estimate coverage (Lynch, 2003).

A range of four ages were chosen at each site from young post canopy closure trees to harvesting age (Table 4). Ages between sites were not exactly the same and for each site, the plots selected fitted into two-year wide age ranges from 3 years to 11 years. Access to information pertaining to age and species limited the range of sites available for selection and where information was inaccessible, no accurate index of productivity was available.

2.1.2   Compartment selection and sample plot selection

Productivity in each potential compartment was estimated by measuring the dbhs of up to 54 trees contained in a 17 m x 19 m plot. These data together with knowledge of the compartment ages were used to calculate the BA, standing volume (Vol) and the mean annual increment (MAI) per hectare. Mean annual increment is a measure of growth rate, calculated as the sum of the tree volumes per hectare divided by the age of the trees. Values of MAI were compared across all the sites and ages and used to select final sample plots to represent a range in MAIs and ages. Sites were ultimately chosen based on current growth performance rather than on climatically-driven levels of potential productivity.

The sample plots were chosen based on the following criteria; relatively even terrain, free of diseases and pests, uniform canopy, and a relatively weed free forest floor. Problems such as bagworm or gummosis appeared to be more common on sites with lower rainfall and lower productivity. The sites at Bloemendal and Mistley were selected respectively as low and medium quality sites based on estimates of volumes and MAIs. A combination of two sites was used for the high quality class (Mountain Home / Seele), as the required range in age could not be found on any one high quality site. This site combination (SeeleMtH) was a merging of two separate sites with similar productivity in order to produce an even age spread on highly productive sites. Table 4 shows the age classes as well as the actual ages of the compartments selected in each of the sites. The trees on the SeeleMtH site were originally planted at 3 x 1.5 m spacing with a resulting initial stocking of 2222 stems per hectare. Mistley however, was planted with a line sowing method, where seeds were planted in lines spaced 3 m apart and thinned to 2000 and 1500 stems per hectare once they achieved heights of 2 m and 7 m, respectively (Smith and Dunlop, 2002). It was not possible to select plots of equal stocking between sites as natural site driven factors and mortality ultimately defined the final stocking for each site.

Table 4: General site characteristics for Bloemendal, Mistley, Seele and Mountain Home.

Study site	Age Class (yr)	Actual Age	Compartment No.	Latitude	Longitude	Altitude (m)	MAT[1] (°C)	MAP[2] (mm)	Actual Annual Rainfall[3] (mm)	Soil Clay (%)	MAI[4] (m³ ha⁻¹ y⁻¹)
Bloemendal	3-5	3.84	14	29°33'	30°28'	835	18	805	753	Topsoil 50 - 60	21.6
	5-7	5.84	12	29°32'	30°28'						18.3
	7-9	7.84	9	29°32'	30°28'					Subsoil 60 –80	14.7
	9-11	9.84	13	29°33'	30°28'						12.5
Mistley	3-5	3.41	A01	29°13'	30°37'	930	17	842	805	Topsoil 25 - 35	26.2
	5-7	5.49	B16	29°11'	30°39'						18.3
	7-9	7.00	B27	29°11'	30°39'					Subsoil 45 - 60	17.9
	9-11	11.25	C01A	29°13'	30°39'						16.6
Seele	3-5	4.29	D27	29°14'	30°30'	1010	17	1000	944	Topsoil 25 –35	35.1
	5-7	7.29	E03	29°15'	30°31'					Subsoil 55 - 00	31.3
Mountain Home	7-9	8.21	D03	29°35'	30°16'	1180	16	1015	984	Topsoil 35 - 45	27.9
	9-11	11.21	D01A	29°35'	30°16'					Subsoil 60 - 80	26.6

[1] Mean annual temperature; [2] mean annual precipitation;

3 mean actual rainfall over current rotation period of the 9-11 year-old crop; [4] mean annual increment (tree volume)

2.1.3 Site and stand information

Altitude, MAP and MAT was taken as the average of all the plots on each site in order to compensate for compartments crossing grid boundaries with large MAP and MAT differences. The presence of nearby rainfall stations provided more accurate estimates of rainfall for the actual stand age at each site. Rainfall for each site was corrected by multiplying the rain-gauge rainfall by the ratio of the sample site grid MAP : rain-gauge grid MAP (Table 4). This correction was done to adjust the rainfall recorded at the rain gauge to closer match that of the site. Geology and soils information were taken from observation at the sites, geological maps and soil data from past ICFR soil analyses and Mondi Forests soil surveys of the sites.

Bloemendal was described by Boden (1991) as a low productivity site with steep slopes and shallow soils, having a high air temperature and low rainfall. Middle Ecca shales (karoo series) dominate the area with the presence of a few dolerite intrusions. The soils however, are fairly deep in some areas with red doleritic soils overlaying saprolite having resulted from colluvial redistribution. Fey and Schönau (1982) described the site as having characteristically high levels of leaching and weathering. Mistley, a Mondi Forest owned timber and sugarcane plantation has

a higher MAP and a marginally lower MAT than Bloemendal (Table 4). The underlying geology is dominated by Natal group sandstone. Smaller areas are underlain by southern shale, southern mudstone and dolerite outcrops. Soils are a fine to medium sandy clay loam with humic topsoils over yellow or red apedal subsoils (Mondi Forests, 2002).

Seele Estate, previously planted to tea and sugarcane, has a higher MAP than Bloemendal and Mistley and a lower MAT than Bloemendal (Table 4). Parent materials comprise mostly shale with dolerite intrusions. Soils are fine sandy clay loams with humic topsoils over yellow or red apedal subsoils. This site is characterised by having good drainage and high topsoil carbon contents as well as a good water holding capacity. Mountain Home, an old pastureland and crop farm, has a similar MAP and MAT to Seele Estate. The parent material is mostly shale with the presence of some dolerite. Soils are fine to sandy clay loams with humic topsoils over yellow or red apedal subsoils The soils generally have a good drainage and water holding capacity with high topsoil carbon contents (Mondi Forests, 2002).

2.1.4   Sample tree selection and measurement of the standing crop

The sample plots within each chosen stand were selected on the same criteria as mentioned previously. These plots were also selected to represent the compartment and assumed to have the same level of variability as the compartment. Once the sample plots were selected, tree dbhs and heights were measured and used to calculate the mean dbh, mean height, plot basal area, total volume and stocking as shown in Table 5. Sample trees were selected by stratifying the dbh distributions of each plot into four classes and selecting the mean of each stratified component. Due to time and resource constraints as well as difficulty in harvesting the trees, only four trees were taken on each of the four plots for the three sites. This sampling method was based on those described by Cherry *et al.* (1998), Deblonde *et al.* (1994) and Snowdon *et al.* (2001). There were 12 sample plots in total with four plots on each of the three study sites. The four plots on each site were of different age; each within an specific age class. A grand total of 48 trees were sampled in this study with four trees sampled in each sample plot.

The individual volumes (V) of the trees (m^3) up to 5 cm tip over bark diameter, and SI at 5 years, were calculated using existing models developed by Schönau (1972). These are shown in Equation 1 and 2 respectively. Basal area was calculated as the sum of the cross sectional areas of all the trees in the plot, scaled up to $m^2 ha^{-1}$ by considering plot size.

$$Log(V) = 1.95322 \text{ x } log(dbh) + 12315 \text{ x } log(h) - 1.74069 \qquad \textbf{[Equation 1]}$$

Where *dbh* is diameter at breast height and *h* is tree height.

$$SI_5 = {}_{10}(1.2524 \text{ x } [(age_{stand})^{-1} - (age_{SI})^{-1}] + log(h_t) \qquad \textbf{[Equation 2]}$$

Where SI_5 is site index at five years, age_{stand} is the stand age in years, age_{SI} is the site index age (5 years in this case) and h_t is the top height (i.e. 80th percentile stand tree height).

2.2   Destructive harvesting and sample analysis

The dry mass of each component was estimated for each tree by the following destructive harvesting procedures; A chainsaw or a hand-held bow saw was used to cut down the tree as close to the ground as possible. The tree was directed to fall onto a plastic sheet laid on the ground in an attempt to catch as many dead branches as possible. Total tree length and distance from the base of the tree to the bottom of the canopy was measured. The bottom of the canopy was taken at the base of the first live branch carrying live foliage. These measurements were used to divide the canopy into three sections. The canopy was separated from the point at which the branches were attached to the main stem. This method is similar to those described by Cherry *et al.* (1998), Deblonde *et al.* (1994) and Snowdon *et al.* (2001).

A. mearnsii has a bi-pinnately compound leaf structure. In the text that follows, the term leaf is taken to mean the whole compound leaf. Thirty leaves were randomly selected from each of the three canopy layers and immediately pressed in a heavy book to prevent the pinnules from closing. All the remaining foliage on the trees was removed at the base of their petioles from each canopy section and weighed in their separate canopy sections. Leaf area for each of the thirty leaves was determined with a LICOR- LI-3100 Leaf Area Meter. These leaves were then oven dried at 70 °C and weighed to determine oven dry mass, used to calculate the specific leaf area (SLA) in $m^2 \text{ kg}^{-1}$ for each leaf. Specific leaf area is the single sided area of the foliage per unit foliage mass in ($m^2 \text{ kg}^{-1}$).

The bark, stem up to 5 cm over bark diameter, dead and live branches were separated and weighed. Masses greater than 3 kg were weighed on a 30 kg balance to a resolution of 1 g, while smaller masses were recorded on a portable 3 kg balance. Three sub-samples were taken from each tree component to determine an average wet to dry mass ratio between the sample in

field and after oven drying. This ratio was multiplied with the total mass taken in field to determine the total dry mass of each separate tree component. All oven drying was done at 70 °C until no further mass loss was observed.

Further stem sub-samples were taken as 2 cm thick cross-sectional discs, cut at 2.4 metre distances along the tree from the base. Density was determined from these stem samples by a water displacement method (Tappi, 1985). This involved saturating the discs with water and then measuring the mass of water displaced by inserting them into a known volume of water. Since the density of water can be taken as 1g cm^{-3} the oven dry mass of each disc divided by the water displaced mass was taken as the wood density.

2.2.1   Measurement of sapwood area

Additional discs were taken from each tree at 1.3 above-ground level and used to determine sapwood area. Heartwood was distinguished as having a distinctly darker colour than that of the sapwood. Sapwood area was estimated by scanning each disk on a flat bed scanner along with a plastic card of known size. The plastic card was used to calibrate the area measuring software in order to obtain accurate measurements. Analysis was performed on a computer using the free UTHSCSA ImageTool program (UTHSCSA, 2002). Whole disc area was digitally calculated by tracing the outside of the debarked stem and subtracting a traced area around the heartwood.

2.2.2   Optical plant area index measurement

The PAI was estimated using a LICOR-LAI2000 plant canopy analyser (PCA). This instrument records the fraction of light below the canopy to the above canopy light at 5 zenith[a] angles through a fish eye lens. The measurements are integrated over the five angles and a gap fraction calculation is used to estimate plant area index at points under a forest canopy (LI-COR, 1992). The gap fraction method is a widely used method of optical leaf area determination using the relationship between leaf area and the probability of light being intercepted as it passes through the canopy. In order to simplify the estimation of LAI by gap fraction, a number of assumptions are made (Chason et al., 1991; LI-COR, 1992). The canopy is assumed to be horizontally homogenous with the foliage elements being small and black, and having a set angular distribution while being randomly distributed azimuthally[b] and in space. As some level of foliar

---

a The angle from the vertical to horizontal plane. (Directly up is 0°)

b A top down view angle between the vertical plane and a rotational direction. (Facing North, East is 90°)

clumping (gathering of leaves into clusters along the branches) and light scattering and transmission of light through the foliage occurs, the assumptions cannot be fully adhered to.

The entire canopy area or PAI is measured with the PCA, as it does not distinguish between foliage, branch and stem elements in making light measurements. A calibration model may be developed to convert PAI to LAI using destructively determined LAI, provided a good relationship exists between the two methods of LAI determination.

A total of 90 PAI samples (3 replications of 30 samples) were taken in each sample plot to capture as much variability as possible. A 45° lens cap was used to cover the sensor lens to obscure the operator from the instrument's field of view. Samples were taken in transects between the 3 m spaced tree rows within each plot. The fifth ring or zenith angle was removed in calculating the PAI with the LICOR-C2000 software to exclude any possible edge effects recorded by this low field of view light sensor.

2.2.3   Nutrient determination

Samples from this study were used determine nutrient concentrations in stands of *A. mearnsii* across four age classes and three site qualities. The sample set of 48 trees comprised stem wood, bark, dead branches, live branches and foliage. Sub-samples of each tree were collected for each sample tree component, except the stem, and dried at 60°C until constant mass. Stem samples were taken as 2.0 cm thick discs at 1.2 m intervals from the base of the stem to 5.0 cm over bark diameter. Five macronutrients, N, P, K, Ca and Mg and four micronutrients, Mn, Fe, Cu and Zn, and Na were assessed on a dry mass nutrient concentration basis (Kalra and Maynard, 1991). Plant material was analysed for total N by Kjeldahl digestion and titration. Phosphorus concentration was determined spectrophotometrically after dry ashing, using the molybdenum blue method and a segmented flow analyser. Flame emission spectroscopy was used for the analysis of K and Ca Mg Mn, Cu, Fe, Zn were analysed using atomic adsorption spectroscopy (Kalra and Maynard, 1991; Kalra, 1998). Since Bloemendal was sampled in early summer (late October) followed by Mistley in mid summer, and then SeeleMtH later in summer (mid February), the effect of time within season may have influenced the nutrient concentrations, particularly in the foliage.

Tree component masses predicted using the allometric relationships and nutrient concentrations were used to estimate masses of nutrients in each tree component. Nutrients contained in the AGB of each tree component were used to estimate nutrient removals for various harvesting

intensities. General sample tree data are shown in Appendix A, Tables A1 to A3 and concentrations are shown by site, age and component and element in Appendix B, Tables B1 to B3.

2.3   ANALYSIS OF DATA

2.3.1   Analysis of general tree and stand growth

Two-way analysis of variance (ANOVA) was performed with no blocking or interactions to test for growth differences between age and sites of the sample plots. The difference between the plot age and the mean age of each age class was used as a covariate to account for the differences in ages of plots within each age class. All statistical analyses were performed using Genstat 5th edition statistical analysis software (VSN, 2001).

2.3.2   Ratios between tree component masses

Relationships between each tree component and: (a) total AGB, (b) woody biomass (Ws), and (c) stem biomass were analysed using multiple linear regression. Woody biomass or "weight of stem" is the sum of all above-ground dry biomass components including bark, but excluding the foliage. Branch bark fraction (Bk) was calculated as the fractional contribution of the branches and bark to Ws. Branch bark fraction and Ws are used as parameters in some process-based models, such as 3-PG.

Multiple linear regression analysis was used to test whether the relationships between components were affected by age or site. By using total AGB, Ws and stem biomass to predict each of the component masses, the influence of age and site on theses relationships was assessed. Plot age was added to the relationship in the regression analysis as a variate and site was used as a grouping factor. Regressions showing a significant improvement for age and/or site were concluded to be influenced by these factors. The effects of addition of age and site were assessed by scrutinising the changes in F-test probabilities, t-test probabilities, regression r^2 and the regression standard error. The addition of site or age to the model was taken as significant if the probability of change was significant at $P<0.05$. The probability of change is the F-test describing if the added variable significantly improves the error accounted for by the new regression model. In some cases other variables such as stocking and tree size were tested in order to exclude other possible influences on the relationships.

2.3.3 Allometric equations for estimation of stand attributes

To estimate the total AGB and biomass of tree components at the plot level, allometric equations were derived by regression from the sample tree data. The small number of trees sampled per plot (due to cost and time constraints) did not allow for enough degrees of freedom in regressing any tree component with dbh on an individual plot basis.

However, bulking all 48 trees together produced adequate degrees of freedom with site and age being incorporated in the subsequent regression equations. Multiple linear regression was used to generate allometric equations with dbh, h, stocking, age and site to best predict the biomass or area of tree components. Age and site were included in the relationships, only if they improved the predictive ability of the equations, assessed in the same manner as above. A maximum of two additional parameters were included in the final prediction equations, so as not to greatly reduce the degrees of freedom, although only one was necessary for most predictions.

2.3.4 Comparing sites and ages

Two-way ANOVA was performed with no blocking or interactions to test for differences between age classes and sites for final biomass levels and leaf areas. Individual leaf data were analysed with general ANOVA to include differences between levels of canopy depth. The difference between the plot age and the mean age of each age class was used as a covariate to take into account the differences in ages of plots within each age class. It was not possible to evaluate the interaction between the ages and sites as the study sites were not replicated. The strength of the results are questionable with this small number of degrees of freedom for age and site and are taken only as an indication of trends in this study.

The mean and standard deviation were calculated for concentrations of nutrients in each tree component. Values were excluded as outliers or re-submitted for analysis that had a difference of twice the standard deviation from the mean concentration of each component. Means for each sample plot were calculated and multiplied with the total biomass (ha^{-1}) to estimate masses of nutrients in the biomass component at the stand level (kg ha^{-1}). There was no reason to use a tree size stratified calculation of nutrient contents within a plot as no relationship or trend was observed between concentration and tree size. Two-way ANOVA was performed with no blocking or interactions to test for differences between age classes and sites for each component's nutrient concentration. Statistical analyses were performed using Genstat 5th edition statistical analysis software (VSN, 2001).

2.3.5 Plant area index, leaf area index and biomass

Simple linear regression was used to find a relationship between PAI and LAI in order to generate a general calibration equation to convert PAI measured by the LICOR- LAI2000 to LAI. Multiple linear regressions were used to find relationships for PAI and age that predict stand productivity or a stand attribute at each site. This was done to test whether PAI can be used to estimate stand attributes other than LAI. The PAI also recorded canopy light interception as a fraction of light intensity below the canopy to light intensity above the canopy. These data were used with LAI estimate the canopy extinction coefficient, which relates to the amount of light interception to LAI. Intercepted light is then shown in relation with biomass production.

CHAPTER 3: ALLOMETRY AND BIOMASS
RESULTS AND DISCUSSION

The following is a study of 12 stands in KwaZulu-Natal, spanning four ages and three site qualities, estimating AGB and allometric relationships for black wattle. Destructive sampling methods described in Chapter 2 were used to calculate the dry biomass of the stem, bark, live branches, dead branches and foliage on a hectare basis for the 12 stands. Measurements of simple tree attributes, such as dbh and h were used with destructively harvested tree component attributes, such as stem and bark biomass, to develop these allometric relationships. These relationships were used to predict more complex tree attributes and were compared across the site and age classes. Optically determined plant area index (PAI) was compared to LAI and stand growth attributes, to test whether suitable relationships exist between optically determined, stand attributed and destructively determined attributes. The relationship between total AGB and PAR was investigated to determine whether a relationship exists between iPAR and AGB.

This chapter describes the differences in growth and distribution of biomass amongst the tree components and between the plots sampled in this study. The leaf area, sapwood area 1.3 m above-ground level, optical canopy measurements and wood density are also indicated and related to growth, site and age.

3.1 Growth and yield

Table 5 shows general characteristics calculated for the sample stand for the four age classes. These include final stocking in stems ha^{-1}, mean diameter at breast height (cm), mean height of the trees (m), basal area of the plot (m^2 ha^{-1}), wood volume (m^3 ha^{-1}), mean annual increment (m^3 ha^{-1} y^{-1}), Site Index at five years (m) (SI) and the mean density of the wood (kg m^{-3}).

Table 5: General mensuration characteristics for each stand.

Study site	Age Class (yr)	Final stocking (stems ha⁻¹)	Mean dbh (cm)	Top height (m)	Basal area (m^2 ha⁻¹)	Volume (m^3 ha⁻¹)	MAI* (m^3 ha⁻¹ y⁻¹)	SI (m)	Wood Density (kg m⁻³)
Bloemendal	3-5	1981	9.7	14.7	15	83	21.6	17.5	515
	5-7	1517	11.4	17.3	16	107	18.3	15.9	586
	7-9	1455	12.0	17.6	17	115	14.7	14.0	566
	9-11	1348	12.1	18.7	16	123	12.5	14.1	642
Mistley	3-5	2291	8.9	15.5	15	90	26.2	20.2	534
	5-7	1796	10.3	16.4	16	101	18.3	15.5	580
	7-9	1393	12.4	18.3	18	125	17.9	15.5	598
	9-11	1176	15.0	21.5	22	187	16.6	15.6	639
SeeleMtH	3-5	1517	13.0	18.8	21	151	35.1	20.6	525
	5-7	1765	13.2	22.4	26	228	31.3	18.4	544
	7-9	1981	12.9	21.3	27	229	27.9	17.0	572
	9-11	2043	13.8	23.3	33	298	26.6	16.9	598

* Denotes the stand MAI at current age and not the maximum MAI for that site.

3.2 General growth of the sample stands

Site quality is used in this study to indicate the ability of a site to supply the growing trees with the necessary resources for growth. Sites of similar ages with a higher site quality will have a higher volume than sites with a low site quality. Site index in Table 5 is an age-equilibrated measure of site quality, yielding comparatively higher values on sites with higher site quality. Mean annual increment and SI are both real-time measures of site quality and are used as practical tools to predict yields at a particular site and rotation age. Site Index calculated for trees younger than five years may be inaccurate and over-inflated as the model was only established to back predict from ages close to and older than five years. Mean height, mean dbh, basal area and volume show an increase with site quality and age.

Maximum mean annual increment and SI will be higher in areas of higher site quality. Current annual increment (annual volume growth) will reach a maximum at canopy closure then decrease with age. The decrease in current annual increment with age is due to a decline in the trees' growth rate with age, as growth vigour decreases. A reduced growth rate may also be due to drought, poor silvicultural practices (e.g. a lack of fertiliser or weeding), poor genetic material or a decrease in stocking. Competition between trees increases with age as resources become depleted, and can only be alleviated by the removal some of the trees from a stand.

Removal of trees by thinning results in a sharp reduction in MAI with the remaining trees exhibiting an increase in MAI from the new base level, followed by the same pattern of growth rate decline. The Bloemendal 9-11 year-old age class experienced a dry period in the first two years of growth, which did not affect the 7-9 year old trees (Table 5). The older trees exhibited a very small volume difference compared to the younger trees having not experienced a similar dry period in early growth stages.

Stocking decreases are expected with age due to natural mortality, as a result of competition for resources, disease or natural thinning. In Table 5 stocking decreases with age for Bloemendal and Mistley sites, but increases at the SeeleMtH site. The reasons for the increase at this site may be due to the stands not being thinned. Wood density seems to increase with age and has a decreasing trend with increased site quality. Stubbings and Schönau (1972) showed density of black wattle timber to vary according to site, with faster growing trees having a lower density. Site variations in density are not clear in this study, although final densities at clear felling age are lowest at the SeeleMtH site.

Differences between sites were significant at the 0.01 probability level with respect to volume and basal area. In terms of volume, site productivity for these sites can be ordered as: Bloemendal < Mistley << SeeleMtH. Bloemendal and Mistley are not significantly different from each other in terms of basal area, but SeeleMtH is significantly different from the other two sites. The initial selection of sites and ranking by site quality as determined by rainfall is in agreement with this ordering by final volume growth.

3.3   Distribution of biomass between tree components

Table 6 shows some correlations between individual tree component masses, tree size measurements and stocking for all sample trees. All tree component masses showed a high degree of correlation between each other, indicating that significant relationships exist between the masses of the individual tree components. Tree component masses were highly correlated with dbh, h and sapwood area, while age and stocking showed lower levels of correlation. A negative correlation is shown in Table 6 between stocking and all components analysed. This implies a decrease in the component mass or size as stocking increases. A high level of correlation between tree components may allow for the prediction of an unknown component from a known one (i.e. stem biomass may be used to estimate branch biomass).

Table 6: Correlations between individual tree dimensions and component masses with levels of significance.

	age	dbh	height	sapwood area	AGB	Ws	stem biomass	bark biomass	live branch biomass	dead branch biomass	foliar biomass	leaf area
dbh	0.494***											
height	0.642***	0.856***										
sapwood area	0.301*	0.961***	0.752***									
AGB	0.606***	0.933***	0.835***	0.873***								
Ws	0.603***	0.941***	0.847***	0.881***	0.998***							
stem biomass	0.605***	0.936***	0.864***	0.876***	0.992***	0.995***						
bark biomass	0.648***	0.915***	0.832***	0.842***	0.984***	0.983***	0.975***					
live branch biomass	0.509***	0.789***	0.615***	0.731***	0.857***	0.854***	0.801***	0.843***				
dead branch mass	0.493***	0.632***	0.512***	0.580***	0.789***	0.751***	0.737***	0.763***	0.691***			
foliar biomass	0.184^{n.s.}	0.874***	0.640***	0.924***	0.814***	0.816***	0.799***	0.768***	0.730***	0.603***		
leaf area	0.238^{n.s.}	0.886***	0.678***	0.920***	0.834***	0.839***	0.827***	0.789***	0.738***	0.587***		
stocking	-0.398**	-0.296*	-0.304*	-0.197^{n.s.}	-0.349*	-0.328*	-0.281^{n.s.}	-0.370**	-0.520***	-0.492***	-0.200^{n.s.}	-0.175^{ns}

* significant at $P < 0.05$, ** significant at $P < 0.01$, *** significant at $P < 0.001$, ^{n.s.} implies not significant

The correlations in Table 6 show significant relationships between all the individual tree biomass components. The correlations between tree components and AGB, Ws and stem mass in Table 6 were increased in some cases by the separate inclusion of site and then age in the linear relationships between them. Tables 7 and 8 show a summary of the mean proportional relationships between the selected tree components and AGB, Ws and stem biomass. The multiple linear regression F probabilities were used as an indication of an influence of age or site on the relationships between these components. The F probability here is the significance of change to the relationships by the addition of age or site to the model (Table 7 and 8). The t probabilities were used to indicate differences between the three sites in their influence on the relationships. Site differences are denoted in Tables 7 and 8 with different a, b or c superscripts having a significant difference at $P < 0.05$. The influence of age and site are shown as an increase (inc) or decrease (dec) with increased age or improved site quality, with corresponding F probabilities.

Table 7: Mean percentage (%) contribution of each component to total AGB across all ages and all sites.

Component	Stem	Bark	Dead Branches	Live Branches	Foliage
Site Quality influence	inc [0.001]	ns	dec [0.016]	dec [0.002]	dec [0.002]
Bloemendal	63.3 [a]	9.4 [a]	6.4 [a]	15.9 [a]	5 [a]
Mistley	64.6 [a]	9.8 [a]	5 [ab]	16.6 [a]	4 [b]
SeeleMtH	72.3 [b]	9.4 [a]	3.3 [b]	11.6 [b]	3.4 [b]
Age Class (yr)	Across all sites				
3-5	63.2	9.7	2.9	17.6	6.5
5-7	69.2	9.1	4.8	12.9	3.9
7-9	65.3	9.6	5.7	15.9	3.4
9-11	69.2	9.7	5.9	12.5	2.8
Age influence	ns	ns	inc [0.01]	dec [0.005]	dec [0.001]

Inc- increase, dec- implies a decrease with increased age or site productivity; ns- no significant change. Sites with different superscripts are significantly different at $P < 0.05$.

Table 7 shows a summary of the proportional contributions of each tree component to AGB with site quality increasing from lowest at Bloemendal to highest at SeeleMtH. Stem biomass contribution to total AGB increased with improved site quality, while all other components, except the bark biomass, decreased in proportion to AGB with improved site quality. Bark

fraction showed no change between sites. Foliage and live branch biomass decreased with increasing age relative to total AGB, while dead branch mass proportion increased with age. The influence of age on dead and live branch ratios was not significant when stocking was used in the multiple regression relationship and the contribution of stem biomass to AGB was also larger at higher stockings (data not shown). These are the only relationships where stocking had an influence. A reduction in branchiness here is most probably attributed to a higher stocking on the sites with a higher site quality. Increased branch mass with increased age may be due to a reduction in stocking through natural tree mortality. The higher stocking on the sites with a higher site quality may be due to lower mortality where sites are capable of supporting a higher stocking with fewer diseased trees, or it may be due to a lack of thinning.

Table 8: Mean bark : stem ratios as well as the ratio of Ws to mean component masses across all ages and sites.

Component	Bark	Leaves	Stem	Bark + branches
Relative to:	Stem	Ws	Ws	Ws
Site Quality influence	$dec^{0.003}$	$dec^{0.002}$	$inc^{0.001}$	$dec^{0.001}$
Bloemendal	0.146a	0.48	0.724	0.328
Mistley	0.136a	0.45	0.742	0.305
SeeleMtH	0.117b	0.32	0.791	0.242
Age Class (yr)	Across all sites			
3-5	0.131	0.55	0.743	0.283
5-7	0.123	0.44	0.762	0.276
7-9	0.135	0.38	0.749	0.302
9-11	0.143	0.30	0.755	0.306
Age influence	ns	$dec^{0.001}$	ns	ns

inc- increase, dec- decrease with increased age or site productivity; ns- no significant change. Sites with different superscripts are significantly different at $P < 0.05$.

Table 8 shows the ratio of leaves : Ws and the proportional contributions of stem and bark + branches to Ws verses site quality (increasing from the lowest at Bloemendal to highest at SeeleMtH). Table 8 also indicates oven dry bark to stem ratios. Relationships between other tree components and stem biomass are not shown for the purpose of brevity. Relationships to Ws are shown as they are useful fractions for some known process-based models.

As shown in Table 8, bark mass decreases relative to stem biomass, with improved site quality. All other components also decreased relative to stem biomass (data not shown). There was no

change in the bark : stem ratio with age, although foliage and live branch proportions decreased, while dead branch proportions increased with increased age (data not shown). Relative to woody biomass, Table 8 shows stem biomass to increase and foliage and Bark to decrease with improved site quality. Increased age resulted in a reduction in the proportion of foliage biomass with no change in Bk and stem proportions.

Biomass studies often involve the comparison of the proportions of total biomass in the various plant components. Site quality, stocking and silvicultural treatment have been linked to differences in the distributions of biomass between the stem, branches and leaves. In *Pinus radiata* decreased stocking has been found to increase the proportion of biomass in branches and leaves, and improved site quality and silviculture to result in increased total leaf biomass, but decreased proportion of leaf to total biomass (Birk, 1992). A similar decrease in branch biomass at higher planting densities has been found with *Eucalyptus* species. Bradstock (1981) and Judd *et al.* (1996) found that foliage biomass increased with age to a maximum then declined. Bark and branch biomass increased with age while dead branch biomass increased, and then stabilised.

Table 9 shows component contributions to the total above-ground living biomass for *A. mearnsii* in two studies by Schönau (1978) and Williams (1927) as well as other similar international study sites. The values for the studies by Schönau and Williams taken from South African sites show similar relationships to those found in this study. The studies by Caldeira *et al.* (2000a, 2001) and Pereira *et al.* (1997) were carried out in Brazil, while the Tandon (1989) study was located in India.

Table 9: Percent contributions of tree components to AGB in other similar studies.

Reference	Age (years)	Foliage (%)	Live branches (%)	Dead branches (%)	Bark (%)	Stem (%)
Caldeira *et al.* (2000a)	2.4	22.2	19.6	0.5	12.4	44.8
Caldeira *et al.* (2001)	2.4	19.9	19.4	2.8	11.9	46.0
Caldeira *et al.* (2000b)	2.4	18.2	19.5	1.2	11.7	49.4
Pereira (1997)	9	2.6	7.1	2.5	8.8	78.9
Tandon *et al.* (1989)	4	14.8	24.6	n.d.*	10.3	50.6
	7	18.2	25.7	n.d.*	9.7	46.5
	10	11.8	22.3	n.d.*	9.3	56.6
Schönau (1978)	10.5	4.8	15.2	4.7	10.4	64.9
	10.5	4.7	13.5	4.6	10.3	66.9
Williams (1927)	8	5.3	11.3	0.0	9.1	74.2

* n.d. not determined

Sites in Table 9 have been arranged according to their productivity from lowest to highest for each study listed. The studies of Caldeira *et al.* (2000a, b; 2001) and Schönau (1978) show stem proportion to be higher on the sites with higher site quality, while other components decreased relative to total AGB. Tandon shows an increase in stem proportion with age, while all other components decrease in relative proportion to AGB. Proportions reported for the non-South African sites are quite different from local results (including this study) with respect to some of the tree components, especially the foliage. The differences may be due primarily to different sampling strategies. Leaf biomass, for instance, was taken as leaves and small twigs in the studies of Tandon *et al.* (1989) and Caldeira *et al.* (2000a, b; 2001), resulting in a far greater foliage biomass than in this study. Other differences such as genetics, silvicultural practices and stocking may have played a role.

Although absolute masses of branches, bark and foliage are higher on good quality sites, the increases in proportional stem masses and decreases in proportional branch, bark and foliage biomass translate to a lower percentage waste on these sites. The general order of biomass

contributions of the components to AGB is as follows: Foliage ≤ Dead Branches < Bark < Live Branches < Stem. With increased age, the fraction of foliage decreases, thus switching the order between dead branches and foliage. Increases in dead branch biomass with age may be due to the lack of natural dead branch pruning, where increasingly more branches are retained on trees as they age.

3.4 Canopy and foliar dynamics

Changes in total foliage biomass, mean individual leaf area, mean individual leaf mass, and SLA were analysed by canopy depth, age and site. Table 10 shows SLA, leaf mass and individual leaf area for each age, site and canopy level. Bloemendal, the lowest productivity site, was significantly different from the other two sites with respect to SLA, leaf mass and leaf area.

Table 10: Individual leaf area, unit leaf mass and specific leaf area related to site, age and canopy layer. (Means for site and age are shown on the right of each section and on the bottom for canopy layer).

Site	Leaf area (cm^2)				Leaf mass (g)				SLA (m^2 kg^{-1})			
	Lower	Middle	Upper	Mean	Lower	Middle	Upper	Mean	Lower	Middle	Upper	Mean
Bloemendal	38.1	41.1	38.9	39.4[a]	0.46	0.54	0.54	0.51[a]	8.4	7.8	7.3	7.8[a]
Mistley	34.4	33.3	33.5	33.7[b]	0.39	0.41	0.45	0.42[b]	8.9	8.4	7.6	8.3[b]
SeeleMtH	34.9	36.0	35.2	35.4[b]	0.38	0.44	0.45	0.43[b]	9.3	8.3	7.9	8.5[b]
Age Class (yrs)	All Sites											
3-5	42.0	43.5	41.2	42.3[a]	0.47	0.55	0.54	0.52[a]	9.2	8.3	7.9	8.5[a]
5-7	33.7	36.2	36.0	35.3[b]	0.40	0.46	0.49	0.45[b]	8.6	8.1	7.6	8.1[a]
7-9	33.7	32.4	32.4	32.8[b]	0.39	0.41	0.45	0.42[b]	8.8	8.0	7.4	8.1[a]
9-11	33.8	35.2	33.9	34.3[b]	0.38	0.43	0.46	0.43[b]	8.9	8.3	7.5	8.2[a]
Mean	35.8[a]	36.8[a]	35.9[a]		0.41[a]	0.46[b]	0.48[b]		8.9[a]	8.2[b]	7.6[c]	

Components with different superscripts are significantly different at $P < 0.05$ for each site and age comparison.

The youngest age class had the highest individual leaf area and individual leaf mass, with no difference between subsequent age classes for all sites (Table 10). A study conducted by Gilmore *et al.* (1995) on *Picea abies* was compared with similar studies on foliar age related decreases in SLA. The results suggested that an accumulation of carbohydrates and a reduction in the rate of soluble carbohydrate export in relation to photosynthetic rate, as the leaves age, are responsible for this SLA reduction. Specific leaf area decreased with increased canopy

height, while individual leaf mass was significantly lower in the bottom canopy section. Leaf area shows no change with canopy position (Table 10). Lower SLA and lower leaf mass in the lower canopy regions may be due to these leaves being older with older leaves having lost a large number of pinnules. Upper canopy leaves may be exposed to more sunlight and may have higher starch storage as a result of receiving more light. Upper canopy leaves may also be more prone to desiccation and therefore have a localised adaptation to wilting by becoming thickened. The upper canopy also contains a larger portion of immature leaves. Bloemendal, the lowest productivity site, was significantly different from the other two sites with respect to SLA, leaf mass and leaf area. Specific leaf area was lower at Bloemendal, with a slightly higher individual leaf area and a somewhat greater individual leaf mass. Leaves of trees on a poorer or drier site may have a lower SLA for similar reasons as upper canopy leaves. Dicks (2001) calculated SLA to be 6 $m^2 kg^{-1}$ for both young and mature trees, while in this study it ranged from 7.3 $m^2 kg^{-1}$ to 9.3 $m^2 kg^{-1}$ with an overall average of approximately 8.2 $m^2 kg^{-1}$.

The total number of leaves in Table 11 shows an increasing trend with increasing site quality but is unaffected by age. This measurement gives an indication of canopy density, with higher numbers of leaves at higher canopy densities. Percentages of leaves by biomass and number in each canopy section are shown in Figure 3.1. Bloemendal had a larger proportion of foliage biomass in the middle canopy section, but a smaller number of leaves in the upper canopy section. The effect of time within season may have influenced canopy structure results. Having a higher proportion of old leaves, the lower SLA, higher leaf pineal mass and area at Bloemendal may have been due to a higher proportion of older leaves, having been sampled near the beginning of the summer growth flush.

If seasonal effects were not involved in leaf size, mass and number, then site factors may have influenced the leaf morphology. Studies conducted by Osório et al. (1998) and Pita and Pardos (2000) on Eucalyptus globulus shows leaf expansion rates, SLA, leaf area, leaf number per tree and LAI to decrease between well watered and water stressed trees. It may be assumed that smaller lighter leaves may be due to a higher leaf turnover rate on the sites with a higher site quality with leaves not attaining a large mass or size before becoming shaded by new leaves. Smaller leaves allow for lower transpiration rates per leaf and lower SLA may allow for greater strength and resistance to wilting. Potentially more sunlight may be captured with a greater number of smaller leaves, as this would increase the potential number of angular distributions of leaves within the canopy.

Table 11: Number of leaves (Millions ha^{-1}) for each age group at each site.

Age Class (yrs)	Bloemendal	Mistley	SeeleMtH	Mean
3-5	5.9	10.8	10.7	9.13[a]
5-7	8.1	9.6	16.6	11.46[a]
7-9	9.5	11.1	12	10.88[a]
9-11	10.4	8.9	13.6	10.96[a]
Mean	8.48[a]	10.1[ab]	13.23[b]	10.6

Values with different a, b or c superscripts are significantly different at P < 0.05
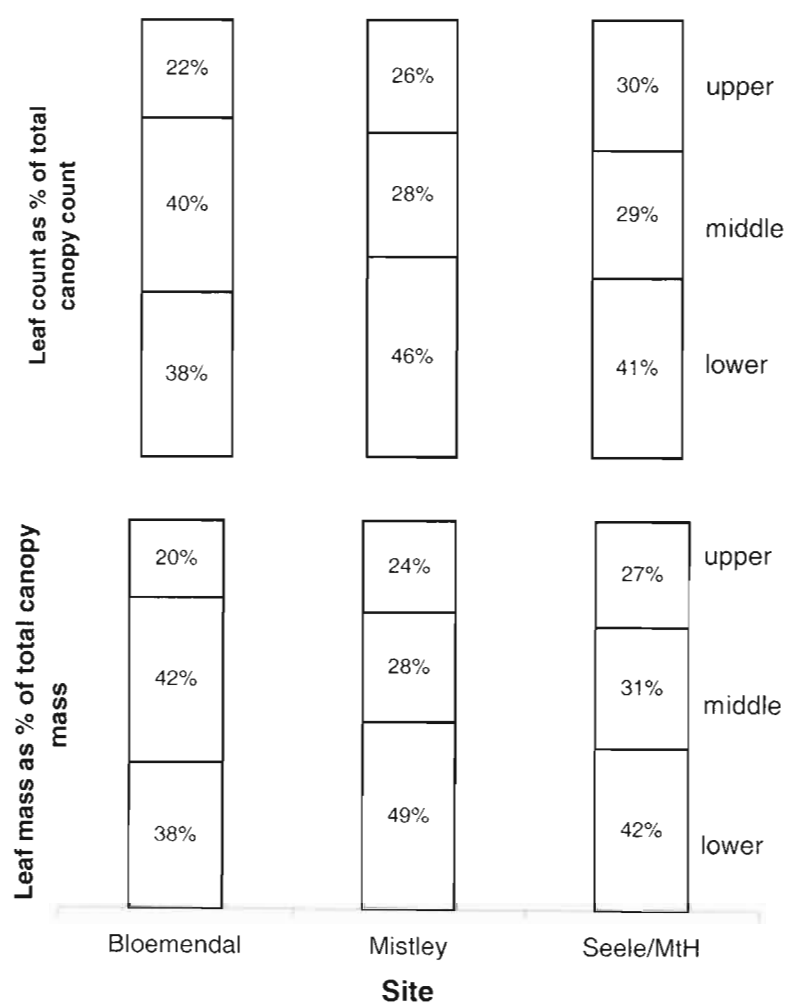
Figure 3.1: Foliage biomass and leaf number in the upper, middle and lower canopy positions as a percentage of the canopy total.

3.5 Models to predict masses of individual tree components

Diameter at breast height is the easiest tree dimension to measure and all components were highly correlated with it, (Table 6. p.38). In some cases the inclusion of additional tree dimension or plot descriptors with dbh in a multiple linear regression was found to improve the predictive ability of an equation. All allometric regressions for predicting tree component biomasses were pooled across all sites, as the inclusion of site in the regression analysis resulted in no improvement of the models. A natural logarithmic transformation was used with some of the relationships in order to improve the residual scatter. Outliers were removed if their residuals were high or they had high leverage, and this was done only if the author had a prior knowledge of the data point being questionable. Results of the regressions are summarised with their equations in Table 12. Full regression results are shown in Appendix C; Tables C1 to C11 with observed plotted against predicted values in Figures C1 to C11.

Table 12: Allometric models to predict masses or areas of individual biomass components, with the r^2 of each regression used to generate them.

Equation No.	Equation	r^2
3	Ws (kg) = 0.1126 x dbh$^{2.5691}$	0.944
4	Stem (kg) = (dbh$^{1.91}$ x ht$^{1.486}$) / 168.174	0.979
5	Bark (kg) = (dbh$^{2.082}$ x (exp(age))$^{0.06433}$) / 42.225	0.946
6	Live branches (kg) = (82.27 x dbh$^{1.826}$) / (stocking$^{0.899}$)	0.704
7	Dead branches (kg) = (dbh$^{1.962}$ x age$^{0.748}$) / (46.06 x exp(0.000842* stocking))	0.677
8	AGB (kg) = (dbh$^{2.3287}$ x (exp(age))$^{0.04158}$) / 6.5995	0.959
9	Sapwood area (cm^2) = (1.231 x dbh$^{1.786}$) / age$^{0.2744}$)	0.970
10	Foliage mass (kg) = Sapwood$^{1.2457}$ / 67.579	0.869
11	Leaf area (m^2) = Sapwood area / 2.882	0.820
12	Foliage mass (kg) = dbh$^{2.268}$ / (51.935 x age$^{0.404}$)	0.861
13	Leaf area (m^2) = dbh$^{1.966}$ / (3.589 x age$^{0.3030}$)	0.820

(dbh is measured in cm, ht in m, age in years, stocking in stems ha^{-1} and sapwood in cm^2)

Equation 3 is the model where dbh is used to predict Ws (Table C1 and Figure C1). Equation 4 is the model used for predicting the stem biomass (Table C2 and Figure C2). Tree height included with dbh produced the best predictive stem biomass model. The addition of height to the stem biomass prediction model may have improved the predictive ability of the model, by taking tree height variation into account in the same manner that Equation 1 for volume does, by

compensating for taller, thinner trees. This results in taller trees having a higher stem biomass per unit dbh.

Although bark biomass was highly correlated with dbh, with an r^2 of 0.83, it was best predicted with the inclusion of age in the model resulting in an r^2 of 0.95, (Equation 5). Regressions for bark biomass are shown in Table C3 and Figure C3. Increased age results in increased bark biomass in this model, by 7% per year for a constant dbh. Live branch and dead branch biomass was less well correlated with dbh than all the other measured tree components, (r^2 of 0.61 and 0.39 respectively) (Table 6). Live and dead branch biomass predictions were improved by including stocking with dbh in the model equations, resulting in an r^2 of 0.70 for live branch biomass, (Equation 6). The prediction of dead branch biomass required an age adjustment, as branch retention from previous years of growth resulted in an additive effect of age on branch biomass. Including stocking and age with dbh in the dead branch biomass predictive model increased the r^2 to 0.68. Higher stocking numbers are known to result in a lower total branch biomass, as increased stocking and closer spacing limits lateral branch growth. Regressions for live branch biomass are shown in Table C4 and Figure C4, while regressions for dead branch biomass are shown in Table C5 and Figure C5. The prediction of AGB was best with the inclusion of age with dbh (Equation 8), with no significant improvement by the addition of stocking. Regressions for AGB are shown in Table C6 and Figure C6.

Sapwood area was highly correlated with dbh having an r^2 of 0.92 (Table 6). The inclusion of age increased the r^2 to 0.97 resulting in the model shown in Equation 9, (Table C7 and Figure C7). Sapwood area was found to have a higher correlation with leaf biomass and leaf area than did dbh with leaf biomass and area. Diameter at breast height had a r^2 of 0.76 for leaf biomass and 0.78 for leaf area, while sapwood area produced an r^2 value of 0.85 for leaf biomass and 0.84 for leaf area. Adding age to the dbh improved the prediction of leaf biomass and area to 0.86 and 0.83. Sapwood area was predicted using Equation 8 and demonstrated as a predictor of leaf biomass and leaf area predicted in Equation 10, (Table C8 and Figure C8) and Equation 11, (Table C9 and Figure C9) respectively. As tree size increases, sapwood area increases, but the proportion of sapwood area to whole stem area is reduced with increased age and increased dbh. Leaf biomass and leaf area were predicted from dbh and age using Equation 12, (Table C10 and Figure C10) and Equation 13, (Table C11 and Figure C11) respectively.

With a given unit of foliage requiring a given unit of sapwood area to supply water, the Huber value (Huber, 1928), calculated as the relationship between leaf area or leaf biomass and

sapwood area is not improved by the inclusion of site or age in this study. This implies that the ratio between conductive tissue and leaf area is unchanged with site or age and that the supply efficiency of the sapwood is unchanged within the site range of this study. Not all sapwood is conductive tissue, as some volumes of sapwood are comprised of parenchyma, needed for storage materials (e.g. starch) (Hillis, 1987).

3.6 Plot masses of tree components

Table 13 gives final biomass per ha of each tree component obtained from the solution of all regression equations for every tree in each of the 12 measured plots (17 m x 19 m). Differences between ages and sites analysed by two-way ANOVA are shown in Table 14. The age and the mean age of each age class used as a covariate had no significant influence on the analyses, except for total dead branch biomass. Rainfall water use efficiency (WUE_r) as defined by Dye (1999) was calculated as the total stem biomass divided by the total cumulative rainfall to give dry biomass production per 1000 mm (1 m) of rain.

Table 13: Final masses and measures of tree components for each plot.

Study site	Age Class (yrs)	Stem (t ha^{-1})	Bark (t ha^{-1})	Live Branch (t ha^{-1})	Dead Branch (t ha^{-1})	Foliage (t ha^{-1})	Total AGB (t ha^{-1})	Sapwood Area (m^2 ha^{-1})	LAI (m^2 m^{-2})	WUE_r (t ha^{-1} m^{-1})
Bloemendal	3-5	48.1	7.2	11.7	2.0	3.8	70.8	10.1	3.5	17.1
	5-7	64.5	8.6	15.1	4.2	4.1	92.2	9.1	3.1	11.8
	7-9	69.6	10.5	16.6	5.9	4.6	101.3	8.8	3.0	9.8
	9-11	76.0	11.5	17.1	7.3	4.5	109.1	7.9	2.7	9.2
Mistley	3-5	52.8	7.0	10.3	1.4	4.7	74.8	10.6	3.8	19.0
	5-7	64.2	8.6	13.3	3.2	4.3	90.3	9.5	3.4	14.6
	7-9	76.3	10.4	17.8	5.9	4.0	108.5	9.4	3.4	13.1
	9-11	118.2	16.8	24.7	12.2	3.8	163.5	9.6	3.5	13.3
SeeleMtH	3-5	92.3	10.1	19.1	4.3	5.2	126.7	12.4	4.4	23.2
	5-7	145.2	15.5	20.7	6.4	6.3	187.6	13.3	4.6	23.0
	7-9	144.1	17.2	19.7	6.2	4.8	185.8	13.6	4.8	21.8
	9-11	190.8	25.5	22.8	8.9	5.7	244.7	14.8	5.3	22.3

Total AGB, stem and bark biomass generally increased as site quality and age increased (Table 13). Foliage biomass also increased with improved site quality, but showed no significant difference between ages. Live and dead branch masses showed no differences between sites with only dead branch biomass increasing significantly with age. Leaf area index and PAI both

produced no significant differences between ages, but were significantly greater as site quality improved. Water use efficiency increased significantly with improved site and decreased with increased age. Bloemendal and Mistley showed no significant differences in any of the analyses performed except for WUE_r. The masses and areas of the components did follow trends with all factors increasing with increased site quality and age. Mistley tended to show a trend of larger component masses and leaf area than Bloemendal, although the least significant difference values indicated there were no significant differences between them (Table 14). Table 14 shows efficiency in terms of water use to be higher on the sites with higher site quality. Water use efficiency decreases with age as incremental growth rate decreases and relatively more rainfall is cumulatively lost through runoff or infiltration, lateral flow or soil surface evaporation. Although rainfall is a useful measure in rain dependent forestry, as a water use efficiency (WUE) measure, it is difficult to compare between sites as losses are largely affected by soil type, topography and rainfall intensity.

Two-way ANOVAs were used to test the same relationships shown in Table 7 and Table 8. These analyses were used as a simple check to determine if the relationships between individual tree component masses were carried through the building-up process to the stand level. These analyses are not shown or discussed in the text as they show the same trends as the individual tree analyses.

Table 14: Mean tree component masses for site and age class.

Site	Stem (t ha^{-1})	Bark (t ha^{-1})	Live branch (t ha^{-1})	Dead branch (t ha^{-1})	Foliage (t ha^{-1})	Total AGB (t ha^{-1})	Sapwood area (m^2 ha^{-1})	LAI (m^2 m^{-2})	WUE_r (t ha^{-1} m^{-1})
Bloemendal	64.5[a]	9.4[a]	15.1[a]	4.8[a]	4.2[a]	93.3[a]	9.0[a]	3.1[a]	20.1[a]
Mistley	77.9[a]	10.7[a]	16.5[a]	5.7[a]	4.2[a]	109.3[a]	9.8[a]	3.5[a]	24.8[b]
SeeleMtH	143.1[b]	17.1[b]	20.6[a]	6.5[a]	5.5[b]	186.2[b]	13.5[b]	4.8[b]	35.3[c]
Age Class (yrs)					All Sites				
3-5	64.4[a]	8.1[a]	13.7[a]	2.6[a]	4.5[a]	90.8[a]	11.0[a]	3.9[a]	33.2[b]
5-7	91.3[ab]	10.9[a]	16.3[a]	4.6[ab]	4.9[a]	123.4[ab]	10.6[a]	3.7[a]	25.9[a]
7-9	96.7[bc]	12.7[a]	18.1[a]	6.0[b]	4.5[a]	131.9[b]	10.6[a]	3.8[a]	24.1[a]
9-11	128.3[c]	17.9[b]	21.5[a]	9.5[c]	4.7[a]	172.4[c]	10.8[a]	3.8[a]	23.7[a]

Values with different superscripts are significantly different at $P < 0.05$ for each site and age comparison.

A higher LAI will lead to greater transpiration at the stand level, which implies a greater water usage on sites capable of supporting a greater area of leaves. Although more rainfall occurs on the sites with higher site quality, the rainfall-based WUE on these sites is higher, therefore

suggesting that the sites with a higher site quality result in more efficient usage of available water. Trees with little water, nutrient, VPD or temperature limitations, may generally have a higher WUE, as stomata are open for longer periods of time enabling more carbon fixation. As light and carbon dioxide are not lacking under South African growing conditions, differences in efficiency may be attributed to temperature, VPD, water and nutrient differences. Decreases in efficiency may occur at high vapour pressure deficits and low soil water availability due to cessation of photosynthesis through stomatal closure. This would translate into less time for carbon dioxide adsorption and reduced photosynthesis. A nutrient deficiency may reduce growth efficiency and WUE by a lack of structural or osmotic elements required for growth, in any of the growth processes from photosynthetic light capture at the chloroplasts, at the structural level or at the osmotic level. Results from fertiliser experiments have shown WUE to increase with added fertiliser, with the increased growth being attributed to the added nutrients. Under conditions of limiting water and nutrients, a reduction in LAI occurs as well as a reduction in the efficiency in converting light energy to biomass (Linder and Rook, 1984). An artificial reduction in LAI by pruning may be the best way to increase WUE. Removal of the lower canopy areas intercepting small amounts of sunlight would reduce the total transpiration area of the canopy and hence reduce the rate of water usage. A reduction in growth would be expected from removal of leaves, but as the leaves on the lower canopy areas are intercepting low quantities of light, net production is low in relation to water loss. Losses in respiration of the lower canopy areas are also eliminated. With a decrease in transpiration and little change in production, WUE is improved (Linder, 1985; Pinkard et al, 1999).

As a tree plantation ages, increases in biomass are expected unless some outside influence such as pests, diseases or adverse weather reduces it. A net decline in plantation growth rate with age may be attributed to an increased demand on maintenance respiration or tree mortality. An increase in respiration is attributed to the maintenance of incrementally larger living structures as the tree ages (Linder, 1985). Ryan et al. (1997) suggested that the decreasing growth rate of surviving trees is more relevant than the increased mortality in explaining decreased production with increased age. Growth is also slowed as trees age due to limited hydraulic flow of water through increasingly longer paths, and the decrease in sensitivity of stomatal closure in relation to VPD. A reduction in hydraulic conductance translates into a reduction in stomatal conductance and to a reduction in photosynthesis (Landsberg and Waring, 1997). A slow age-related decline in soil water availability of a site or reduced availability of nutrients may also result in a reduced growth rate. Nutrients may be made unavailable by being "locked up" in the tree biomass, forest floor biomass and soil organic material. Soil water availability has been

shown to slowly decline in forest soils throughout the rotation, with field capacity never being reached in a mature plantation until clear felling (Calder, 1991).

Differences in yields between sites may be expected and are attributed to site quality. A suboptimal level of water and nutrient availability (i.e. lower site quality) will naturally result in a resource limitation or stress that may be translated into a reduced growth rate and lower site quality. Climatic variation between the years within a rotation may also influence the growth rate and result in different levels of productivity over successive rotations. It will therefore be necessary to take several estimates of PAI throughout a rotation and within seasons for this variable to be used in standing biomass predictions.

Total biomass generally increases with improved silviculture and higher site quality and stand age. Linder (1985) compared allocation to stem biomass as a fraction of AGB and demonstrated an increase in stem allocation with fertilisation, in irrigation and fertilisation experiments on *Eucalyptus* and pine species. This shows that improving the site quality not only increases total biomass, but also results in a greater allocation of biomass to the marketable stem portion. An increase in stocking will also produce an increase in biomass, up to a point where further stocking increases produce no further biomass increases. The point of optimal biomass with stocking is usually not the same as that for optimal marketable product.

3.7   Comparison of optical and destructive estimates of leaf area index

The use of dbh and age to estimate leaf area was more effective than dbh alone, (Figure C11, Table C11), and when plotted with PAI produced a better fit than LAI predicted by dbh alone, although yielding a similar relationship (Ghebremicael *et al.*, 2003). Sapwood area may also be used as a leaf area predictor, although a destructive measure, it can be predicted in this study from dbh and age. Leaf area index predicted by dbh was compared with remotely sensed normalized difference vegetation index (NDVI), to ascertain the effectiveness of satellite predicted LAI (Ghebremicael *et al.*, 2003). Sapwood area was not available during the analysis of the satellite study and dbh plus age was not tested in leaf area predictions. The ability of a non-destructive method to predict the leaf area of a canopy is useful where LAI is needed.

An increase in leaf area would require a greater area of sapwood as verified by Shinozaki *et al.* (1964) who found that plants conserved tree cross-sectional area so that the area of the stem is almost equal to that of the twigs. The 'Shinozaki Pipe Model' describes the plant form as a series of pipes packed together at ground level that diverge and branch away from each other. The

cross-sectional area of all the twigs combined is close to that of the base of the main branch and then to that of the main stem, so that the cross-sectional area is conserved (Shinozaki *et al.*, 1964). Deviations from the Pipe Model can, in most cases, be accounted for by the exclusion of the bark and the heartwood, only considering the living sapwood. There is a correlation between leaf quantity and the sapwood area of individual branches and the stems of the whole tree. Using sapwood area in this study may have compensated for heartwood and bark thickness, which may vary across site, age, and tree spacing.

Table 15 shows the PCA to slightly under predict LAI with a slope of 1.14, although to a lesser extent than that found in previous studies. In similar work by Battaglia *et al.* (1998) for *E. nitens* and Hingston *et al.* (1995), for *E. globulus,* the PCA was shown to under-predict the LAI by a factor of 1.51. The under-prediction of LAI by the PCA has been attributed to foliar clumping and scattering of light by the leaves, which are both deviations from the previously stated assumptions. Over-estimation attributed to the stems and branches accounting for a large portion of the PAI reading has been shown only when LAI is very low (Chason *et al.*, 1991; Smith *et al.*, 1991; Deblonde *et al.*, 1994). Differences between sites and ages could not be assessed in this study, as too few data points exist to form an unbiased regression.

Table 15: Regression predicting leaf area index from LAI-2000 plant area index.		
	d.f.	m.s.
Regression	1	179.379 [pr 0.001]
Residual	46	0.06613
Total	47	15.00889
r^2		0.895
SE		0.257
PAI (slope)		1.1396 [pr 0.001]
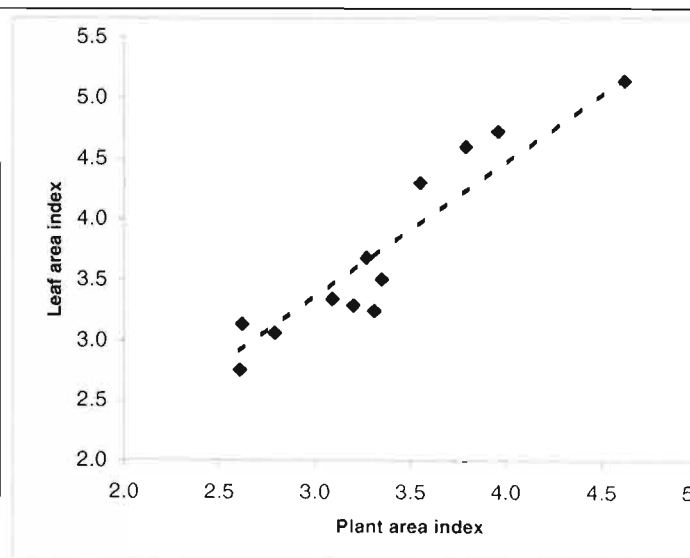
Figure 3.2 Observed LAI vs. LAI-2000-predicted PAI.

3.8 Intercepted radiation and growth

Photosynthetically active radiation consists of wavelengths of solar radiation that are utilized by plant biochemical processes in photosynthesis to convert light energy into biomass. The light energy in turn can be converted into the number of photons of light intercepted by foliage, which, in forests, is directly related to the quantity of carbon assimilated from the atmosphere (Landsberg and Waring, 1997). Approximately 47% of this assimilated carbon is lost through respiration and the remainder is partitioned between leaves, roots and woody biomass (Landsberg and Waring, 1997, Waring, 1998). Partitioning between stand components may be influenced (within limits) by growth resource availability. It follows that there should be some relationship between absorbed PAR and AGB produced (Linder, 1985; Beadle, 1997).

Forest growth may be linearly related to light interception, allowing for the correlation of growth with LAI or light interception (McMurtrie *et al.*, 1994; Battaglia *et al.*, 1998). Current radiation-use efficiency is dependent on vapour pressure deficit (VPD), temperature, and light and should decrease as the leaves age and with increased respiration as tree size increases (Mariscal *et al*, 1999). A decrease in efficiency effectively translates into less structural carbon sequestrated per unit water used or light intercepted. Linder (1985), in a study comparing species across Sweden, New Zealand and Australia showed a linear trend for light interception plotted against AGB production. The study compares pine and *Eucalyptus* species with deviations from the linearity being attributed to species differences or climatic stresses. A negative intercept for the linear trend in his study was attributed to varying levels of below ground allocation. The quantity of AGB produced per unit of intercepted PAR has been estimated as 0.45 g MJ^{-1} for *Eucalyptus* species in Australia (Beadle, 1997).

The quantity of light absorbed at a given LAI and the increase of light absorption with cumulative LAI is dependent on the canopy extinction coefficient (k) (Gazarini *et al.*, 1990). Intercepted PAR can be estimated by multiplying PAR with an interception fraction calculated using the equation after (Linder, 1985):

$$I = I_0 \times e^{-k \times LAI} \quad \textbf{Equation 13}$$

Where I is the flux density of radiation below the canopy and I_0 is the flux density of radiation above the canopy, LAI is leaf area index and k is the light extinction coefficient.

Dividing I by I_o gives the fraction of non-intercepted light below the forest canopy. This light fraction as recorded by the PCA is plotted as an exponential function (Figure 3.3). The light fraction recorded by the PCA assumes no scattering of light by the foliage (LI-COR, 1992). Equation 14 shows the exponential function (derived from Table 16) describing the reduction in below canopy light with increasing LAI. The constant in the equation may describe a 35% light interception by non-foliar portions of the tree canopy and the –k is the canopy extinction coefficient as in Equation 13. Plotting PAI and the fraction of non-intercepted light below the forest canopy give a constant of 1 (data not shown). It is therefore assumed that the constant in the LAI-based relationship is related to branch and stem attributes. The value of k calculated in this study is approximately 0.50 (Table 16) and is similar to that found in many other studies that estimate utilisable light in relation to LAI (Landsberg and Waring, 1997).

Fraction of non-intercepted light $= 0.651 \times e^{-0.495 \times LAI}$ **Equation 14**

Table 16: Nonlinear regression predicting extinction coefficient from leaf area index and fraction of light below the tree canopy.

	d.f.	m.s.
Regression	2	$0.0789889^{Fpr\ 0.001}$
Residual	10	0.0002494
Total	12	0.0133727
r^2		0.835
SE		0.0158
Constant		$0.651^{tpr\ 0.001}$
-k		$-0.495^{tpr\ 0.001}$
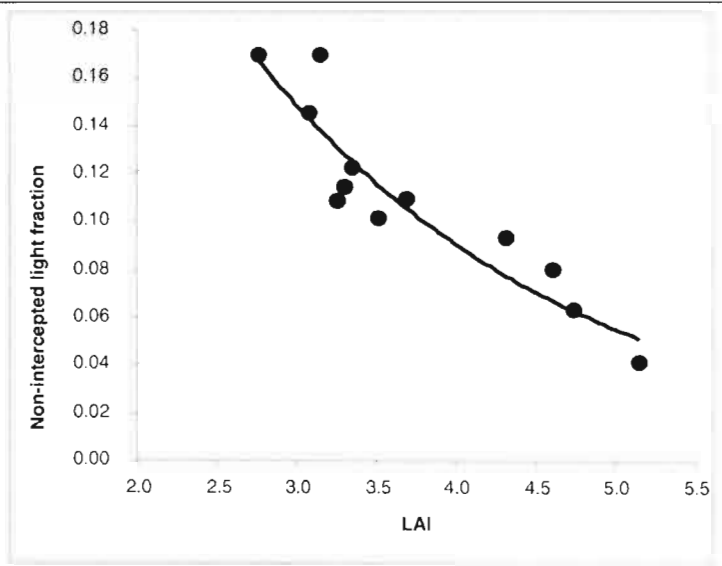
Figure 3.3 LAI plotted against non-intercepted light fraction.

Annual gridded estimates of radiation obtained from gridded estimates (Schulze, 1997) were converted into PAR by multiplying solar radiation by a factor of 0.45 (Newbould, 1967). With PAR as I_o, the extinction coefficient (Table 16) and allometrically derived LAI are used to calculated I using Equation 13. Intercepted PAR was calculated as the difference between I and

I_o. Above-ground productivity per unit of intercepted light energy was calculated by dividing annual AGB by iPAR.

Annual total PAR, iPAR and above-ground productivity expressed in energy units (g MJ^{-1}) of intercepted light energy are shown in Table 17. It is assumed that the LAI measured in the 5-11 year age group is a fair reflection of the average LAI during the rotation. This assumption may not hold for the 3-5 year old stands as the early development of LAI and growth rate are unknown, and can be strongly influenced by growth resource availability (du Toit and Dovey, 2004), hence it is excluded from Table 17.

The relationship between intercepted PAR and AGB is shown in Figure 3.4 to demonstrate the deviation of the 3 – 5 year age class from the older classes. A simple line is plotted through the 5 – 11 year old tree data to visually demonstrate the closeness to a linear relationship. Deviation from the line in young stands (Fig 3.4) may be due to higher initial LAI or faster growth as more leaves may be exposed to light, or soil water levels may have been higher early in the rotation. No regression was performed as this is not based on incremental growth data in relation to LAI or actual solar radiation. Solar radiation estimates were not adjusted for cloud cover effects as cloud cover was unknown.

Table 17: Annual PAR. iPAR, and AGB production per unit light energy for three sites in the KwaZulu-Natal Midlands.

Site	Age	Annual PAR (GJ m^{-2} yr^{-1})	iPAR (GJ m^{-2} yr^{-1})	AGB/iPAR (g MJ^{-1})
Bloemendal	5.8	3.60	2.83	0.56
Mistley	5.5	3.61	2.95	0.56
SeeleMtH	7.3	3.71	3.33	0.77
Bloemendal	7.8	3.60	2.80	0.46
Mistley	7.0	3.61	2.94	0.53
SeeleMtH	8.2	3.61	3.28	0.69
Bloemendal	9.8	3.62	2.68	0.41
Mistley	11.2	3.50	2.88	0.50
SeeleMtH	11.2	3.49	3.23	0.68
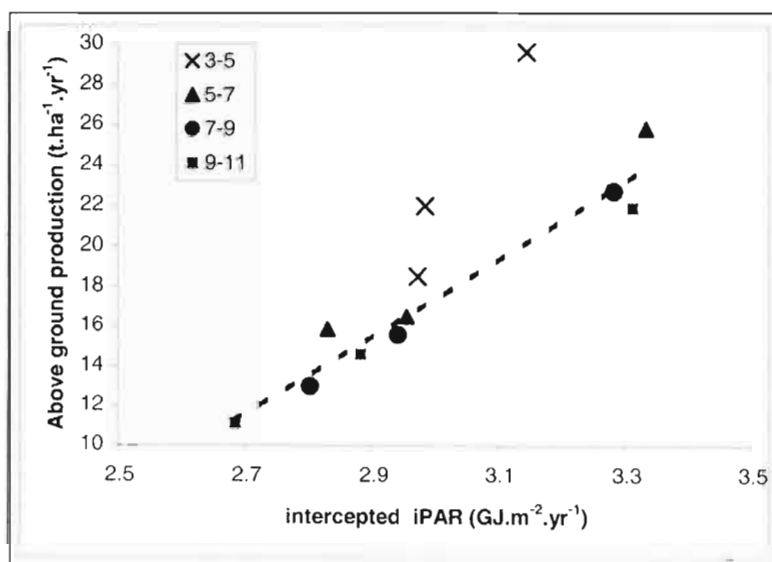
Figure 3.4 The relationship between AGB production and intercepted radiation (iPAR) for stands of different age.

Closure of the pinnules during water stress or high evaporative demand may also have caused a more negative intercept than that of Linder, (1985) in Figure 3.4. Stomata are found on both the adaxial and abaxial sides of the leaves, with the abaxial stomata remaining exposed after the pinnules have closed. It is unknown as to whether or not the stomata remain open after the pinnules close, allowing for continued transpiration. If they do remain open, then the leaves will continue to photosynthesise, but perhaps at a lower rate per unit total surface area as a result of a lower level of light interception. Pinnule closure may serve to partially reduce water loss, along with increased leaf heat loss by increased air movement. The interception of light by non-foliar portions of the tree canopy may also affect the relationship in Table 17, Figure 3.4 as these relate all intercepted light into AGB. Stem and perhaps branch area in relation to LAI changes with age and may contribute to different levels of light interception at various ages. This may need to be explored further with defoliated canopies in order to further the understanding of this issue.

3.9   Predictions of tree attributes with PAI

The good relationship between light interception and growth suggests that a light-based tool such as the PCA may serve as a useful instrument for current biomass estimation. This requires that a good relationship exists between PAI readings and some measure of yield or biomass. Relationship between productivity and age with PAI are shown in Tables D1 to D5 and Figures D1 to D5 (Appendix D), summarized as Equations 14 to 18 in Table 18. Measurement of PAI alone cannot be used to predict biomass as past growth or age is not taken into account; growth is cumulative and PAI is dynamic.

The use of PAI was preferred over LAI as PAI is an independent light-based measure of the canopy structure. Leaf area index and biomass are both predicted from dbh in this study and are thus related to each other. Although LAI may give rise to better predictions of each productivity estimate, the light-based estimate of PAI may be preferred as it is not possible to easily estimate LAI without using destructive harvesting. Plant area index determined here is that found in the post canopy closure (comparatively stable) state. Plant area index or LAI increases from near zero at planting to a maximum or peak value, decreasing after canopy closure to a relatively stable state (du Toit and Dovey, 2004). All PAI values in this study were measured during the stable phase.

Table 18: Equations to predict stand dimensions from plant area index.

Equation No.	Equation	r^2
14	BA (m^2) = 7.76 x PAI + 0.898 x age – 12.06	0.889
15	Vol (m^3) = 80.6 x PAI + 13.4 x age – 212	0.888
16	AGB (kg) = 60.97 x PAI + 11.57 x age – 156.7	0.896
17	Stem (kg) = 52.72 x PAI + 896 x age - 145	0.892
18	Bark (kg) = 5.417 x PAI + 1.387 x age - 15.59	0.967

A good relationship exists between PAI with age and stem volume, basal area, AGB, stem biomass and bark biomass at the stand level (Table 18). With known age and PAI, the relationships can be used to predict volume, stem biomass, and bark biomass for PAIs between 2 and 5, ages between 3 and 11 years. For example, a PAI of 3 at 10 years may be used to predict a volume of 164 m^3, a stem biomass of 103 t ha^{-1} and a bark biomass of 14.5 t ha^{-1}. These predictions are generated with a small number of points over a narrow range of biomass estimates. Additional sampling and measurements are required to make the predictions more robust and reliable.

Leaf area index and leaf biomass are the most site-sensitive tree components and are known to show great variation with age, season and site quality (Pierce and Running, 1988; Gower and Norman, 1991; Deblonde *et al.*, 1994). Leaf area index is required for the estimation of CO_2 flux, evapotranspiration, rainfall interception and dry atmospheric deposition (Chason *et al.*, 1991). Differences in growth rate may even be predicted between sites or silvicultural practices in terms of LAI differences that are presumably directly related to the availability of growth resources. Using LAI or PAI to predict growth or potential growth may have some merit, provided that the predictive relationships developed in this study are supplemented with wider ranging datasets. Leaf area index may in this manner be used as a supplement to site index as it may better represent short-term (annual) site changes and ranges in site quality. Site index is an integrated measure of site quality at a specific age, while LAI may be used as a dynamic assessment index.

CHAPTER 4: NUTRIENT DISTRIBUTIONS AND POOLS
RESULTS AND DISCUSSION

The nutrient pools and fluxes in South African black wattle stands (four age classes in each of three sites) are discussed in this chapter, with the implications of removal through various harvesting intensities. The three sites ranked into levels of productivity according to total AGB were as follows: Bloemendal is a low productivity site while SeeleMtH is regarded as a high productivity site. Mistley, although having no statistically significantly difference from Bloemendal (Table 14, p.49), is ranked as a medium productivity site for ease of reference. The concentrations of nutrients in each tree component are discussed in relation to norms for related species, tree component, site and age. Nutrient concentrations were used with the AGB data to estimate quantities of nutrients held in the various biomass components for the four age classes on the three sites. Nutrient contents are discussed in relation to the contribution of each tree component to the above-ground nutrient pool, termed nutrient distribution. These data were used to describe nutrient distributions in the AGB and to predict nutrient loss through various levels of harvesting intensity. Various harvesting intensities are shown in relation to nutrient removal with other inputs and outputs considered in a budget-type approach.

4.1 Nutrient concentrations

The mean concentrations of nutrients for each site in this study are compared with "adequate" ranges suggested for *A. dealbata* and *A. decurrens* (Boardman *et al.,* 1997) and foliar nutrient ratios relative to N after Linder (1995) in Table 19. The comparative values are from samples of young fully expanded foliage, while those in this study are from a mix of old and young foliage. Concentration differences between sites and age classes are shown with later reference to Table 21 and Table 22. All the macro nutrients presented in Table 19 are within the ranges described as adequate for *A. dealbata* and *A. decurrens*, except for P and K. The nutrient ranges show P to be lower than the optimal levels for the two other wattle species and K may be at the lower end of these acceptable ranges. Levels of Zn and Mn (especially for SeeleMtH) are lower than the reported range, but are not necessarily below required levels.

Table 19: Foliar nutrient concentrations and ratios of *A. mearnsii* as a mean of all ages and sites in contrast to "adequate" values cited in literature.

		Foliar nutrient concentrations			*A dealbata*	*A. decurrens*
Nutrient	Units	Bloemendal	Mistley	SeeleMtH		
N	%	2.52	2.66	2.98	2.40 - 3.90	2.04 - 3.00
P	%	0.09	0.10	0.10	0.10 - 0.17	0.35 - 0.80
K	%	0.56	0.72	0.78	0.55 - 0.93	0.65 - 1.00
Ca	%	0.63	0.55	0.49	0.12 - 0.86	0.33 - 0.47
Mg	%	0.21	0.19	0.20	0.14 - 0.22	0.15 - 0.20
Na	%	0.08	0.07	0.10	0.01 - 0.06	
Mn	mg kg^{-1}	143.2	86.6	23.4		195.0 – 325.0
Fe	mg kg^{-1}	333.8	241.0	223.7		
Cu	mg kg^{-1}	6.7	6.7	9.3		> 3.0
Zn	mg kg^{-1}	15.7	15.4	17.1		23.0 – 29.0

Foliar nutrient ratios relative to N (with N fixed at a value of 100)

Nutrient ratio	Ideal ratios [a]	Bloemendal	Mistley	SeeleMtH
N	100	100.0	100.0	100.0
P/N	10	3.5	3.7	3.4
K/N	35	22.4	27.1	26.3
Ca/N	2.5	24.8	20.9	16.4
Mg/N	4	8.4	7.2	6.6
Na/N	-	-	-	-
Mn/N	0.05	0.57	0.33	0.08
Fe/N	0.2	1.32	0.91	0.75
Cu/N	0.03	0.03	0.03	0.03
Zn/N	0.05	0.06	0.06	0.06

[a] Ratios for non-N-fixing species (conifers) after Linder (1995)

Fertiliser studies conducted on black wattle in the same areas as this study have shown an improvement in growth with additions of P and K at planting (du Toit, 2002a). The low values of P and K in Table 19 may therefore be a true indication of a nutrient limitation, although this should be determined from samples of young fully expanded foliage to be comparable to published norms. Foliar age and time of year may have affected the results here, as foliar

concentrations vary with age, time of year and canopy position (Grove *et al.,* 1996). Phosphorus concentrations are generally low, as is the case in the older, highly leached soils in the study area. With a relatively low rainfall, less leaching of Ca and Mg may occur. This may result in generally higher concentrations of these elements compared to higher rainfall sites.

4.2 Concentrations of nutrients in various tree components

Tree component nutrient concentrations across all ages and sites are shown in Table 20. Foliage generally had the highest concentration of all nutrients, except for Ca, which was highest in the bark. The stem generally had the lowest concentrations of all elements, except for K, which was lowest in the dead branches. Bark had the second highest concentrations only for N and Mg. Calcium, Mn and Fe concentrations were higher in the dead than in the live branches. Second-, third- and fourth-ranked levels of concentration were dependent on the plant part and element in question.

Table 20: Nutrient concentrations in each tree component across all ages and sites.

Part	N	P	K	Ca	Mg	Na	Mn	Fe	Cu	Zn
Foliage	2.72[a]	0.095[a]	0.689[a]	0.562[a]	0.200[a]	0.083[a]	88.15[a]	266.84[a]	7.58[a]	16.09[a]
Bark	1.01[b]	0.022[b]	0.280[b]	0.868[b]	0.098[b]	0.025[b]	21.78[b]	67.41[b]	1.46[b]	4.54[b]
Live branches	0.66[c]	0.030[c]	0.358[c]	0.228[c]	0.071[c]	0.030[bc]	22.95[bc]	80.42[c]	3.18[b]	9.79[c]
Dead branches	0.44[d]	0.013[d]	0.052[d]	0.268[c]	0.055[d]	0.014[c]	31.02[bc]	136.90[c]	2.75[c]	6.44[d]
Stem	0.15[c]	0.008[d]	0.076[d]	0.052[d]	0.019[c]	0.012[d]	11.38[c]	23.19[d]	1.32[c]	1.17[e]
LSD	0.084	0.0053	0.0805	0.0117	0.0586	0.0106	14.230	18.980	0.704	1.309

Components with different superscripts in a given column are significantly different at $p < 0.01$; LSD = least significant difference.

The order of concentrations of P, Ca and Mg were similar to those in a South African *A. mearnsii* study by Williams (1927), with K concentrations in the live branches lower than in the bark. An age series study by Tandon *et al.* (1988) in India, which excluded dead branches, yielded a similar order of concentrations for the macronutrients, except for K, where bark concentrations were higher than the live branches concentrations. A Brazilian *A. mearnsii* study by Calderia *et al.* (2000a) on 2-year-old trees revealed a similar order of concentrations as this study for N, K, and Mg. Calcium concentration was slightly higher in the foliage than the bark in that study, while P concentration in the bark was higher than in the live branches.

E. globulus and *Eucalyptus* clone studies have also given similar patterns with concentrations of N, P, K and Mg highest in the leaves, and Ca highest in the bark (Judd *et al.,* 1996; Laclau *et*

al., 2000). A study in Congo on *Eucalyptus* clones (Laclau *et al.,* 2000) showed P, Ca and Mg concentrations to be higher in the live branches than in the stem, as in Table 20. Nitrogen and Mg followed the same trend as data calculated from a South African *E. grandis* study (du Toit and Scholes, 2002), with an increase in concentration from the stem to the branches, bark and foliage, respectively. The *E. grandis* study shows P and K to have lower concentrations in the live branches than in the bark. Calcium and Mg followed the same trend in the *E. grandis* study as in this study, except that the bark Mg concentrations were higher than the foliar concentrations in the *E. grandis* study. The orders of concentrations was also the same for N, P, K and Ca, in 7-year-old trees in Brazil (Pereira *et al.,* 2000) although dead branch concentrations of P and Ca were higher than the stem concentrations. Magnesium followed a similar order of concentrations in the 7-year-old trees in Brazil as in this current study, except that the bark concentrations were lower than the live branch concentrations.

Concentration differences between plant parts are due to differences in nutrient sink strengths (associated with metabolic rates) between tree components (Raven *et al.,* 1992). Large differences in concentration between the live branches and the leaves may point to leaves as a stronger sink for nutrients. Lowest concentrations of K in the dead branches may be mostly due to high levels leaching from the dead branches by rainfall and not only re-mobilisation during branch senescence. Actively growing and metabolising plant parts such as the cambium, meristem and the foliage will have a greater demand for most nutrients (Raven *et al.,* 1992).

4.3 Concentrations of nutrients in relation to site and age class

Tree component concentrations that are significantly different between sites, and between age classes are summarised in Tables 21 and 22, respectively. Foliar N, K and Cu concentrations were lower, and Mn and Fe higher for Bloemendal than SeeleMtH. Magnesium concentration was lowest and Zn was highest in the live branches at SeeleMtH. Stem wood P and Ca concentrations were lowest at SeeleMtH, while Cu was lowest at Bloemendal. Dead branch N and Cu concentrations were highest and P concentrations the lowest at SeeleMtH. All other element concentrations showed no significant differences between sites. Iron concentration in the leaves and N in the dead branches (Db) was higher in older age classes than the younger (Table 22). Stem wood Zn concentration was highest at age 7 – 9 years, with no age related trends. All other element concentrations showed no significant differences between age classes.

Table 21: Nutrients with significantly different concentrations between sites.

Component	Leaves					Live branches		Stem wood			Dead branches		
	N	K	Mn	Fe	Cu	Mg	Zn	P	Ca	Cu	N	P	Cu
Nutrient	(%)	(%)	(mg kg^{-1})	(mg kg^{-1})	(mg kg^{-1})	(%)	(mg kg^{-1})	(%)	(%)	(mg kg^{-1})	(%)	(%)	(mg kg^{-1})
Bloemendal	2.52^a	0.56^a	154.1^a	333.8^a	6.72^a	0.08^a	9.75^{ab}	0.012^a	0.06^a	0.58^a	0.38^a	0.016^a	1.82^a
Mistley	2.66^{ab}	0.72^b	86.6^b	241.0^b	6.68^a	0.07^{ab}	7.26^a	0.009^a	0.05^{ab}	1.96^b	0.43^a	0.014^a	2.60^a
SeeleMtH	2.98^b	0.78^b	23.7^b	225.7^b	9.35^b	0.06^b	12.36^b	0.004^b	0.04^b	1.42^b	0.51^b	0.009^b	3.82^b
LSD	0.333	0.129	65.30	41.59	2.049	0.017	3.880	0.0030	0.011	0.812	0.062	0.0043	1.206

Components with different superscripts within a column are significantly different at $p < 0.05$; LSD = least significant difference.

Table 22: Nutrients with significantly different concentrations between age classes.

Age Class	Fe-leaves (mg kg^{-1})	Zn-Stem (mg kg^{-1})	N-Db (%)
3-5	221.9^a	0.72^a	0.39^a
5-7	266.5^{ab}	1.55^b	0.42^a
7-9	276.3^b	1.66^b	0.45^{ab}
9-11	302.7^b	0.75^a	0.52^b
LSD	48.02	0.724	0.072
F. probability	0.032	0.033	0.022

Components with different superscripts within a column are significantly different at $p < 0.05$; LSD = least significant difference.

There were no real relationships between nutrient concentrations and productivity between the sites or age classes. Above-ground biomass for these sites, (Table 14; p. 49) show Bloemendal and Mistley to have no significant differences in productivity. However, Table 21 shows concentration differences between these sites for some elements in various plant parts. SeeleMtH, which was very different in productivity from both Bloemendal and Mistley, had little or no significant differences in concentrations compared with these lower producing sites. There is, however, a trend of increasing foliar N and Mg concentration, and decreasing branch K and stem wood P and K concentration in comparing the low, medium and high productivity sites.

This study shows lower concentrations of some nutrients on better sites, which may be a result of soil supply differences (due to differences in base status), or plant tissue dilution with faster growth on higher quality sites. A higher nutrient concentration may not be interpreted as an indication of better growth potential, although increased foliar N may be a result of improved N-fixation on the better sites. Favourable soil conditions that increase tree carbohydrate supply to the root nodules have been shown to increase N-fixation (Binkley and Giardina, 1997). Soil water, aeration and subtle P supply differences between the sites may have influenced the rate of N-fixation either directly at the root nodule level, or indirectly by increasing tree carbohydrate supplies to the root nodules.

4.4   Concentration as an efficiency indicator

Concentration of nutrients in a harvested component may be used as an indication of nutrient use efficiency. Lower stem P and K concentrations and higher stem biomass on the better quality SeeleMtH site may translate into superior levels of nutrient use efficiency. The same principle applies to live branch K and dead branch P concentration. However, a larger biomass production will mostly result in higher levels of nutrient removal on better sites than on poorer sites, regardless of concentration differences between sites. Black wattle, with higher N concentrations, may appear to use N less efficiently than other species, which may be due to luxury consumption levels through N-fixation. Soil N availability may not be driving the high N concentrations.

4.5   Factors that may have influenced concentrations

High levels of variability between concentrations within sites and age classes have resulted in low significance levels between ages and sites. Any trend may be due to the sample collection strategy as seasonal differences in samples occurred (samples collected in early summer at Bloemendal compared to late summer at SeeleMtH). This may be related to mobilisation or

immobilisation of nutrients in the trees and forest floor, or climatically driven changes in soil nutrient uptake throughout the season. Differences between sites may also be a result of differences in soil supply potential or dilution within fast-growing plant parts. A similar underlying shale geology intruded by dolerite across all the sites in this study may have resulted in too narrow a range in soil chemical properties to allow for large differences in nutrient concentrations.

4.6   Nutrient distribution in the above-ground biomass

In Table 23 nutrient proportion data calculated from this study are compared with other studies on *A. mearnsii* in South Africa (Williams, 1927) and Brazil (Pereira *et al.*, 2000), and with *E. grandis* (du Toit, 2003) and pine (Carlson and Allen, 2001) data from studies in South Africa. All masses in Table 23 have been "normalised", for comparative purposes, to a utilisable stem mass of 100 t ha^{-1} by expressing nutrient distribution as a percentage of the total. This allows for a comparison of relative differences in nutrient export per unit biomass produced, with a fixed stem production. The original total AGBs for each study were 160, 217, 159, 135, 161 t ha^{-1}, respectively. Both stem and bark are commonly removed in black wattle and pine harvesting, while stem-only removal is practiced with *Eucalyptus*. Each element is shown as a nutrient mass percentage contained in each tree portion in relation to above-ground total nutrient mass.

The biomass distributions are relatively similar for the five studies in Table 23 with some small differences in stem and branch mass proportions. Nutrient distributions differ in relation to nutrient element and study in question. Potassium had the greatest fractions in the branches, followed by the bark, stem and foliage, respectively. Calcium had the greatest fraction in the bark, while Mg fractions were highest in the stem for the black wattle studies. The P distribution in this study decreased from the branches to the stem, foliage and bark, respectively. Nitrogen percentage was the lowest in the foliage in this study, but second highest in the pine and *E. grandis* studies.

Although the foliage comprises only 3% to 5% of the AGB in each study shown in Table 23, this component contains a relatively large portion of individual nutrients (10% - 30%). Although bark comprises only 9% of the AGB in this study (Table 23), it contains one third to one half of the above-ground Ca, due to the relatively high concentrations of this element (Table 20). The opposite is true for nutrients held in the stem wood; with a relatively high proportion of stem mass, nutrient proportions are relatively low. These differences are mostly due to large concentration differences between tree components (Table 20). The canopy portions (branches and leaves) shown in Table 23 comprise 21% of the AGB, but contain between one and two thirds of the nutrients held in these components. In most cases, the stem wood and bark

combined contained most of the above-ground nutrients, due to the high stem mass proportion (70%) and the high bark concentrations.

Nutrient masses and distributions are not similar when comparing the three black wattle studies in Table 23. The total N fraction for the Brazilian study was notably different in both mass and nutrient distribution compared to this study. Stem concentrations of N in the Brazilian study were six times higher than in this study. The proportion of nitrogen was lowest in the branches of the seven-year-old trees in the Brazilian study (7%), but was highest in this study (29%). The other South African study (Williams, 1927) shows a similar distribution of most nutrients compared to this study, except for K. In comparing wattle in this study with the South African pine and *E. grandis* studies, some apparent differences and similarities in nutrient distributions can be seen. The black wattles in Table 23 seem to be more efficient than the other species in the total quantity of P held in the AGB with respect to total biomass production. Calcium was the only element in this black wattle study that had a similar distribution to the *E. grandis* and pine studies, while the distribution of P compared only with the pine study. The black wattles contain far greater amounts of K and P in the stem and bark than the pines.

The proportion of biomass exported by stem-only removal in *A. mearnsii* appears higher than the pine and *E. grandis* studies, and even higher with bark included. Wattle holds, in the potentially harvested products, more N and K than the other species, and more Ca and Mg than the *E. grandis*. Large proportions of Ca and Mg are potentially removed in black wattle harvesting and since *Eucalyptus* is debarked on site a much smaller portion of Ca is potentially exported. The fraction of P is similar for the potentially harvested portion between species. Almost half the P contained in the ABG is exported through black wattle and pine bark and stem harvesting and stem-only harvesting of *Eucalyptus*.

Table 23: Distribution of above-ground macronutrients for stands of *A. mearnsii*, *E. grandis* and *Pinus patula*, equalised to 100 t ha^{-1} of utilisable stem mass.

Species	Element	Total (kg ha-1)	Distribution (%)					Common harvesting (%)
			Stem	Bark	Branches	Leaves	Capsules	
A. mearnsii RSA [1]	AGB (t ha-1)	142.9	70	9	18	3	-	79
A. mearnsii RSA [2]		134.7	74	9	11	5	-	83
A. mearnsii Brazil [3]		126.8	79	9	10	3	-	88
E. grandis RSA [4]		148.7	67	7	19	4	2	67
P. patula RSA [5]		156.8	64	9	23	5	-	73
A. mearnsii RSA [1]	N	540.8	26	24	29	21	-	50
A. mearnsii RSA [2]		nd	nd	nd	nd	nd	-	nd
A. mearnsii Brazil [3]		1207.4	72	11	7	10	-	83
E. grandis RSA [4]		344.4	32	10	20	29	8	32
P. patula RSA [5]		428.4	21	16	34	29	-	37
A. mearnsii RSA [1]	P	20.4	30	14	35	20	-	44
A. mearnsii RSA [2]		16.1	35	16	35	16	-	50
A. mearnsii Brazil [3]		12.5	16	22	33	30	-	38
E. grandis RSA [4]		32.0	45	10	17	17	10	45
P. patula RSA [5]		46.1	26	17	34	23	-	43
A. mearnsii RSA [1]	K	200.6	34	18	33	15	-	52
A. mearnsii RSA [2]		219.5	44	16	13	27	-	59
A. mearnsii Brazil [3]		160.7	13	26	42	19	-	39
E. grandis RSA [4]		243.9	30	14	30	14	12	30
P. patula RSA [5]		138.2	14	18	45	24	-	32
A. mearnsii RSA [1]	Ca	241.0	20	46	24	10	-	66
A. mearnsii RSA [2]		283.4	46	30	12	13	-	75
A. mearnsii Brazil [3]		279.1	34	38	14	14	-	72
E. grandis RSA [4]		348.8	20	34	24	14	7	20
P. patula RSA [5]		112.2	20	36	28	16	-	57
A. mearnsii RSA [1]	Mg	55.7	33	23	29	15	-	55
A. mearnsii RSA [2]		74.4	58	12	13	17	-	69
A. mearnsii Brazil [3]		102.7	43	20	20	17	-	63
E. grandis RSA [4]		117.0	18	33	27	14	8	18
P. patula RSA [5]		83.3	17	24	49	10	-	41

Superscripts denote data from [1] This study; [2] Williams (1927); [3] Pereira *et al.* (2000) ; [4] du Toit (2003); [5] Carlson and Allen (2001) (Nutrient distributions for all sites and ages in Table E1, Appendix E); nd refers to not determined

Biomass distribution changes with site and age (Table 14), with increases in proportional stem mass on the higher quality sites and decreases in proportional masses of all other components. Using a general mean concentration per tree component across all sites and age classes will result in an increase in the proportion of nutrients held in the stem relative to the total. However, lower concentrations of live branch K and stem wood P and K for the higher quality sites (Table 21) influence the nutrient proportions between sites by dampening the effects of the proportional biomass differences between them (see Table E2, Appendix E).

In most cases, the nutrient distributions in this study did not completely agree with those in the other black wattle studies. This may be due to different sampling strategies, time of sampling, or laboratory analysis techniques. It is highly likely that the nutrient status of the trees may have also affected the distributions in these studies. The distinction between utilisable and non-utilisable stem may have been different in each of the black wattle studies, resulting in different stem or branch proportions. The study by Williams (1927) did not include dead branches in the calculations, and the pine study used live branch nutrient concentrations to calculate dead branch nutrient masses.

4.7 Harvesting practices and nutrient removal

Average nutrient masses for components of 7- to 11-year-old *A. mearnsii* stands are shown in Table 24; masses of all nutrients for all ages and sites shown in Table E1 (Appendix E) and per tree component in Tables F1 to F3 (Appendix F). Harvesting intensity has a large influence on the quantity of nutrients removed. In most cases, bark and stem harvesting increases removal of P, K and Mg by one third and triples Ca removal compared to stem-only harvesting. Adding 75% branch harvesting (as a percentage of total branches) doubles removal for P, K and Mg, and increases Ca removal four fold. Branch removal increases removals of all nutrients by about one third in all cases relative to stem and bark harvesting. Compared to stem-only harvesting, N removal is doubled and tripled by addition of bark and branches, respectively. A 75% branch removal in addition to stem harvesting, increases potential K and Mg export by a third, and doubles nutrient removal of all other nutrients.

Table 24: Average nutrient masses (kg ha^{-1}) for 7 to 11 year old stand components of *A. mearnsii* .

	Stem	Bark	Branches	Leaves	Total
AGB	112.5	15.3	27.5	4.6	159.9
N	159.6	144.5	174.2	128.1	606.4
P	7.1	3.3	8.1	4.7	23.2
Ca	52.7	125.7	64.9	26.6	269.8
Mg	20.3	14.1	18.3	9.4	62.1
K	73.8	41.0	74.3	32.8	221.9
Na	11.7	3.4	6.8	3.7	25.6
Mn	5.2	1.7	3.2	3.1	13.3
Fe	10.1	5.4	12.8	11.0	39.3
Cu	0.5	0.1	0.4	0.3	1.4
Zn	0.6	0.3	1.3	0.7	2.9

Total nutrients held in the AGB are shown in Appendix E, Table E2

In past studies little work has been conducted on micronutrients contained in the biomass and the effects of biomass removal. Losses of these nutrients are not seen as important an issue as macronutrients losses. A micronutrient deficiency is easy to remedy by small soil or foliar fertiliser additions to the forest system. Micronutrients are distributed similarly to the macronutrients, with the stem and branches containing large proportions (Table E2, Appendix E), with the bark containing the smallest proportions of these nutrients in all cases.

Although this study shows high levels of potential K export through biomass removal, this estimate may be altered by increased K losses from soils through base cation leaching and in-field leaching of K out of the harvested biomass. Losses in harvesting may be reduced by allowing the biomass to stand for a short period on the site after clear felling. This will allow the K, which is found only as a soluble salt in plant tissue, to leach from the biomass, thereby reducing the quantities removed (Mackensen, *et al.*, 1996*)*. It is uncertain as to how long it would take for optimal leaching to occur, or how prevailing weather conditions affect this, although the timber quality may deteriorate if left too long on the site. Branches are left in the field to dry before firewood collection, which may drastically reduce the amount of K contained in the branches.

4.8 Simple nutrient budgets

An incomplete nutrient budget for the mean of the 7- to 11-year-old stands, showing all the major processes involved in adding and removing macronutrients from the forest system is

presented in Table 25. This budget technique gives no indication of the soil supplying potential of the sites involved. Additions by fertiliser have been calculated from South African forestry recommendations (du Toit, 2002a) and losses by harvesting are calculated from data in this study. Burning, assuming moderate intensity fires and branch removal (firewood as 75% of branches and tree tops), have been included as common practices in South Africa. Unknown additions and losses have been estimated or set to general values taken from other studies as listed in Table 25. Erosion losses have been assumed low, as occurs with responsible silvicultural practices. Responsible practices that minimise erosion allow only one of the following: steep slopes, soil tillage or residue burning (du Toit, 2002b). All fluxes regarded as uncertain in wattle stands have been shaded.

The influences of N-fixing trees on soil nutrient sustainability may differ from other tree species, although N additions may compensate for harvesting removals. There is, however, uncertainty with regards to the amount of N added to the site, although estimates are between 50 and 150 kg N ha^{-1} yr^{-1} (Binkley and Giardina, 1997). Leaching losses are unknown for all the elements, although leaching of P may be low due to P-fixing soils, and low levels of available P. Leaching in Table 25 is estimated from a catchment study of a pine plantation on shale-derived soils. The accelerated rate of base cation leaching (K, Ca and Mg) under N-fixing conditions due to associated high leaching rates of NO_3^- anions coupled with these cations is also uncertain (Binkley and Giardina, 1997). The losses of these elements may be far higher in this study than stated in Table 25, provided that the rainfall is high enough to leach them below the rooting zone. Johnson et al. (1988) and Van Miegroet and Cole (1984) compare leaching in *Alnus rubra* and Pseudotsuga menziesii showing a ten-fold increase in base cation leaching under the N-fixing *A. rubra* compared to the P. menziesii. The leaching of Ca and Mg were 10 times greater and K two times higher in the N-fixing trees. The soils in their studies were, however, far richer in base cations than those in the catchment study in Table 25.

The resultant budget balance cannot be calculated, as there is both missing and uncertain data. Various levels of harvesting in Table 25 show relatively large amounts of potential K, Ca and Mg export, increasing with higher harvesting intensities. For instance, the harvesting of bark in addition to stem wood greatly increases the quantities of nutrients exported (15% – 50% increase), although the bark constitutes only 9% of the AGB.

Table 25: Simple representation of an annual nutrient input-output budget for the 7 to 11-year old stands showing areas of limited knowledge and data needs.

Nutrients	N	P	K	Ca	Mg	Reference
Annual system inputs (kg ha^{-1} y^{-1})						
Atmospheric deposition	15.2	1.0	8.6	20.7	4.5	(Van Wyk, 1990); (Lowman, 2003)
Weathering	0.0	0.2	1.9	1.7	0.3	(Owens and Watson(1979), (Fey, cited in Scholes and Scholes 1999)
N-fixation	50-150	0.0	0.0	0.0	0.0	(Binkley and Giardina, 1997)
Fertilisation	0.0	1.5-3.0	0.0-3.0	0.0	0.0	(du Toit, 2002a)
Total Inputs	65-165	2.7-4.2	10.5 - 13.5	22.4	4.8	
Annual system losses (kg ha^{-1} y^{-1})						
Leaching	Pot. high (1.0)	Low (0.10)	Pot. high (2.3)	Pot. high (8.0)	Pot. high (7.3)	(du Toit, 2002a) (Simpson 1991)
Erosion	0.2	0.05	0.5	0.05	0.2	(du Toit and Scholes, 2002)
Burning losses	Pot. high 11.2	Low 0.80	Low 3.6	Low 0.5	Low 0.9	(Beard, 1961) (du Toit and Scholes. 2002).
Totals with: Stem-only removal	>>16.2	>0.76	>>7.9	>>5.3	>>2.2	This study
Stem and bark removal	>>30.6	>1.09	>>12.0	>>17.9	>>3.6	This study
Stem, bark and 75% branch removal	>>43.7	>1.70	>>17.6	>>22.8	>>5.0	This study

Low and Pot. high implies low and potentially high values may occur, *respectively*, for reasons given in the text.

> Implies greater than value shown.

>> Implies much greater than value shown, due to uncertainty in the shaded cells
(Greater values are expected with leaching and burning losses).

Assume responsible silvicultural practices that minimise erosion.

A general idea of whether the nutrient budget is negative and to what extent the losses exceed the gains can be judged in some cases without knowledge of losses by leaching and burning on a specific site. However, caution is needed with an N-fixing crop as mobile anions are added to the system through N-fixation, and subsequent nitrification, increasing base cation leaching. Nitrogen, due to high inputs from fixation, may have a strongly positive budget balance with a net gain to the forest system. Phosphorus in the absence of fertilisation additions may tend towards a negative budget. Soil fixing or immobilisation of P also reduces the availability of atmospheric or fertilisation P additions, especially under N-fixing trees. In areas where the

intensity of harvesting is high with stem, bark and branch removal, additions may not compensate for the losses. The leaching and hence final balance of base cations may far exceed that replaced by natural inputs. These losses need to be quantified in order to truly assess the severity of losses.

CHAPTER 5: CONCLUSIONS AND RECOMMENDATIONS

The indications from this study are that simple allometric measures do exist between component masses or area and tree dimensions for *A. mearnsii*. Diameter at breast height is the easiest tree dimension to measure that can be used to predict stem and bark biomass irrespective of site or age, while the prediction of branch biomass, foliage biomass and leaf area may be site- and age-dependent. Leaf area index can be assessed with optical measures and the optical estimations may be used to predict yields. Certain relationships do change with site and age, although these changes can be attributed to stocking changes, affecting branching or age and branch retention, resulting in higher dead branch masses with increased age. As implied by the data in this study, a higher productivity site can result in more tree resources being allocated to stem biomass production as opposed to foliage, branches and bark. High site quality results in not only higher levels of total biomass, stem wood and bark, but lower percentages of harvesting residue. Harvest residue comprises mostly branches and leaves left behind on the site after a harvesting operation has been completed.

Management practices that optimise stocking for a site may thus result in less resources being allocated into branches and more into the leaves. Stocking optimisation also reduces the incidence of disease, increases bark quality and allows for easier bark stripping (Sherry, 1971). As plantation fires are fueled by the forest floor (comprised mainly of plantation residue and fallen dead branches), a reduction in branches will reduce the fuel load and fire risk. This may need to be considered in terms of the decomposition rates of a site, as cooler sites may have a lower branch proportion but a higher level of forest floor fuel load due to slower decomposition rates. A benefit of having larger and more numerous branches is in supplying the firewood fuel needs for the local community around a site. The high-density wood is preferred as a source of firewood having a high calorific value and low ash content (Sherry, 1971). However this firewood removal may affect the sustainability of the forest, as valuable nutrients may be removed from the site.

As the bark yield is estimated in terms of site index and bark to stem ratios, an improvement in site quality will reduce the bark to stem ratio. This may result in an over prediction of bark yield on the sites with higher site quality or an under prediction on poorer sites, if simple prediction parameters alone are used. A separate study by Schönau (1978), shows a similar decrease in bark to stem ratio and bark thickness with increased SI. He formulated a prediction of bark based on mean dbh, latitude and site index. In his model, an increase in latitude and site index predicted a reduction in bark biomass relative to the stem size.

Bark biomass, stem biomass and the ratios between bark and stem biomass in this study are similar to those calculated in Schönau's study. In that study, bark to stem ratio ranged from 14% on good sites to 22% on poorer sites, calculated on a wet biomass basis, compared to 14% to 20% wet biomass ratios for this study. Samples in the study by Schönau (1978) were not oven-dried, but air-dried, so direct dry biomass comparisons cannot be made.

Root biomass was not estimated in this study, although it is a valuable component in understanding the allocation of resources between plant parts. Including coarse and fine roots in the biomass estimations will change the reported proportional allocation to whole tree biomass allocation. Growth efficiency and WUE values are calculated based on AGB, as very few studies exist that include root biomass estimation. Calculations of total plantation biomass and turnover would require the inclusion of forest floor biomass, litterfall, root turnover and soil organic matter in this study. Calculations of gross primary production or total mass of carbohydrates assimilated would require measurements of plant and soil respiration.

The information in this study may be used to estimate some of the parameters for the 3-PG process based growth model for *A. mearnsii*. Observed final volumes, component masses and LAI compared to 3-PG predicted values might be used to test the predictive ability of the model for the 12 plots in this study. This would form a simple validation of the model across the three sites and four age class range in this study. In a simple model parameterisation study by Dicks (2001) undertaken for *A. mearnsii* in South Africa for one age over two sites the constant and power in the Ws predictive equation were found to be 0.12 and 2.52 respectively. The values in this study were found to be 0.11 and 2.57 respectively (data not shown). The foliage to Ws ratio in this study was around 0.03 while that calculated by Dicks (2001) was approximately 0.15, for trees having a dbh of 20 cm. Dicks (2001) reported the branch and bark fraction of Ws to be 0.4 at canopy closure and 0.3 for mature trees while in this study, trees had values ranging from 0.2 to 0.4.

Satellite normalized difference vegetation index data taken in conjunction with the biomass data can be compared and may be used to form models to predict the total tree biomass or biomass of the tree components. This would be useful in remotely assessing the productivity of *A. mearnsii* sites across a broad spatial area. Optically predicted biomass with the PCA can be very useful for rapid assessments of current plantation production. Even though important variables such as timber and bark masses can be predicted with these relationships, the range in tree sizes needs to be extended to both larger and smaller trees. Drier sites need to be added to the dataset as well as wetter sites to further extend the observations made in this study. The data forming the PAI

predictions of volume and basal area can easily be appended or validated by recording PAI for sites where the age, volume and basal area are known.

Using spatially estimated PAR with the PAR-based biomass predictions in this study can be used to generate a spatial prediction of productivity for black wattle provided LAI is known. The linear relationship assumes a direct relationship between biomass production and intercepted light. Prediction of LAI from soil, climatically or remotely sensed variables might enable the model to estimate the maximum potential productivity on any site. Past droughts, diseases or pest infestations may reduce the actual productivity of a site and estimates of productivity may be higher than the actual when based on current LAI values.

Relationships between components and the effect of site quality in terms of water availability and nutrient status can be best validated by the establishment of trials that use irrigation and fertilisation as the basis of their treatments assessing the effects on biomass and allocation of biomass. Trials of this type would need to be replicated through a range in areas with greater temperature and VPD differences. Data from this work point to trends and relationships that exist within and across an age and site series of commercial *A. mearnsii* plantations that may be used in planning new hypotheses, only to be tested through more complex trial designs.

Relatively small differences in concentrations of nutrients between sites and age classes in this study may allow for a universal concentration to be used for each tree component and nutrient. This may be applied to other biomass studies to generate nutrient contents. The influence of site on nutrient concentration is not as great as it is on biomass in this study; even with slightly lower concentrations, an increase in biomass results in greater removal of nutrients.

Nutrient pool sizes are dependent on biomass pools sizes of various tree components with different biomass levels responsible for different nutrient exports. Structures that increase in biomass with age will hold more nutrients and therefore contribute relatively more to the export of nutrients with harvesting. Higher quality sites with larger biomass will result in larger nutrient export. Harvesting intensity and choice of component harvested has a great influence on nutrient export. In areas where bark is harvested, the soil supply of nutrients needs to be considered in relation to the quantity that is removed in harvesting.

This study may be useful to the forest plantation industry in determining the availability of branch (fuel wood) resources. Having an idea of the nutrient removal involved in removing the branches from a site will help managers to decide whether or not branch collection should be allowed. If nutritional sustainability is included as a criterion in certified plantation forestry

practices then this study will assist in providing basic data of nutrition loss through harvesting. This can be weighed-up in a nutrient budget approach with respect to the available nutrients on a site to assess the nutrient loss in relation to site nutrient reserves. The losses of the macronutrients are large in relation to the amounts that are added by natural processes and may need to be supplemented with fertilisation. Calcium and Mg may be relatively cheap to replace where lime and gypsum are freely available, but K is often expensive to replace, but should be considered in areas of low soil supply.

The information on the processes that make up the nutrient budget is inadequate. The pools of nutrients in the soil and forest floor as well as the fluxes and cycling of nutrients in and between the pools needs to be quantified. There is clearly a need to improve estimates of fixation, leaching and burning losses in wattle in relation to atmospheric inputs, stand parameters and management practices such as burning. Much more work is needed in assessing the long-term changes of soil chemistry and fertility under N-fixing *A. mearnsii*. Simple models need to be compiled to allow growers to assess these issues in relation to their growing conditions. Using the nutrient budget approach in conjunction with nutrient pool information may be a useful tool in supplying information to help growers maintain the soil nutrient supply and hence sustain productivity. This information needs to be synthesised into a practical recommendation so that forest managers can be familiarised with the impacts of various management practices on fertility, productivity and sustainability in general. Developing such strategies requires additional soil process research over broader soil types and growing conditions.

REFERENCES

Allen, J.A. Pimentel, D.P. and Lassoie, J.P. 1988. Fuelwood production and use in rural Swaziland: A case-study of two communities. *Forest Ecology and Management* 25(3-4):239-254.

Art, H.W. and Marks, P.L. 1971. A summary table of biomass and net annual primary production in forest ecosystems of the world. *Forest biomass studies IUFRO-Section 25. XVth IUFRO Congress*, Gainesville, Florida, USA, March 15-20.

Bartelink, H.H. 1998. A model of dry matter partitioning in trees. *Tree Physiology* 18:91-101.

Battaglia, M. Cherry, M.L. Beadle, C.L. Sands, P.J. and Hingstone, A. 1998. Prediction of leaf area index in eucalypt plantations: effects of water stress and temperature. *Tree Physiology* 18: 521-528.

Beadle, C.L. *1997*. Stand development and productivity. In: Nambiar, E. K. S. and Brown, A. G. (*eds*) Management of Soil, Nutrients and Water in Tropical Plantation Forests. p.169-*212*. Australian Centre for International Agricultural Research (ACIAR), Canberra.

Beard, J.S. 1961. Further Evidence on Burning Versus Non-Burning In Wattle Silviculture. *The South African Forestry Association* 38:7-10.

Binkley, D. 1986. Harvesting, site preparation, and regeneration. In: Binkley, D. (ed). *Forest nutrition management* Wiley, New York, pp.161-187.

Binkley, D. and Giardina, C. 1997. Nitrogen-fixation in tropical forest plantations. *In: Nambiar, E. K. S. and Brown, A. G. (eds)* Management of Soil, Nutrients and Water in Tropical Plantation Forests. Australian Centre for International Agricultural Research (ACIAR), Canberra. pp.169-212

Birk, E.M. 1992. Biomass and nutrient distribution in radiata pine in relation to previous land use 1. Biomass. *Australian Forestry Research* 55:118 - 125.

Birk, E.M. 1993. Biomass and nutrient distribution in radiata pine in relation to previous land use. II. Nutrient accumulation, distribution and removal. *Australian Forestry Research* 56(2):148-156.

Boardman, R. Cromer, R.N. Lambert, M.J. and Webb, M.J. 1997. Forest plantations. *In:* Reuter, D.J. and Robinson, J.B. *(eds) Plant Analysis: An Interpretation Manual.* 2nd Edition. CSIRO Publishing, Collingwood, Australia. pp.503-566.

Boden, D.I. 1991. Intensive site preparation on steep land: the effect of hydrological processes and growth of *Eucalyptus grandis* at 18 months. *In: Proceedings of 1991 IUFRO Symposium; Intensive Forestry: The role of* eucalypts.

Bond-Lamberty, B. Wang, C. and Gower, S.T. 2002. Above-ground and below-ground biomass and sapwood area allometric equations for six boreal tree species of northern Manitoba. *Canadian Journal of Forestry Research* 32:1441-1450.

Bradstock, R. 1981. Biomass in an Age Series of *Eucalyptus grandis* plantations. *Australian Forestry Research* 11:111-127.

Caldeira, M.V.W. Schumacher, M.V. dos Santos, E.M. Tedesco, N. and Pereira, J.C. 1999. Estimativa do contcudo de nutrientes em um povoamento jovem de *Acacia mearnsii De Wild.* estabelccido na regiao sul do Brasil. *Ciencia Florestal* 29(1/2):53-65.

Caldeira, M.V.W. Schumacher, M.V. Neto, R.M.R. Watzlawick, L.F. and dos Santos, E.M. 2001. Quantificacao da biomassa acima do solo de *Acacia mearnsii* De Wild. procedencia Batemans Bay, Australia (Quantification of above-ground biomass in stand of *Acacia mearnsii* De Wild. Batemans Bay provenance, Australia). *Ciencia Florestal* 2:79-91.

Caldeira, M.V.W. Schumacher, M.V. Tedesco, N. and dos Santos, E.M. 2000a. Ciclagem de nutrientes em *Acacia mearnsii* De Wild. V. Quantifica cao do conteudo de nutrientes na biomassa aerea de *Acacia mearnsii* De Wild. procedencia Australiana. *Ciencia Rural.* 30(6):977-982.

Caldeira, M.V.W. Schumacher, M.V. Tedesco, N. Pereira, J.C. and dos Santos, E.M. 2000b. Producao de biomassa em uma procedencia Australiana de *Acacia mearnsii De Wild.* plantada no sul do Brasil. *Rivista Arvore* 24(2):201-206.

Calder, I.R. 1991. A water use and growth model for *eucalyptus* plantations in water limited conditions. In: Calder, I.R. Hall, R.L.& Adlard, P.G.*(eds)* Growth and water use of forest plantations. Bangalore conference proceedings. pp.301-317.

Carlson, C.A. and Allan, R. 2001. A pilot study into the above-ground biomass of a mature *Pinus patula* stand. *ICFR Bulletin Series* 20/2001, Institute for Commercial Forestry Research, Pietermaritzburg. 41pp.

Catchpole, W.R. and Wheeler, C.J. 1992. Estimating plant biomass: A review of techniques. *Australian Journal of Ecology* 17:121-132.

Chason, J.W. Baldocchi, D.D. and Huston, M.A. 1991. A comparison of direct and indirect methods for estimating forest canopy leaf area. *Agricultural and Forest Meteorology* 57:107-128.

Chavangi, N.A. Taylor, D.R.F. and Mackenzie, F. 1992. Household based tree planting activities for fuelwood supply in rural Kenya: The role of the Kenya Woodfuel Development Programme. Routledge, London, and New York, USA.

Cherry, M. Hingston, A. Battaglia, M. and Beadle, C. 1998. Calibrating the LI-COR LAI-2000 for estimating leaf area index in eucalypt plantations. *Tasforests* 10:75-82.

Compton, J.E. and Cole, D.W. 1991. Impact of harvest intensity on growth and nutrition of successive rotations of Douglas-fir. Forest Research Institute, *Long term Field Trials to Assess Environmental Impacts of Harvesting.* Bulletin No. 161. Rotorua, New Zealand.

Cromer, R.N. and Williams, E.R. 1982. Biomass and Nutrient Accumulation in a Planted *E. globules* (*Labill.*) Fertilizer Trial. Australian Journal of Botany. 30:65-78

Cromer, R.N. Barr, N.J. Williams, E.R. and McNaught, A.M. 1985. Response to fertiliser in a *Pinus radiata* plantation 1: Above-ground biomass and wood density. *New Zealand Journal of Forest Science* 15:71-88.

Cromer, R.N. Cameron, D.M. Lennon, S. Rance, S.J. Ryan, P.A. and West, P.W. 1995. Response of *E. grandis* to fertiliser and irrigation, to five years-of-age. CSIRO, *A report on Eucalyptus grandis* for Shell Australia. pp.1-20.

Cromer, R.N. Cameron, D.M. Rance, S.J. Ryan, P.A. and Brown, M. 1993. Response to nutrients in *Eucalyptus grandis.* 1. Biomass accumulation. *Forest Ecology and Management* 62:211-230.

Deblonde, G. Penner, M. and Royer, A. 1994. Measuring leaf area index with the LI-COR LAI-2000 in Pine Stands. *Ecology* 75(5):1507-1511.

Dicks, M. 2001. A preliminary validation of the 3-PG forest growth and water use model for *Acacia mearnsii* in Southern Africa. *CSIR Environmental report No.* ENV-D-I 2000-16, *CSIR, Pretoria.* 21p.

du Toit B. 2003. Effects of site management operations on the nutrient capital of a eucalypt plantation system in South Africa. *Southern African Forestry Journal* 199:15- 26.

du Toit, B. 2002. Long-term ecological sustainability of wattle plantations. In: Dunlop, R.W. and MacLennan, L.A. *(eds) Black Wattle: The South African Research Experience.* Institute for Commercial Forestry Research, Pietermaritzburg. pp.135-144.

du Toit, B. 2002a. Wattle nutrition. In: Dunlop, R.W. and MacLennan, L.A. *(eds) Black Wattle: The South African Research Experience.* Institute for Commercial Forestry Research, Pietermaritzburg. pp.47-64.

du Toit, B. 2002b. Long term ecological sustainability of wattle plantations. In: Dunlop, R.W. and MacLennan, L.A. *(eds) Black Wattle: The South African Research Experience.* Institute for Commercial Forestry Research, Pietermaritzburg, South Africa, pp.135-144.

du Toit, B. and Scholes, C. 2002. Nutritional sustainability of *Eucalyptus* plantations: A case study at Karkloof, South Africa. *Southern African Forestry Journal* 195:63-72.

du Toit, B. and Dovey, S.B. 2004. Effect of site management on leaf area, biomass development and stand growth efficiency of *Eucalyptus grandis* stand in South Africa. (Submitted for publication.)

Duke, J.A. (ed). 1981. *Handbook of legumes of world economic importance.* Plenum Press, New York. pp.55

Dunlop, R.W. and Hagedorn, S. 1998. Final report on two Australian *Acacia mearnsii* (Black Wattle) provenance trials established In KwaZulu-Natal and south eastern Mpumulanga. Institute for Commercial Forestry Research, *Bulletin* 7/98. Pietermaritzburg, South Africa. pp.15

Dunlop, R.W. and MacLennan, L.A. *(eds)* 2002. *Black Wattle: The South African Research Experience.* Institute for Commercial Forestry Research, Pietermaritzburg, South Africa. 166p.

Dye, P.J. 1999. How efficiently do *Eucalyptus* plantations use rainfall? *Deliverable Report, CSIR Environmental report no. ENV-P-1 98204 31 March 1999 CSIR, Pretoria.*

Edwards, M.B.P. 2000. What if all the SA timber plantations were to disappear? *Southern African Forestry Journal* 189:1-2.

Environmental Systems Research Institute (ESRI), I.A.S. Redlands, California, USA. 2000. ArcGIS 8.1 (Software) Ed. Redlands, California, USA.

Fey, M.V. and Schönau, A.P.G. 1982. Soils of Bloemendal field experiment station. *Annual Report.* 81/82, Wattle Research Institute, pp.109-113.

Fisher, R.F. and Binkley, D. *(eds)* 2000. *Ecology and Management of Forest Soils* John Wiley & Sons, inc. New York.

Garbutt, D.C.F. Metelerkamp, D.P. and Schönau, A.P.G. 1978. Plantation biomass as a source of energy. Unpublished, *Wattle Research Institute Report* 6/78

Gazarini, L.C. Araujo, M.C.C. Borralho, N. and Pereira, J.S. 1990. Plant area index in *Eucalyptus globulus* plantations determined indirectly by a light interception method. *Tree Physiology* 7:107-113.

Ghebremicael, S.T. Ahmed, F.B. and Smith C.W. 2003. Estimating the Leaf Area Index of Black Wattle (*Acacia mearnsii*) from Landsat ETM+ Satellite Imagery. *ICFR Bulletin Series* 07/2003, Institute for Commercial Forestry Research, Pietermaritzburg.

Gilmore, D.W. Seymour, R.S. Halteman, W.A. and Greenwood, M.S. 1995. Canopy dynamics and the morphological development of *Abies balsamea*: effects of foliage age on specific leaf area and secondary vascular development. *Tree Physiology* 15:47–55.

Gower, S.T. and Norman, J.M. 1991. Rapid estimation of leaf area index in conifer and broad-leaf plantations. *Ecology* 72(5): 1896-1900.

Grove, T.S. Thomson, B.D. and Malajczuk, N. 1996. Nutritional physiology of *Eucalyptus*: Uptake, distribution and utilisation. In: Attiwill, P.M. and Adams, M.A. *(eds) Nutrition of* eucalypt CSIRO, Australia, pp.77-108.

Herbert, M.A. 1993. Site requirements of exotic hardwood species. Institute for Commercial Forestry Research, *Bulletin* 2/93. Pietermaritzburg, South Africa.

80

Higman, S. Bass, S. Judd, N. Mayers, J. and Nussbaum, R. *(eds)* 2000. *The Sustainable Forestry Handbook, IIED*, London.

Hillis, W.E. (ed.) 1987. *Heartwood and tree exudates.* Springer Verlag, Berlin.

Hingston, F.J. Galbraith, J.H. and Dimmock, G.M. 1995. Evaluating the effects of soils and climate on productivity of *Eucalyptus globulus* plantations on contrasting sites in south west of Western Australia. Final Report to Rural Industries Research and Development Corporation. Project CSF-41A. 67p.

Hitchcock, H.C. and McDonnell, J.P. 1995. Biomass measurement: A synthesis of the literature. Tennessee Valley Authority, Division of Land and Forest Resources, Norris, Tennessee. 52p.

Huber, B. 1928. Weitere quantitative Untersuchungen über das Wasserleitungssytem der Pflanzen. *Jahrb Wiss Bot.* 67:877–959.

Hunter, I. 2001. Above-ground biomass and nutrient uptake of three tree species (*Eucalyptus camaldulensis, Eucalyptus grandis* and *Dalbergia sisso*) as affected by irrigation and fertiliser, at 3 years of age, in southern India. *Forest Ecology and Management* 144:189-199.

Johnson, D.W. Kelly, J.M. Swank, W.T. Cole, D.W. Vanmiegroet, H. Hornbeck, J.W. Pierce, R.S. and Vanlear, D. 1988. The Effects of Leaching and Whole-tree Harvesting on Cation Budgets of Several Forests. *Journal of Environmental Quality* 17(3):418-424.

Jorgenson, J.R. Wells, C.G. and Metz, L.J. 1975. The nutrient cycle : Key to continuous forest production. *Journal of Forestry* 73:400-403.

Judd, T.S. Bennett, L.T. and Weston, C.J. 1996. The response of growth and foliar nutrients to fertilizers in young *Eucalyptus globulus* plantations in Gippsland, south-eastern Australia. *Forest Ecology and Management 82:87-101.*

Kalra, Y.P. and Maynard, D.G. 1991. Methods manual for forest soil and plant analysis. Forestry Canada, Northwest region, Northern Forestry Centre, Edmonton, Alberta. Inf. Rep. NOR-X-319.

Kalra,Y.P. 1998. Reference methods for plant analysis, CRC Press, New York.

Kumar, B.M. George, S.J. Jamaludheen, V. and Suresh, T.K. 1998. Comparison of biomass production, tree allometry and nutrient use efficiency of multipurpose trees grown in woodlot and silvopastoral experiments in Kerala, India. *Forest Ecology and Management* 112:145-163.

Laclau, J.-P. Bouillet, J.P. and Ranger, J. 2000. Dynamics of biomass and nutrient accumulation in a clonal plantation of *Eucalyptus* in Congo. *Forest Ecology and Management* 128:181-196.

Landsberg, J.J. and Waring, R.H. 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *Forest Ecology and Management* 95:209-228.

LI-COR, I. ed. 1992. *LAI-2000 Plant canopy analyser: instruction manual*, Lincoln, Nebrasca.

Linder, S. 1985. Potential and actual production in Australian forest stands. In: Landsberg, J.J. and Parsons, W. *Research for forest management*, CSIRO, Melbourne pp.11-35.

Linder, S. and Rook, D.A. 1984. Effects of mineral nutrition on carbon dioxide exchange and partitioning of carbon in trees. *Nutrition of plantation forests* Academic Press *(eds)*, London, pp211-236.

Linder, S. 1995. Foliar analysis for detecting and correcting nutrient imbalances in Norway spruce. *Ecological Bulletins 44: 178-190.*

Little, K.M. Eccles, N. Oscroft, D. Viero, P. and Eastwood, T. 1996. Growth of eucalypt on slash managed and burned sites in Zululand. *Institute For Commercial Forestry Research Bulletin* 3/96.

Lowman, G.R.P. 2003. Deposition of nitrogen to grassland versus forested areas in the vicinity of Sabie, Mpumalanga. University of Witwatersrand Press, Johannesburg, South Africa. 119p.

Lynch, S.D. 2003. The Development of an Improved Gridded Database of Annual, Monthly and Daily Rainfall. 1156/0/1, Water Research Commission, Pretoria, South Africa.

Mackensen, J., Hölscher, D., Klinge, R. and Fölster, H. 1996. Nutrient transfer to the atmosphere by burning of debris in eastern Amazonia Forest Ecology and Management 86:121-128

Madgwick, H.A.I. Jackson, D.S. and Knight, P.J. 1977. Above-ground dry matter, energy, and nutrient contents of trees in an age series of *Pinus radiata* plantations. *New Zealand Journal of Forest Science* 7(3):445-478.

Mariscal, M.J. Orgaz, F. and Villalobos, F.J. 1999. Radiation-use efficiency and dry matter partitioning of a young olive (*Olea europaea*) orchard. *Tree Physiology* 20:65–72.

McMurtrie, R.E. Gholz, H.L. Linder, S. and Gower, S.T. 1994. Climatic factors controlling the productivity of the pine stands: a model-based analysis. *Ecological Bulletins 43: 173-188.*

Medhurst, J.L. Battaglia, M. Cherry, M.L. Hunt, M.A. White, D.A. and Beadle, C.L. 1999. Allometric relationships for *Eucalyptus nitens* (Deane and Maiden) Maiden plantations. *Trees* 14(2): 91-101.

Misra, R.K. Turnbull, C.R.A. Cromer, R.N. Gibbons, A.K. and LaSala, A.V. 1998. Below and above-ground growth of *Eucalyptus nitens* in a young plantation. 1. Biomass. *Forest Ecology and Management* 106:283-293.

Moller, I.S. 2000. Calculation of biomass and nutrient removal for different harvesting intensities. *New Zealand Journal of Forest Science* 30(1/2):29-45.

Mondi Forests. 2002. Management Plan - Paper Value Chain, Internal company document.

Morris, A.R. 1992. Dry matter and nutrients in the biomass of an age series of *Pinus patula* plantations in the Usutu Forest, Swaziland. *Southern African Forestry Journal* 163:5-11.

Mroz, G.D. Jurgensen, M.F. and Frederick, D.J. 1985. Soil nutrient changes following whole tree harvesting on three northern hardwood sites. *Soil Science Society of America Journal* 49:1552-1557.

Muneri, A. 1997. Kraft pulping properties of *Acacia mearnsii* and *Eucalyptus grandis* grown in Zimbabwe. *Southern African Forestry Journal* 179:13-19.

Nackaerts, K. Coppin, P. Muys, B. and Hermy, M. 2000. Sampling methodology for LAI measurements with LAI-2000 in small forest stands. *Agricultural and Forest Meteorology* 101:247-250.

Naidu, S.L. Dellucia, E.H. and Thomas, R.H. 1998. Contrasting patterns of biomass allocation in dominant and suppressed loblolly pine. *Canadian Journal of Forestry Research* 28:1116-1124.

Nambiar, E.K.S. 1996. Sustained productivity of forests is a continuing challenge to soil science. *Soil Science Society of America Journal* 60:1629-1642.

Negi, J.D.S. and Sharma, S.C. 1985. Biomass and nutrient distribution in an age series of *Eucalyptus* hybrid plantation in Tamil Nadu. I. Distribution of organic matter. *Indian Forester 111(*12):1113-1124.

Newbould, P.J. 1967. Methods for Estimating the Primary Production of Forests. *IBP Handbook No. 2.* Blackwell, Oxford and Edinburgh.

Noble, A.D. Donkin, M.J. Smith, C.W. Cromer, R.N. Sands, P.J. and Kirschbaum, M.U.F. 1991. The importance of soil properties as indicators of site quality for *Eucalyptus grandis* on the Zululand coastal plain. In: Schönau, A.P.G. (ed). *Proceedings of the International Union of Forestry Research Organizations Symposium on Intensive Forestry : The Role of eucalypts.*, Durban, Vol 1, pp.433-491.

Norris, C.H. Stuart, R. and Friendmond, S. 1995. Plantation Residue Management. *Institute For Commercial Forestry Research Annual Research Report* 94/95.

Norton, S.A. and Young, H.E. 1976. Forest Biomass utilization and nutrient budgets. *16th Int. Con. of IUFRO Univ. of Maine :55-73.*

Olbrich, K. Christie, S.I. Evans, J. Everard, D. Olbrich, B. and Scholes, R.J. 1997. Factors influencing the long term sustainability of the South African forest industry. *Southern African Forestry Journal* 178:53-58.

Osório, J. Osório, M.L. Chaves, M.M. and Pereira, J.S. 1998. Water deficits are more important in delaying growth than in changing patterns of carbon allocation in *Eucalyptus globulus. Tree Physiology* 18:363-373.

Owens, L.B. and Watson, J.P. 1979. Rates of weathering and soil formation on granite in Rhodesia. *Soil Science Society of America Journal* 43:160-166.

Parresol, B.R. 1999. Assessing tree and stand biomass: A review with examples and critical comparisons. *Forest Science* 45(4):573-593.

Parrotta, J.A. 1999. Productivity, nutrient cycling, and succession in single- and mixed-species plantations of *Casuarina equisetifolia, Eucalyptus robusta,* and *Leucaena leucocephala* in Puerto Rico. *Forest Ecology and Management* 124:45-77.

Pereira, J.C. Caldeira, M.V.W. Schumacher, M.V. Hoppe, J.M. and dos Santos, E.M. 2000. Estimativa do conteudo de nutrientes em um povoamento de *Acacia mearnsii* De Wild. no Rio Grande do sul, Brasil. *R. Arvore.* 24(2):193-199.

Pereira, J.C. Schumacher, M.V. Hoppe, J.M. Caldeira, M.V.W. and dos Santos, E.M. 1997. Producao de biomassa em um povoamento de *Acacia mearnsii De Wild.* no estado do Rio Grande do sul. *Rivista Arvore* 21(4):521-526.

Pierce, L.L. and Running, S.W. 1988. Rapid estimation of coniferous forest leaf area index using a portable integrating radiometer. *Ecology* 69(6):1762-1767.

Pinkard, E.A. Battagila, M. Beadle, C.L. and Sands, P.J. 1999. Modelling the effect of physiological responses to green pruning on net biomass production of *Eucalyptus nitens. Tree Physiology* 19:1-12.

Pita, P. and Pardos, J.A. 2000. Growth, leaf morphology, water use and tissue water relations of *Eucalyptus globulus* clones in response to water deficit. *Tree Physiology* 21:599-607.

Ranger, J. and Turpault, M.P. 1999. Input-output nutrient budgets as a diagnostic tool for sustainable forest management. *Forest Ecology and Management* 122:139-154.

Ranger, J. Marques, R. Colin-Belgrand, M. Flammang, N. and Gelhaye, D. 1995. The dynamics of biomass and nutrient accumulation in a Douglas-fir (*Pseudotsuga menziesii* Franco) stand studied using a chronosequence approach. *Forest Ecology and Management* 72:167-183.

Raven, P.H. Evert, R.F. Eichhorn, S.E. 1992. Biology of Plants, Ed 5. Worth Publishers, New York.

Richards, B.N. and Charley, J.L. 1983. Mineral cycling processes and system stability in the Eucalypt forest. *Forest Ecology and Management* 7:31-47.

Ryan, M.G. Binkley, D. and Fownes, J.H. 1997. Age-related decline in forest productivity: pattern and process. *Advances in Ecological Research* 27:214-262.

Santana, R.C. Barros, N.F. and Comerford, N.B. 2000. Above-ground biomass, nutrient content, and nutrient use efficiency of *Eucalypt* plantations growing in different sites in Brazil. *New Zealand Journal of Forest Science* 30(1/2):225-236.

Scholes, R. J. and Scholes, M.C. 1999. Nutrient imbalances following conversion of grassland to plantation forests in South Africa. In Smaling, E.M.A. Oenema, O. and Fresco, L.O. *(eds) Nutrient Disequilibria in Agroecosystems.* CAB International. Chapter 9, pp.175-189.

Scholes, R.J. Smith, R.E. Van Wilgen, B.W. Berns, J. Evans, J. Everard, D. Forsth, G.G. Scott, D.F. Van Tienhoven, M. and Viljoen, P.J. 1995. The costs and benefits of plantation forestry: Case studies from Mpumulanga. Council for Scientific and Industrial Research, *Environmentek* Report FOR-DEA 939. Pretoria.

Schönau, A.P.G. 1970. Timber / bark weight ratios for black wattle. Report for 1969-1970, Wattle Research Institute, Pietermaritzburg. pp.46-52.

Schönau, A.P.G. 1972. Metric timber volume, percentage utilization and stump and kerf wastage tables for Black Wattle, *Acacia mearnsii.* Wattle Research Institute, *Annual Report* 71/72. Pietermaritzburg. pp.39-47.

Schönau, A.P.G. 1978. Provisional biomass estimates of black wattle. *Wattle Research Institute. Unpublished Report.* 3/78, Pietermaritzburg, South Africa.

Schönau, A.P.G. and Boden, D.I. 1982. Preliminary biomass studies in young eucalypt. *Southern African Forestry Journal* 120:24-28.

Schulze, R.E. Maharaj, M. Lynch, S. Howe, B. and Melvil-Thomson, B. *(eds)* 1997. *South African Atlas of Agrohydrology and-Climatology.* Department of Agricultural Engineering, University of Natal, Pietermaritzburg, South Africa. pp.17-29.

Sherry, S.P. 1971. The black wattle (*Acacia mearnsii de Wild.*). *University of Natal Press.* 402p.

Shinozaki, K. Yoda, K. Hozumi, K. and Kira, T. 1964. A quantitative analysis of plant form - the Pipe Model Theory. I. Basic analyses. *Japanese Journal of Ecology* 14:97-105.

Simpson, D.E. 1991. Quantification of the effects of land use on runoff water quality of selected catchments in Natal: Final report to the Water Research Commission. WRC Report 237/1/91, Division of Water Technology, CSIR, South Africa. ISBN1 874858 22 5

Smith, C.W. and Dunlop, R.W. 2002. Plantation establishment, re-establishment and regeneration. In: Dunlop, R.W. and MacLennan, L.A. *(eds) Black Wattle: The South African Research Experience.* Institute for Commercial Forestry Research, Pietermaritzburg. pp.135-144.

Smith, F.W. Sampson, D.A. and Long, J.N. 1991. Comparison of leaf area index estimates from tree allometrics and measured light interception. *Forest Science* 37(6):1682-1688.

Snowdon, P. 1985. Alternative sampling strategies and regression models for estimating forest biomass. *Australian Forestry Research* 15:353-366.

Snowdon, P. 1992. Ratio methods for estimating forest biomass. *New Zealand Journal of Forest Science* 22(1):54-62.

Snowdon, P. Raison, J. Keith, H. Montagu, K. Bi, H. Ritson, P. Grierson, P. Adams, M. Burows, W. and Eamus, D. 2001. Protocol for Sampling Tree and Stand Biomass. *National Carbon Accounting System. Technical Report No.* 31, Australian Greenhouse Office, Canberra, 66p.

Spangenberg, A. Grimm, U. da Silva, J.R.S. and Folster, H. 1996. Nutrient store and export rates of *Eucalyptus urograndis* plantations in eastern Amaconia (Jari). *Forest Ecology and Management* 80:225-234.

Steyn, M.S. 1937. Analysis of wattle leaves (Translated from Afrikaans). Union Department of Forestry, *Report* 3002/5/20/1. Pietermaritzburg. pp.1-18.

Stubbings, J.A. and Schonau, A.P.G. 1972. Density and air-drying rate of the timber of black wattle (*Acacia mearnsii*). *Wattle Research Institute report for 1971 – 1972,* Wattle Research Institute. pp36-38.

Switzer, G.L. and Nelson, L.E. 1972. Nutrient accumulation and cycling in loblolly pine (Pinus taeda L.) plantation ecosystems : The first twenty years. *Soil Science Society of America Journal* 36:143-147.

Tandon, V.N. Pande, M.C. and Singh, R. 1988. Biomass estimation and distribution of nutrients in five different aged *Eucalyptus grandis* plantation ecosystems in Kerala state. *Indian Forester* 4:184-199.

Tandon, V.N. Pande, M.C. and Singh, R. 1989. Organic matter production and distribution of nutrients in plantations of *Acacia mearnsii* in Nilgiris, Tamil Nadu. *Indian Forester* 115(5): 286-295.

TAPPI. 1985. Basic density and moisture content of pulpwood *TAPPI Method* T258 om-85.

Thompson, D.A. and Matthews, R.W. 1989. The storage of carbon in trees and timber. Forest Research Station, *Research information note* 160. Farnham.

UTHSCSA. 2002. ImageTool program. (developed at the University of Texas Health Science Center at San Antonio, Texas and available from the Internet by anonymous FTP from ftp://maxrad6.uthscsa.edu).

van Laar, A. 1982. Sampling for above-ground biomass for *Pinus radiata* in the Bosboukloof catchment at Jonkershoek. *South African Forestry Journal* 123(1982):8-13.

Van Miegroet, H. and Cole, D.W. 1984. The impact of nitrification on soil acidification and cation leaching in red alder (*Alnus rubra Bong.*) ecosystem. *Journal of Environmental Quality* 13(4):586-590.

Van Wyk, D.B, 1990. Atmospheric deposition at selected sites in the mountain catchments of South Africa. In Proceedings of the 1st IUAPPA regional Conference on Air Pollution:

Towards the 21st Century. National Association for clean air, 24-26 October 1990, Pretoria, South Africa. Vol 1, Paper No. 8.

Veldtman, D.G. Rivers-Moore, N.A. and Atkinson, P.R. 1995. Preliminary estimate of leaf area indices in black wattle (*Acacia mearnsii*). Institute for Commercial Forestry Research, *Annual Report* 94/95. Pietermaritzburg, South Africa. pp.1-5.

VSN. 2001. GenStat Fifth Edition. VSN International Ltd, Lawes Agricultural Trust, Oxford.

Waring, R.H. and Running, S.W. *(eds)* 1998. *Forest ecosystems: Analysis at multiple scales,* Second Edition, Academic Press, San Diego. 370p.

Waring, R.H. and Schlesinger, W.H. 1985. The carbon balance of trees. In: Waring, R.H. and Schlesinger, W.H. *(eds) Forest Ecosystems: Concepts and Management* Academic Press, Inc. Orlando, Florida, pp.7-37.

Waring, R.H. Landsberg, J.J. and Williams, M. 1998. Net primary production of forests: A constant fraction of gross primary production? *Tree Physiology* 18:129-134.

Williams, C.O. 1927. South African Tanning Materials, (Part 1), (The Black Wattle). *Science Bulletin.* 63, Cedara, pp.1-72.

Worrell, R. and Hampson, A. 1997. The influence of some forest operations on the sustainable management of forest soils-a review. *Forestry* 70(1):61-85.

Xu, D. Dell, B. Malajczuk, N. and Gong, M. 2002. Effects of fertilisation on productivity and nutrient accumulation in a *Eucalyptus grandis x E. urophylla* plantation in southern China. *Forest Ecology and Management* 161:89-100.

APPENDICES

Appendix A: Sample tree data for each site and for all ages

Table A1: Sample tree data for all ages at Bloemendal.

Age Class	Age (y)	Dbh (cm)	Under-bark Diameter (cm)	Height (m)	Canopy depth (m)	Stem mass (kg)	Bark mass (kg)	Dead branch mass (kg)	Live branch mass (kg)	Foliar mass (kg)	Mean SLA (kg m⁻²)	leaf area (m²)	Sapwood area (cm²)	Wood Density (kg.m³)
3-5	3.8	6.4	5.8	10.4	4.4	6.13	0.71	0.27	0.80	0.48	9.4	4.5	24.52	452
		8.8	8.1	13.4	6.3	17.67	3.23	0.50	6.24	3.43	8.4	29.0	41.40	581
		10.6	9.8	14.6	7.9	25.38	3.87	1.20	12.50	4.41	7.9	34.8	58.57	536
		12.4	11.5	14.6	7.2	29.31	4.35	2.78	5.71	3.13	7.1	22.2	69.83	479
5-7	5.8	9.0	8.3	15.1	6.3	25.82	3.65	2.67	9.37	1.78	8.3	14.8	36.61	656
		11.1	10.3	17.8	6.2	37.39	5.36	3.78	5.02	1.77	7.2	12.7	50.40	504
		13.0	12.1	17.5	7.9	59.06	8.00	4.13	17.55	3.58	7.1	25.3	74.68	636
		15.0	14.0	17.4	7.8	62.56	8.99	5.94	7.76	3.84	7.1	27.2	98.42	551
7-9	7.8	10.1	9.3	16.2	6.6	28.68	5.08	3.89	5.50	2.13	7.9	16.9	51.00	561
		12.0	11.1	17.4	7.8	42.38	5.42	3.26	10.96	2.80	7.3	20.6	67.34	543
		14.1	13.2	17.2	6.9	65.70	11.99	2.86	21.91	5.82	8.2	47.7	84.74	574
		15.9	14.9	17.7	9.3	79.85	11.30	9.75	19.16	5.26	7.8	41.2	97.11	581
9-11	9.8	10.4	9.6	16.8	5.7	39.82	6.19	7.46	10.35	1.57	7.6	12.0	41.79	653
		12.6	11.7	17.8	6.2	58.38	7.39	13.30	14.37	3.09	7.5	23.2	68.76	602
		14.3	13.3	19.6	5.5	94.81	14.06	8.93	16.42	5.93	8.4	49.8	85.79	662
		17.1	16.0	18.8	7.6	112.29	14.93	9.74	22.41	5.80	7.8	45.2	115.34	642

Table A2: Sample tree data for all ages at Mistley.

Age Class	Age (y)	Dbh (cm)	Under-bark Diameter (cm)	Height (m)	Canopy depth (m)	Stem mass (kg)	Bark mass (kg)	Dead branch mass (kg)	Live branch mass (kg)	Foliar mass (kg)	Mean SLA (kg m^{-2})	leaf area (m^2)	Sapwood area (cm^2)	Wood Density (kg.m^3)
3-5	3.4	7.0	6.3	10.3	4.3	7.60	2.33	0.34	5.80	1.05	11.5	6.1	26.75	507
		9.2	8.6	14.1	4.9	21.09	2.96	0.43	6.10	2.07	9.2	19.0	48.66	520
		10.9	10.1	14.2	5.8	30.51	5.05	2.14	5.81	2.30	7.7	17.7	65.45	549
		13.2	12.3	16.2	7.8	50.88	7.27	0.90	11.52	5.20	6.9	36.1	99.48	554
5-7	5.5	7.9	7.4	13.9	3.3	15.12	2.14	1.55	3.57	1.04	10.1	10.5	30.27	537
		10.4	9.5	15.9	3.9	31.41	4.41	1.67	5.11	1.88	7.3	13.8	50.70	543
		11.6	10.8	16.0	5.8	41.96	5.12	2.49	7.12	2.63	7.7	20.3	63.56	594
		13.1	12.2	15.6	7.2	51.12	6.59	2.40	13.86	4.59	7.4	33.8	77.63	631
7-9	7.0	9.9	9.0	15.7	6.1	29.91	5.18	4.38	10.18	1.26	9.0	11.4	40.17	588
		11.5	10.5	16.0	6.4	35.55	7.13	7.10	8.85	1.91	8.5	16.3	52.70	566
		13.6	12.8	17.9	10.7	63.06	7.59	3.12	23.70	2.63	8.3	21.8	76.55	610
		15.8	14.7	19.2	6.0	99.26	14.11	13.33	21.12	5.36	6.9	36.8	94.26	614
9-11	11.2	12.3	11.5	19.8	9.1	61.73	8.11	1.83	12.76	2.34	8.9	20.9	49.86	604
		14.7	13.6	19.2	9.1	95.11	15.60	2.28	26.17	2.59	8.2	21.2	80.95	641
		17.6	16.5	22.1	6.3	143.73	21.05	13.85	22.11	4.09	7.4	30.2	96.92	623
		20.0	18.9	21.7	6.7	203.96	26.72	31.16	38.13	7.65	7.9	60.7	132.83	669

Table A3: Sample tree data for all ages at SeeleMtH.

Age Class	Age (y)	Dbh (cm)	Under-bark Diameter (cm)	Height (m)	Canopy depth (m)	Stem mass (kg)	Bark mass (kg)	Dead branch mass (kg)	Live branch mass (kg)	Foliar mass (kg)	Mean SLA (kg m^{-2})	leaf area (m^2)	Sapwood area (cm^2)	Wood Density (kg.m^3)
3-5	4.3	9.3	8.8	15.6	4.4	24.99	3.27	0.51	5.14	2.41	8.4	20.3	48.02	493
		11.6	10.8	17.2	5.2	39.68	5.01	3.84	8.16	2.30	8.5	19.4	64.97	529
		13.8	13.0	18.2	8.6	59.17	7.68	0.97	13.00	4.46	8.4	37.5	83.94	528
		16.0	15.0	19.8	6.6	78.08	10.00	3.66	11.90	4.40	8.1	35.8	105.32	525
5-7	7.3	9.2	8.6	17.6	5.6	24.44	3.30	1.68	4.15	0.96	9.8	9.4	37.24	510
		12.0	11.2	19.7	5.3	51.86	6.73	1.98	7.64	2.09	9.1	19.0	60.51	541
		15.3	14.4	22.2	7.8	104.28	12.42	5.31	11.50	4.48	8.7	38.8	91.29	570
		18.4	17.2	23.1	6.3	144.19	15.91	8.05	15.09	7.14	7.2	51.3	131.48	566
7-9	8.2	10.7	9.9	15.8	7.4	30.81	4.75	2.85	6.78	0.69	9.3	6.4	49.00	572
		13.1	12.2	19.6	9.6	70.50	9.79	1.68	16.34	3.84	8.1	31.2	61.49	572
		15.6	14.9	20.1	8.1	88.10	11.44	2.01	16.46	3.69	8.7	32.0	88.61	560
		17.9	16.8	20.4	10.8	127.71	12.54	4.97	16.98	4.18	8.2	34.3	109.70	571
9-11	11.2	9.5	8.7	14.4	8.0	24.30	3.79	0.25	4.96	1.58	10.3	16.2	31.71	528
		12.5	11.5	18.8	6.0	59.45	8.98	2.21	4.94	1.84	10.0	18.4	56.64	573
		15.2	14.1	22.8	6.0	126.43	15.98	9.47	13.21	2.63	7.9	20.7	85.87	669
		18.3	17.1	23.3	6.5	148.26	17.80	6.06	16.83	4.74	9.0	42.6	122.53	615

Appendix B: Mean concentrations of nutrients in tree components

Table B1: Concentrations of nutrients in foliage and bark for all sites and ages.

Age Class (yrs)	Element	Foliar Concentrations			Bark Concentrations		
		Bloemendal	Mistley	SeeleMtH	Bloemendal	Mistley	SeeleMtH
3-5		2.388	2.890	3.088	1.120	0.935	1.053
5-7	N (%)	2.633	2.540	2.835	1.091	0.870	1.078
7-9		2.635	2.498	3.215	0.883	0.898	0.898
9-11		2.428	2.693	2.765	1.095	1.058	0.965
3-5		0.081	0.100	0.115	0.022	0.017	0.025
5-7	P (%)	0.080	0.095	0.078	0.027	0.023	0.021
7-9		0.100	0.093	0.108	0.023	0.023	0.016
9-11		0.093	0.101	0.098	0.028	0.023	0.019
3-5		0.532	0.758	0.834	0.213	0.225	0.394
5-7	K (%)	0.590	0.583	0.785	0.306	0.216	0.333
7-9		0.574	0.775	0.842	0.257	0.351	0.196
9-11		0.561	0.763	0.674	0.306	0.326	0.241
3-5		0.742	0.530	0.465	0.901	0.903	1.116
5-7	Ca (%)	0.605	0.611	0.440	0.625	1.019	0.799
7-9		0.564	0.548	0.335	0.828	0.918	0.980
9-11		0.593	0.530	0.785	0.756	0.999	0.570
3-5		0.253	0.193	0.185	0.098	0.083	0.117
5-7	Mg (%)	0.193	0.190	0.195	0.091	0.106	0.110
7-9		0.209	0.183	0.183	0.084	0.123	0.081
9-11		0.189	0.203	0.226	0.106	0.103	0.081
3-5		0.070	0.075	0.079	0.029	0.016	0.017
5-7	Na (%)	0.093	0.114	0.095	0.032	0.021	0.039
7-9		0.099	0.035	0.111	0.034	0.012	0.039
9-11		0.064	0.039	0.120	0.015	0.009	0.031
3-5		230.33	78.72	21.50	41.74	27.31	12.17
5-7	Mn (ppm)	146.04	54.58	19.90	13.51	9.94	17.17
7-9		131.28	93.49	25.17	17.50	20.99	9.32
9-11		108.72	119.71	28.37	15.60	32.61	43.47
3-5		300.84	197.42	167.41	56.58	91.06	44.36
5-7	Fe (ppm)	337.81	217.68	243.97	39.50	66.78	74.30
7-9		355.48	238.45	235.06	49.39	69.67	79.62
9-11		341.20	310.33	256.48	79.20	81.86	76.60
3-5		8.16	7.02	8.24	1.51	1.13	1.56
5-7	Cu (ppm)	6.07	6.52	7.86	2.32	1.52	1.36
7-9		6.15	7.33	11.24	0.69	1.23	1.76
9-11		6.48	5.86	10.06	1.88	1.37	1.12
3-5		15.72	14.72	17.12	4.69	3.59	4.60
5-7	Zn (ppm)	14.64	17.01	13.11	4.33	5.36	5.07
7-9		16.66	15.72	19.79	5.11	3.76	4.15
9-11		15.67	14.29	18.62	5.07	4.52	4.26

Table B2: Concentrations of nutrients in live and dead branches for all sites and ages.

Age Class (yrs)	Element	Live Branch			Dead Branch		
		Bloemendal	Mistley	SeeleMtH	Bloemendal	Mistley	SeeleMtH
3-5		0.605	0.598	0.725	0.320	0.383	0.463
5-7	N (%)	0.667	0.558	0.735	0.407	0.395	0.448
7-9		0.555	0.638	0.653	0.385	0.418	0.543
9-11		0.855	0.690	0.673	0.423	0.543	0.583
3-5		0.026	0.019	0.020	0.013	0.013	0.008
5-7	P (%)	0.032	0.030	0.021	0.019	0.014	0.005
7-9		0.031	0.032	0.040	0.015	0.014	0.010
9-11		0.043	0.036	0.031	0.016	0.017	0.012
3-5		0.247	0.297	0.450	0.017	0.035	0.070
5-7	K (%)	0.452	0.279	0.389	0.197	0.021	0.046
7-9		0.295	0.490	0.249	0.040	0.035	0.020
9-11		0.369	0.505	0.279	0.040	0.081	0.018
3-5		0.244	0.235	0.220	0.191	0.279	0.310
5-7	Ca (%)	0.235	0.280	0.189	0.297	0.353	0.245
7-9		0.193	0.253	0.100	0.204	0.245	0.127
9-11		0.272	0.224	0.292	0.220	0.358	0.383
3-5		0.078	0.054	0.062	0.045	0.042	0.055
5-7	Mg (%)	0.088	0.092	0.067	0.076	0.060	0.050
7-9		0.069	0.074	0.042	0.046	0.061	0.033
9-11		0.091	0.074	0.058	0.060	0.072	0.067
3-5		0.024	0.021	0.029	0.009	0.008	0.010
5-7	Na (%)	0.041	0.052	0.027	0.047	0.017	0.013
7-9		0.033	0.016	0.028	0.023	0.009	0.005
9-11		0.030	0.013	0.044	0.017	0.009	0.005
3-5		31.83	21.66	19.37	34.46	26.35	22.30
5-7	Mn (ppm)	34.47	17.35	23.45	23.63	24.75	24.98
7-9		15.48	23.70	28.09	26.69	30.21	48.23
9-11		18.85	26.38	14.74	27.01	34.53	49.14
3-5		79.65	74.33	72.74	118.66	165.09	100.34
5-7	Fe (ppm)	104.60	66.02	75.30	77.77	107.38	142.84
7-9		62.32	88.15	70.23	118.64	144.45	187.85
9-11		132.06	64.50	75.15	113.47	170.47	195.81
3-5		2.20	6.52	3.44	1.61	2.52	3.54
5-7	Cu (ppm)	2.17	2.85	2.99	1.97	1.49	4.72
7-9		1.65	3.11	3.25	1.60	2.93	3.37
9-11		2.63	2.52	4.78	2.12	3.44	3.66
3-5		8.10	7.04	12.22	5.41	2.97	10.91
5-7	Zn (ppm)	9.64	7.39	13.31	6.74	6.84	4.46
7-9		8.20	6.74	14.61	5.58	4.91	9.12
9-11		13.08	7.87	9.32	5.86	3.31	11.20

Table B3: Concentrations of nutrients in stem wood for all sites and ages.

Age Class (yrs)	Element	Stem Bloemendal	Mistley	SeeleMtH
3-5		0.150	0.138	0.145
5-7	N (%)	0.123	0.217	0.143
7-9		0.138	0.170	0.138
9-11		0.175	0.140	0.130
3-5		0.013	0.008	0.006
5-7	P (%)	0.010	0.011	0.006
7-9		0.010	0.009	0.002
9-11		0.013	0.011	0.002
3-5		0.058	0.049	0.097
5-7	K (%)	0.100	0.073	0.078
7-9		0.083	0.109	0.046
9-11		0.093	0.067	0.041
3-5		0.077	0.054	0.044
5-7	Ca (%)	0.053	0.052	0.043
7-9		0.049	0.048	0.036
9-11		0.071	0.045	0.048
3-5		0.018	0.017	0.022
5-7	Mg (%)	0.019	0.017	0.018
7-9		0.018	0.020	0.021
9-11		0.018	0.016	0.019
3-5		0.010	0.006	0.012
5-7	Na (%)	0.017	0.022	0.009
7-9		0.015	0.008	0.013
9-11		0.010	0.005	0.013
3-5		16.83	11.02	12.21
5-7	Mn (ppm)	8.49	7.27	15.55
7-9		8.98	11.74	15.23
9-11		9.66	10.65	8.92
3-5		19.90	17.97	22.26
5-7	Fe (ppm)	33.34	34.25	23.52
7-9		39.07	20.90	9.48
9-11		25.25	14.93	20.33
3-5		0.33	1.29	1.54
5-7	Cu (ppm)	1.15	1.76	1.54
7-9		0.50	2.27	1.68
9-11		0.34	1.35	0.91
3-5		0.33	0.64	1.20
5-7	Zn (ppm)	1.95	1.39	1.32
7-9		1.78	1.11	2.09
9-11		0.91	0.60	1.02

Appendix C: Regression results for prediction of component masses or areas

Tables and figures in Appendix D and E are formatted such that the statistical regression fit is tabulated with the appropriate constants and coefficients. All the observed and predicted values are shown alongside in a figure to demonstrate the goodness of fit. Outliers or extreme values that were excluded in the regression models are shown in the graphical representation.

Table C1: Regression predicting woody biomass as $\ln(Ws)$ from $\ln(dbh)$.

	d.f.	m.s.
Regression	1	$17.70034^{Fpr\ 0.001}$
Residual	46	0.02344
Total	47	0.41626
r^2		0.944
SE		0.153
Constant		$-2.184^{tpr\ 0.001}$
$\ln(dbh)$		$2.5691^{tpr\ 0.001}$

Fpr is the F test probability, tpr is the t test probability and ln is the natural logarithm
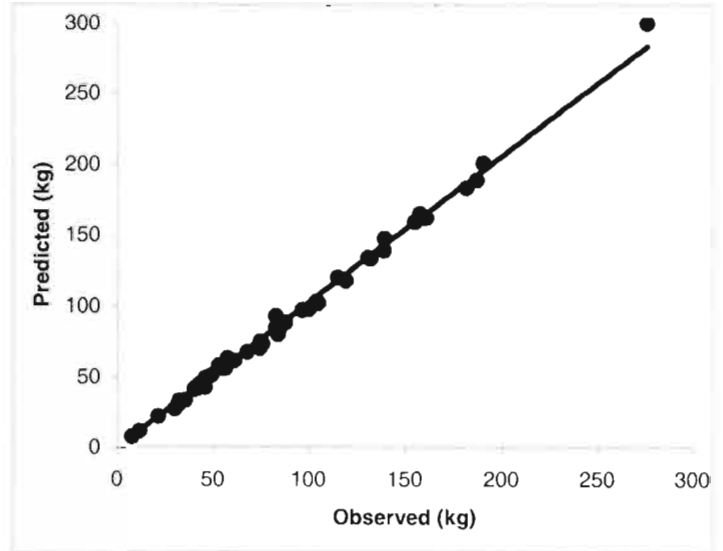
Figure C1: Observed vs. Predicted Ws.

Table C2: Multiple linear regression predicting stem biomass as $\ln(stem\ biomass)$ from $\ln(dbh) + \ln(height)$.

	d.f.	m.s.
Regression	2	$8.419369^{Fpr\ 0.001}$
Residual	40	0.008494
Total	42	0.408536
r^2		0.979
SE		0.0922
Constant		$-5.125^{tpr\ 0.001}$
$\ln(dbh)$		$1.91^{tpr\ 0.001}$
$\ln(height)$		$1.486^{tpr\ 0.001}$

Fpr is the F test probability, tpr is the t test probability and ln is the natural logarithm
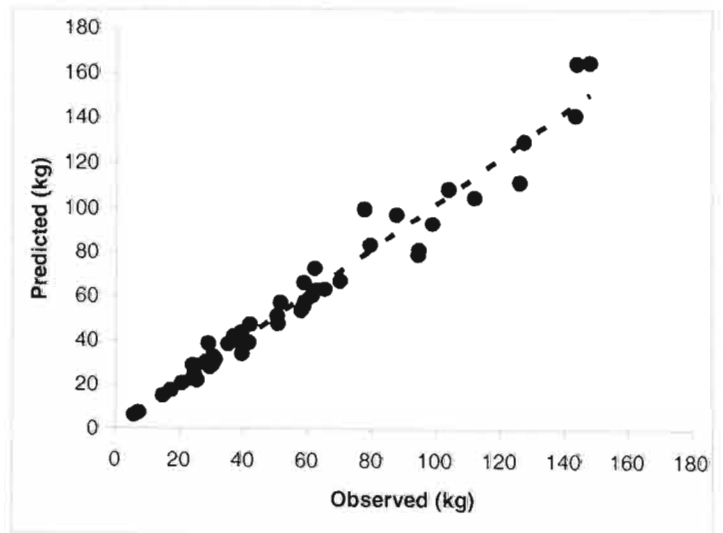
Figure C2: Observed vs. Predicted stem biomass.

Table C3: Multiple linear regression predicting bark biomass ln(Bark Biomass) from ln(dbh) + age.

	d.f.	m.s.
Regression	2	7.10474 $^{Fpr\ 0.001}$
Residual	44	0.01846
Total	46	0.34057
r^2		0.946
SE		0.136
Constant		-3.743 $^{tpr\ 0.001}$
ln(dbh)		2.082 $^{tpr\ 0.001}$
age		0.06433 $^{tpr\ 0.001}$

Fpr is the F test probability, tpr is the t test probability and ln is the natural logarithm
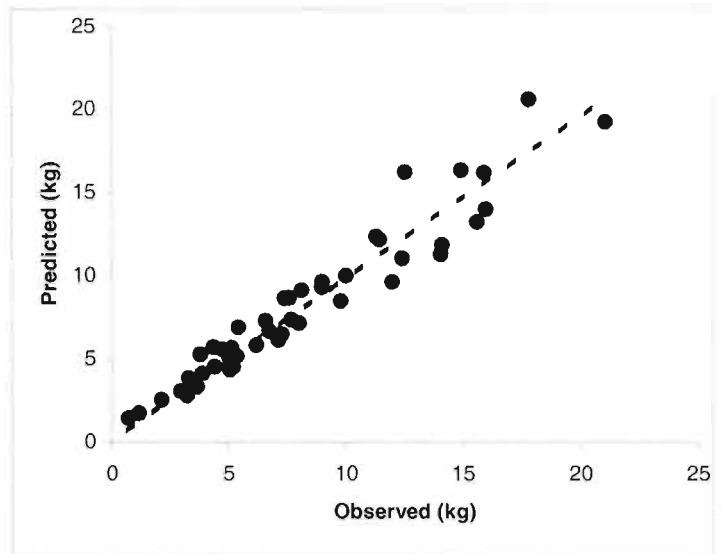
Figure C3: Observed vs. Predicted bark biomass.

Table C4: Multiple linear regression predicting live branch biomass as ln(live branch biomass) from ln(dbh) + ln(stocking).

	d.f.	m.s.
Regression	2	4.60163 $^{Fpr\ 0.001}$
Residual	42	0.08837
Total	44	0.29829
r^2		0.704
SE		0.297
Constant		4.41 $^{tpr\ 0.028}$
ln(dbh)		1.826 $^{tpr\ 0.001}$
ln(Stocking)		-0.899 $^{tpr\ 0.001}$

Fpr is the F test probability, tpr is the t test probability and ln is the natural logarithm
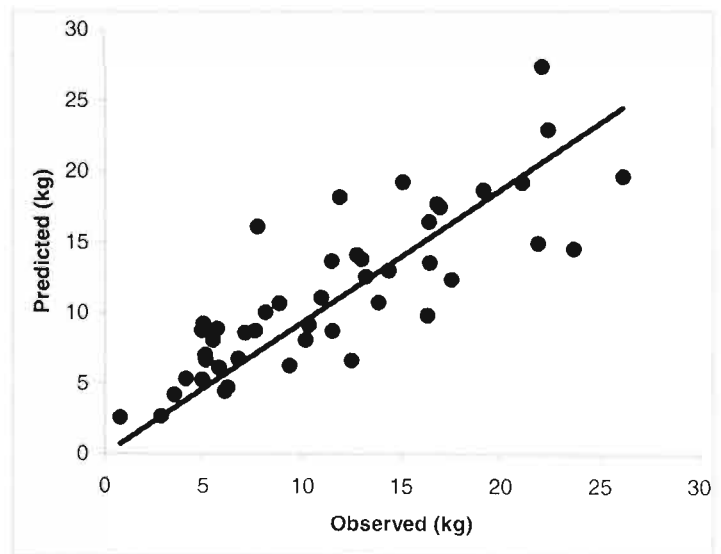
Figure C4: Observed vs. Predicted live branch biomass.

Table C5: Multiple linear regression predicting dead branch biomass as ln(dead branch biomass) from ln(dbh) + stocking + ln(age).

	d.f.	m.s.
Regression	3	11.3561
Residual	43	0.3434
Total	46	1.0616
r^2		0.677
SE		0.586
Constant		-3.83 tpr=0.002
ln(dbh)		1.962 tpr=0.001
Stocking		-0.000842 tpr=0.008
ln(age)		0.748 tpr=0.015

Fpr is the F test probability, tpr is the t test probability and ln is the natural logarithm
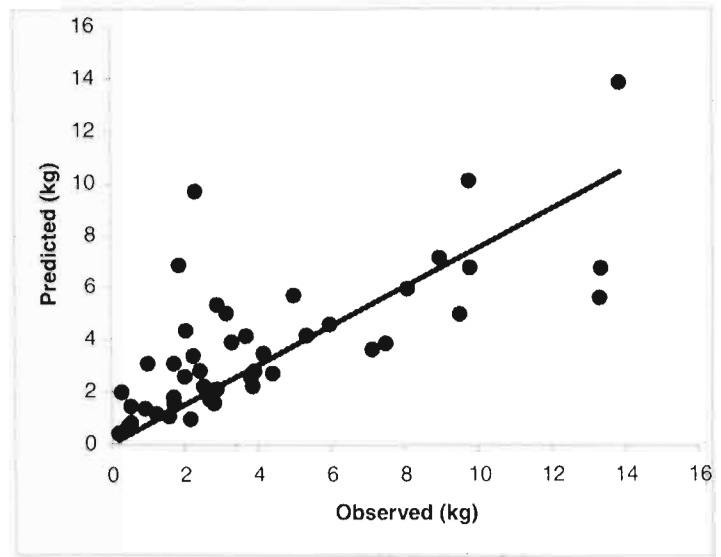
Figure C5: Observed vs. Predicted dead branch biomass.

Table C6: Multiple linear regression predicting AGB as ln(AGB) from ln(dbh) + age.

	d.f.	m.s.
Regression	2	17.4907 Fpr=0.001
Residual	45	0.7101
Total	47	18.2008
r^2		0.959
SE		0.127
Constant		-1.887 tpr=0.001
ln(dbh)		2.3287 tpr=0.001
age		0.04158 tpr=0.001

Fpr is the F test probability, tpr is the t test probability and ln is the natural logarithm
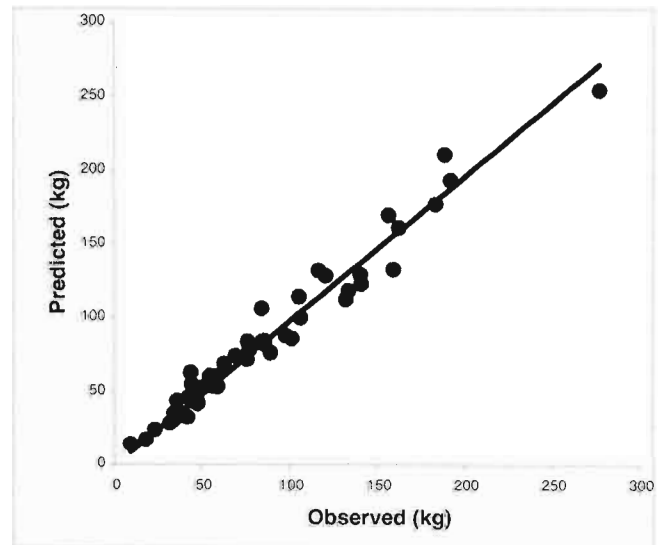
Figure C6: Observed vs. Predicted sapwood area.

Table C7: Multiple linear regression predicting sapwood area as ln(Sapwood) from ln(dbh)+ ln(age).

	d.f.	m.s.
Regression	2	4.077692 $^{Fpr<0.001}$
Residual	45	0.005315
Total	47	0.178608
r^2		0.970
SE		0.0729
Constant		4.813 $^{tpr<0.001}$
ln(dbh)		1.7861 $^{tpr<0.001}$
ln(age)		-0.2744 $^{tpr<0.001}$

Fpr is the F test probability, tpr is the t test probability and ln is the natural logarithm

Table C8: Regression predicting foliar biomass as ln(leaf biomass) from ln(sapwood area).

	d.f.	m.s.
Regression	1	12.34235 $^{Fpr<0.001}$
Residual	41	0.04403
Total	42	0.33685
r^2		0.869
SE		0.21
Constant		-9.95 $^{tpr<0.001}$
ln(Sapwood)		1.2457 $^{tpr<0.001}$

Fpr is the F test probability, tpr is the t test probability and ln is the natural logarithm
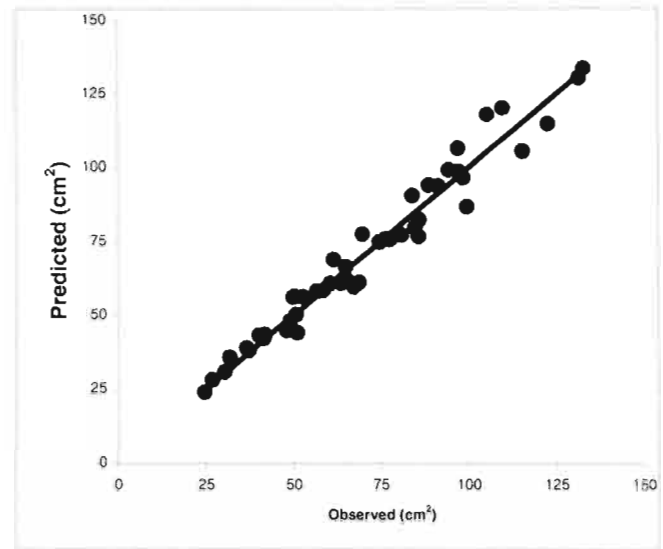
Figure C7: Observed vs. Predicted sapwood area.
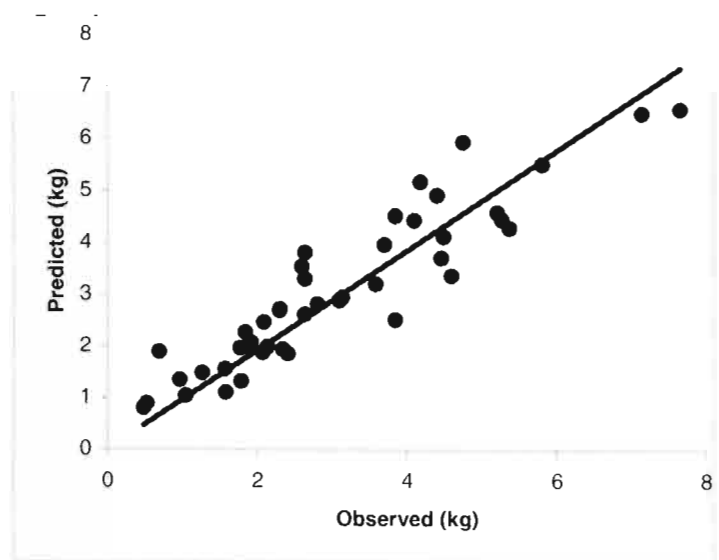
Figure C8: Observed vs. Predicted leaf biomass.

Table C9: Regression predicting leaf area from sapwood area.

	d.f.	m.s.
Regression	1	4.70710 [Fpr<0.001]
Residual	40	0.04634
Total	42	0.26828
r^2		0.827
SE		0.215
Constant		-1.278 [tpr<0.001]
ln(dbh)		1.966 [tpr<0.001]
ln(age)		-0.3030 [tpr<0.004]

Fpr is the F test probability, tpr is the t test probability

Figure C9: Observed vs. Predicted leaf area.

Table C10: Regression predicting foliar biomass as ln(leaf biomass) from ln(dbh)+ ln(age).

	d.f.	m.s.
Regression	2	6.13845 [Fpr<0.001]
Residual	40	0.04679
Total	42	0.33687
r^2		0.861
SE		0.216
Constant		-3.950 [tpr<0.001]
ln(dbh)		2.268 [tpr<0.001]
ln(age)		-0.4044 [tpr<0.001]

Fpr is the F test probability, tpr is the t test probability and ln is the natural logarithm.
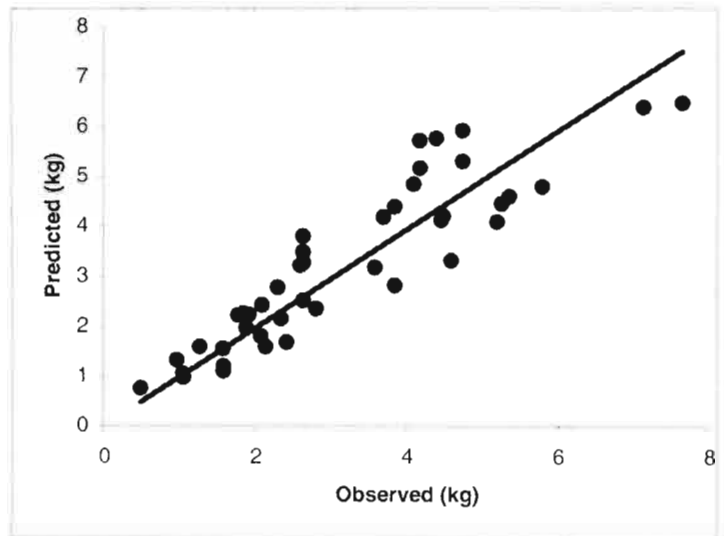
Figure C10: Observed vs. Predicted leaf biomass.

Table C11: Regression predicting leaf area as ln(leaf area) from ln(dbh)+ ln(age).

	d.f.	m.s.
Regression	1	31936.23 [Fpr 0.001]
Residual	43	26.79
Total	44	752.01
r^2		0.831
SE		5.18
Sapwood		0.34694 [tpr< 0.001]

Fpr is the F test probability, tpr is the t test probability
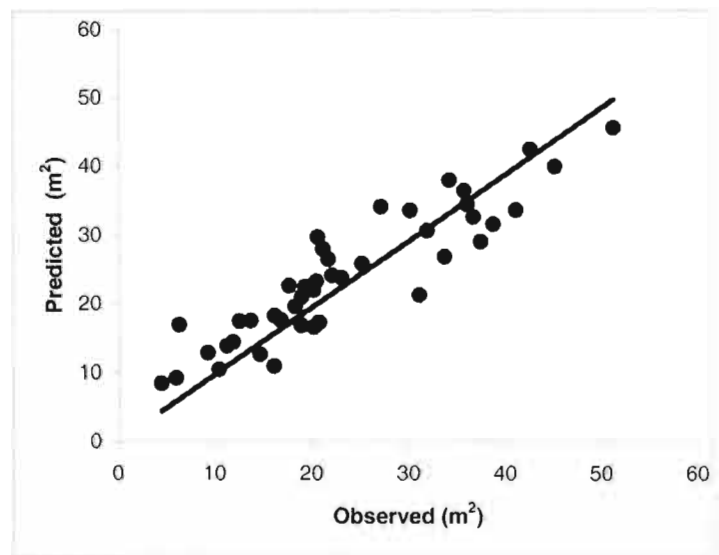
Figure C11: Observed vs. Predicted leaf area.

Appendix D: Regression results for prediction of stand level attributes from plant area index

Table D1: Regression predicting Basal area from plant area index and age.

	d.f.	m.s.
Regression	2	167.214 $^{Fpr\ 0.001}$
Residual	9	3.718
Total	11	33.444
r^2		0.889
SE		1.93
Constant		-12.06 $^{tpr\ .007}$
PAI		7.76 $^{tpr\ 0.001}$
Age		0.898 $^{tpr\ .003}$

Fpr is the F test probability, tpr is the t test probability
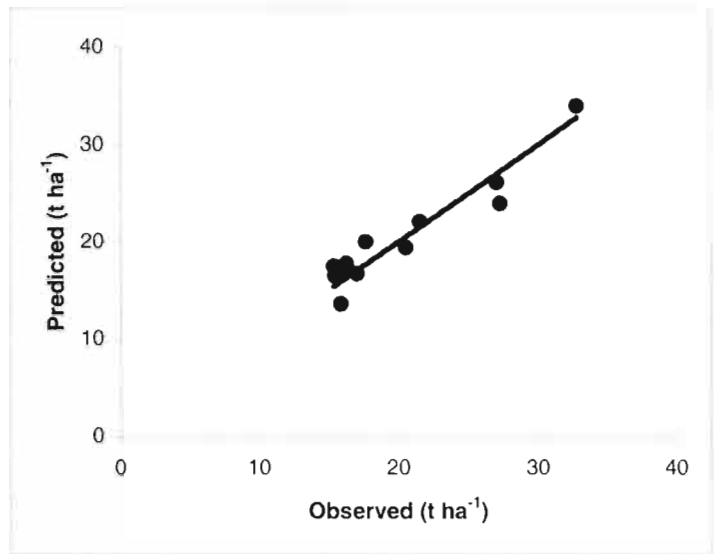
Figure D1: Observed vs. PAI predicted basal area.

Table D2: Regression predicting stand volume from plant area index and age.

	d.f.	m.s.
Regression	2	22902.2 $^{Fpr\ 0.001}$
Residual	9	510.9
Total	11	4582.1
r^2		0.888
SE		22.6
Constant		-212 $^{tpr\ 0.001}$
PAI		80.6 $^{tpr\ 0.001}$
Age		13.4 $^{tpr\ 0.001}$

Fpr is the F test probability, tpr is the t test probability
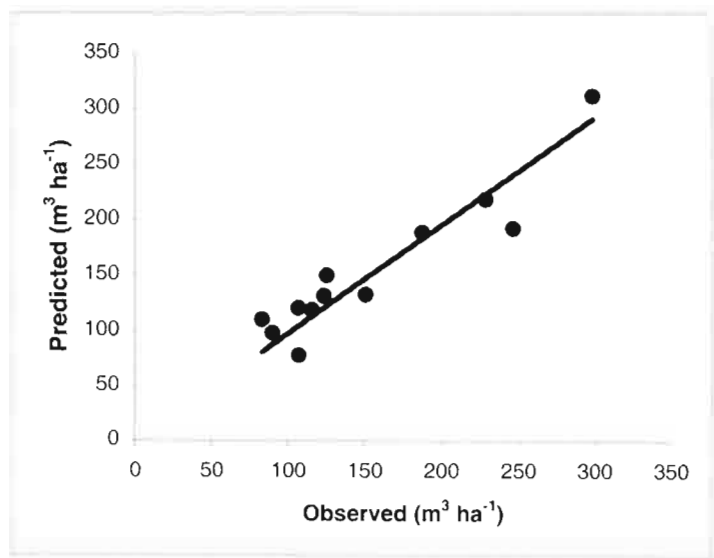
Figure D2: Observed vs. PAI predicted volume.

Table D3: Regression predicting above-ground biomass from plant area index and age.

	d.f.	m.s.
Regression	2	14634.3 $^{Fpr=0.001}$
Residual	9	303.3
Total	11	2908.9
r^2		0.896
SE		17.4
Constant		-156.7 $^{tpr=0.001}$
PAI		60.97 $^{tpr=0.001}$
Age		11.57 $^{tpr=0.001}$

Fpr is the F test probability, tpr is the t test probability
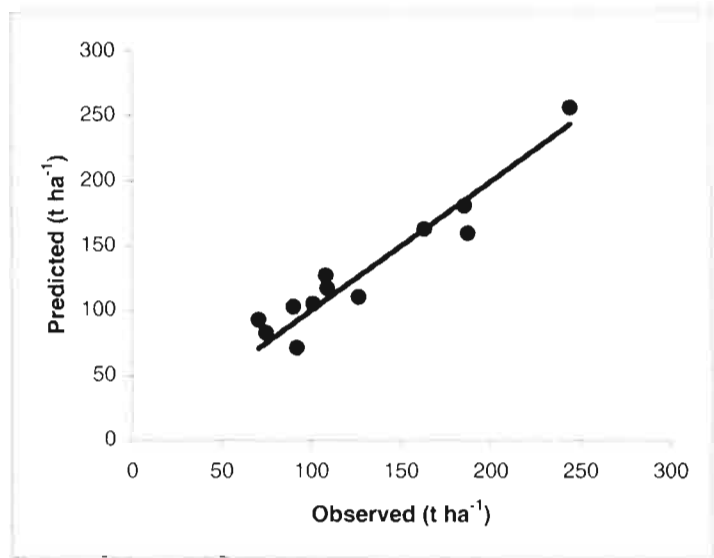
Figure D3: Observed vs. PAI predicted AGB.

Table D4: Regression predicting stem biomass from plant area index and age.

	d.f.	m.s.
Regression	2	9963.3 $^{Fpr=0.001}$
Residual	9	215.2
Total	11	1987.6
r^2		0.892
SE		14.7
Constant		-145 $^{tpr=0.001}$
PAI		52.72 $^{tpr=0.001}$
Age		8.96 $^{tpr=0.001}$

Fpr is the F test probability, tpr is the t test probability
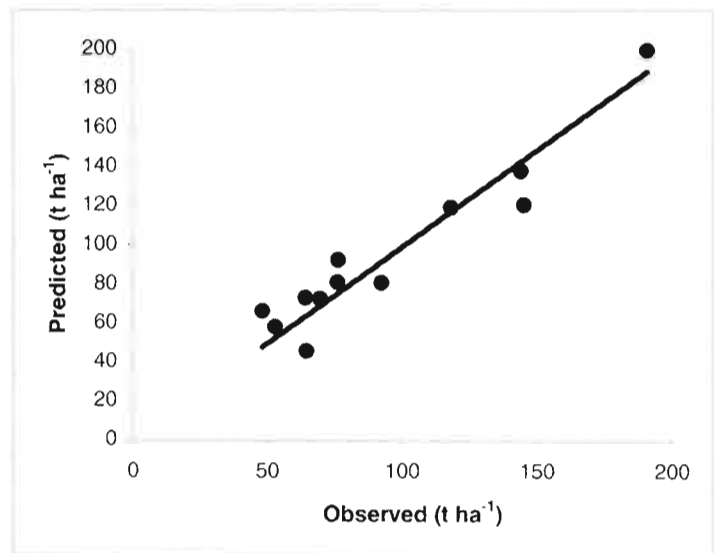
Figure D4: Observed vs. PAI predicted stem biomass.

Table D5: Regression predicting bark biomass from plant area index and age.

	d.f.	m.s.
Regression	2	156.5523 $^{Fpr\ 0.001}$
Residual	9	0.9657
Total	11	29.2542
r^2		0.967
SE		0.983
Constant		-15.59 $^{tpr\ 0.001}$
PAI		5.417 $^{tpr\ 0.001}$
Age		1.387 $^{tpr\ 0.001}$

Fpr is the F test probability, tpr is the t test probability
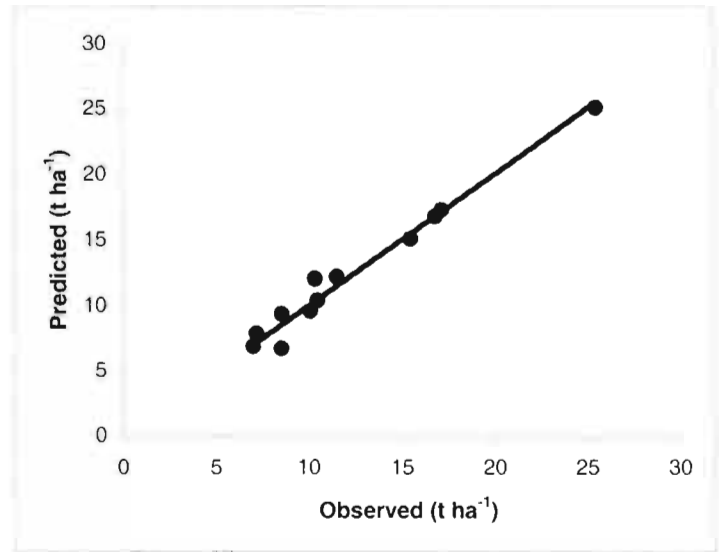
Figure D5: Observed vs. PAI predicted bark biomass.

Appendix E: Nutrient mass data for all *A. mearnsii* ages, sites and elements

Table E 1: Masses of nutrients contained in the AGB for all sites and ages.

Study site	Age Class (yr)	AGB (t ha⁻¹)	N (kg ha⁻¹)	P (kg ha⁻¹)	K (kg ha⁻¹)	Ca (kg ha⁻¹)	Mg (kg ha⁻¹)	Na (kg ha⁻¹)	Mn (kg ha⁻¹)	Fe (kg ha⁻¹)	Cu (kg ha⁻¹)	Zn (kg ha⁻¹)
Bloemendal	3-5	72.76	320	14.0	92.3	162.3	35.4	12.5	24.2	36.7	0.9	2.1
	5-7	96.39	398	17.9	191.2	160.6	44.5	25.6	15.1	45.4	1.2	3.1
	7-9	107.21	424	20.1	162.0	190.6	44.8	25.4	12.9	45.5	0.7	2.9
	9-11	116.39	545	26.0	197.3	229.9	54.5	18.5	12.6	48.5	0.9	3.0
Mistley	3-5	76.27	340	12.3	108.3	145.0	30.1	10.2	13.3	34.7	1.8	2.0
	5-7	93.53	409	17.4	127.8	195.6	42.3	28.3	8.8	39.4	1.6	2.7
	7-9	114.39	462	19.7	240.5	212.9	51.9	12.0	14.1	37.3	1.9	2.3
	9-11	175.63	682	31.2	298.0	340.2	70.4	12.8	15.8	35.8	1.3	2.1
SeeleMtH	3-5	130.96	558	17.7	261.6	232.4	56.1	22.5	10.3	30.7	1.6	3.2
	5-7	194.03	732	21.8	297.6	268.9	72.0	30.7	12.7	37.6	1.6	3.1
	7-9	191.95	670	19.2	190.8	263.0	62.9	36.0	13.2	31.2	1.8	3.9
	9-11	253.65	856	22.9	242.6	382.4	87.8	49.1	11.2	37.7	1.5	2.8

Table E 2: Distribution (%) of above-ground macronutrients for all sampled stands of *A. mearnsii.*

		Macronutrients						Micronutrients					
		Total (kg ha⁻¹)	Stem (%)	Bark (%)	Dead Branch (%)	Live Branch (%)	Leaves (%)	Total (kg ha⁻¹)	Stem (%)	Bark (%)	Dead Branch (%)	Live Branch (%)	Leaves (%)
		N						Na					
Study site	Bloemendal	94.9	22	23	4	24	26	8.4	41	13	5	24	17
	Mistley	126.7	27	21	5	21	26	7.3	44	10	4	23	19
	SeeleMtH	196.7	28	23	5	21	24	16.2	47	15	2	20	17
Age Class (yr)	3-5	406.1	23	21	2	22	32	15.1	40	12	1	23	25
	5-7	513.4	27	21	4	21	26	28.2	44	12	4	22	17
	7-9	518.4	27	22	5	22	24	24.5	47	14	4	20	15
	9-11	694.3	26	26	7	23	18	26.8	45	12	5	24	14
		P						Mn					
Study site	Bloemendal	7.5	39	12	4	25	20	5.3	33	9	4	18	36
	Mistley	7.7	37	11	4	24	23	4.9	38	12	5	20	25
	SeeleMtH	5.3	26	16	3	28	27	6.2	52	13	6	21	8
Age Class (yr)	3-5	14.7	35	12	2	20	31	15.9	43	12	4	19	22
	5-7	19	40	13	3	23	21	12.2	42	8	4	24	22
	7-9	19.7	29	13	4	32	23	13.4	43	9	5	19	24
	9-11	26.7	33	15	5	29	18	13.2	36	17	6	17	24
		K						Fe					
Study site	Bloemendal	55.1	34	16	2	32	16	14.1	32	9	5	25	29
	Mistley	58.9	30	16	1	34	19	10.6	28	15	8	23	25
	SeeleMtH	86.9	35	19	1	28	18	9.1	26	14	9	25	25
Age Class (yr)	3-5	154.1	29	15	1	31	24	34	29	13	8	26	24
	5-7	205.6	36	15	2	31	16	40.8	36	11	6	23	25
	7-9	197.8	35	16	1	31	17	38	28	13	8	23	27
	9-11	246	32	21	2	33	13	40.7	24	14	8	25	28
		Ca						Cu					
Study site	Bloemendal	39.7	21	39	6	19	14	0.3	28	12	4	28	28
	Mistley	37.8	17	46	7	18	12	0.8	49	6	3	26	16
	SeeleMtH	61.6	21	49	6	14	10	0.7	41	6	5	26	22
Age Class (yr)	3-5	179.9	20	44	4	17	15	1.4	33	8	4	32	23
	5-7	208.4	21	41	6	19	13	1.5	48	9	4	21	18
	7-9	222.2	18	51	5	15	10	1.5	45	6	4	22	23
	9-11	317.5	21	42	10	18	10	1.3	32	9	5	31	23
		Mg						Zn					
Study site	Bloemendal	11.8	26	20	6	27	20	0.6	20	13	4	41	22
	Mistley	13.4	28	22	7	25	19	0.4	19	14	4	38	26
	SeeleMtH	27.9	40	23	5	17	16	0.7	20	10	6	44	20
Age Class (yr)	3-5	40.5	31	20	3	22	25	2.5	14	13	5	43	25
	5-7	52.9	30	21	5	26	18	3	25	12	4	39	19
	7-9	53.2	35	22	5	21	17	3	26	11	4	37	22
	9-11	70.9	31	23	9	23	14	2.7	15	13	5	44	23

Appendix F: Mean contents of nutrients in tree components

Table F1: Nutrients contained in foliage and bark for all sites and ages.

Age Class	Element	Leaves			Bark		
		Bloemendal	Mistley	SeeleMtH	Bloemendal	Mistley	SeeleMtH
3-5		90.5	134.8	159.2	80.7	65.7	106.4
5-7	N (kg ha⁻¹)	108.6	109.0	177.8	93.3	74.5	166.9
7-9		120.3	100.8	155.7	92.7	92.9	154.1
9-11		108.5	102.3	157.2	126.2	177.8	245.8
3-5		3.1	4.7	5.9	1.6	1.2	2.6
5-7	P (kg ha⁻¹)	3.3	4.1	4.9	2.3	1.9	3.2
7-9		4.5	3.7	5.2	2.4	2.4	2.7
9-11		4.2	3.9	5.6	3.2	3.9	4.9
3-5		20.2	35.4	43.0	15.3	15.8	39.8
5-7	K (%)	24.3	25.0	49.2	26.2	18.5	51.6
7-9		26.2	31.3	40.8	27.0	36.4	33.6
9-11		25.1	29.0	38.3	35.3	54.8	61.3
3-5		28.1	24.7	24.0	64.9	63.5	112.8
5-7	Ca (kg ha⁻¹)	25.0	26.2	27.6	53.5	87.3	123.8
7-9		25.8	22.1	16.2	86.9	95.0	168.2
9-11		26.5	20.1	44.6	87.2	168.0	145.1
3-5		9.6	9.0	9.5	7.1	5.8	11.8
5-7	Mg (kg ha⁻¹)	7.9	8.2	12.2	7.8	9.1	17.0
7-9		9.6	7.4	8.9	8.8	12.7	13.8
9-11		8.4	7.7	12.9	12.2	17.2	20.5
3-5		2.7	3.5	4.1	2.1	1.1	1.7
5-7	Na (kg ha⁻¹)	3.8	4.9	6.0	2.7	1.8	6.1
7-9		4.5	1.4	5.4	3.6	1.3	6.7
9-11		2.8	1.5	6.8	1.8	1.4	7.9
3-5		8.7	3.0	0.8	3.0	2.0	0.9
5-7	Mn (kg ha⁻¹)	5.5	2.1	0.8	1.0	0.7	1.2
7-9		5.0	3.5	1.0	1.3	1.5	0.7
9-11		4.1	4.5	1.1	1.1	2.4	3.1
3-5		11.4	7.5	6.3	4.1	6.6	3.2
5-7	Fe (kg ha⁻¹)	12.8	8.3	9.3	2.8	4.8	5.4
7-9		13.5	9.0	8.9	3.6	5.0	5.7
9-11		12.9	11.8	9.7	5.7	5.9	5.5
3-5		0.3	0.3	0.3	0.1	0.1	0.1
5-7	Cu (kg ha⁻¹)	0.2	0.2	0.3	0.2	0.1	0.1
7-9		0.2	0.3	0.4	0.0	0.1	0.1
9-11		0.2	0.2	0.4	0.1	0.1	0.1
3-5		0.6	0.6	0.6	0.3	0.3	0.3
5-7	Zn (kg ha⁻¹)	0.6	0.6	0.5	0.3	0.4	0.4
7-9		0.6	0.6	0.8	0.4	0.3	0.3
9-11		0.6	0.5	0.7	0.4	0.3	0.3

Table F2: Nutrients contained in live and dead branches for all sites and ages.

Age Class (yrs)	Element	Live Branch			Dead Branch		
		Bloemendal	Mistley	SeeleMtH	Bloemendal	Mistley	SeeleMtH
3-5		70.5	61.8	138.6	6.4	5.5	19.7
5-7	N (kg ha⁻¹)	100.6	74.1	151.9	17.0	12.8	28.8
7-9		92.4	113.8	128.3	22.6	24.6	33.5
9-11		146.3	170.3	153.3	30.9	66.1	52.0
3-5		3.1	2.0	3.8	0.3	0.2	0.3
5-7	P (kg ha⁻¹)	4.8	4.0	4.4	0.8	0.5	0.3
7-9		5.1	5.8	7.8	0.9	0.8	0.6
9-11		7.3	9.0	7.1	1.2	2.1	1.0
3-5		28.8	30.7	86.0	0.3	0.5	3.0
5-7	K (%)	68.2	37.0	80.3	8.2	0.7	2.9
7-9		49.1	87.5	48.9	2.3	2.1	1.2
9-11		63.1	124.7	63.6	2.9	9.9	1.6
3-5		28.5	24.3	42.1	3.8	4.0	13.2
5-7	Ca (kg ha⁻¹)	35.4	37.2	39.0	12.4	11.4	15.8
7-9		32.2	45.1	19.6	12.0	14.4	7.8
9-11		46.6	55.3	66.5	16.1	43.6	34.2
3-5		9.0	5.6	11.9	0.9	0.6	2.3
5-7	Mg (kg ha⁻¹)	13.3	12.2	13.9	3.2	1.9	3.2
7-9		11.4	13.2	8.3	2.7	3.6	2.0
9-11		15.6	18.3	13.2	4.4	8.8	5.9
3-5		2.8	2.2	5.5	0.2	0.1	0.4
5-7	Na (kg ha⁻¹)	6.2	7.0	5.5	2.0	0.5	0.8
7-9		5.5	2.9	5.6	1.3	0.5	0.3
9-11		5.0	3.1	10.1	1.2	1.1	0.4
3-5		3.7	2.5	2.3	0.7	0.5	0.4
5-7	Mn (kg ha⁻¹)	4.0	2.0	2.7	0.5	0.5	0.5
7-9		1.8	2.8	3.3	0.5	0.6	1.0
9-11		2.2	3.1	1.7	0.5	0.7	1.0
3-5		9.3	8.7	8.5	2.4	3.3	2.0
5-7	Fe (kg ha⁻¹)	12.2	7.7	8.8	1.6	2.2	2.9
7-9		7.3	10.3	8.2	2.4	2.9	3.8
9-11		15.4	7.5	8.8	2.3	3.4	3.9
3-5		0.3	0.8	0.4	0.0	0.1	0.1
5-7	Cu (kg ha⁻¹)	0.3	0.3	0.3	0.0	0.0	0.1
7-9		0.2	0.4	0.4	0.0	0.1	0.1
9-11		0.3	0.3	0.6	0.0	0.1	0.1
3-5		0.9	0.8	1.4	0.1	0.1	0.2
5-7	Zn (kg ha⁻¹)	1.1	0.9	1.6	0.1	0.1	0.1
7-9		1.0	0.8	1.7	0.1	0.1	0.2
9-11		1.5	0.9	1.1	0.1	0.1	0.2

Table F3: Nutrients contained in stem and total AGB for all sites and ages.

Age Class (yrs)	Element	Stem			Total AGB		
		Bloemendal	Mistley	SeeleMtH	Bloemendal	Mistley	SeeleMtH
3-5		72.2	72.6	133.8	320	340	558
5-7	N (kg ha⁻¹)	79.0	139.0	206.8	398	409	732
7-9		95.8	129.7	198.1	424	462	670
9-11		132.9	165.4	248.0	545	682	856
3-5		6.0	4.2	5.1	14.0	12.3	17.7
5-7	P (kg ha⁻¹)	6.7	6.9	9.1	17.9	17.4	21.8
7-9		7.1	7.1	2.9	20.1	19.7	19.2
9-11		10.1	12.5	4.3	26.0	31.2	22.9
3-5		27.7	25.9	89.8	92.3	108.3	261.6
5-7	K (%)	64.3	46.7	113.6	191.2	127.8	297.6
7-9		57.5	83.3	66.3	162.0	240.5	190.8
9-11		70.8	79.7	77.7	197.3	298.0	242.6
3-5		36.9	28.5	40.4	162.3	145.0	232.4
5-7	Ca (kg ha⁻¹)	34.4	33.5	62.8	160.6	195.6	268.9
7-9		33.8	36.2	51.2	190.6	212.9	263.0
9-11		53.6	53.1	92.0	229.9	340.2	382.4
3-5		8.8	9.1	20.5	35.4	30.1	56.1
5-7	Mg (kg ha⁻¹)	12.3	10.9	25.8	44.5	42.3	72.0
7-9		12.4	15.1	29.9	44.8	51.9	62.9
9-11		13.9	18.3	35.3	54.5	70.4	87.8
3-5		4.8	3.3	10.8	12.5	10.2	22.5
5-7	Na (kg ha⁻¹)	10.9	14.1	12.3	25.6	28.3	30.7
7-9		10.4	5.9	18.0	25.4	12.0	36.0
9-11		7.6	5.7	23.8	18.5	12.8	49.1
3-5		8.1	5.3	5.9	24.2	13.3	10.3
5-7	Mn (kg ha⁻¹)	4.1	3.5	7.5	15.1	8.8	12.7
7-9		4.3	5.6	7.3	12.9	14.1	13.2
9-11		4.6	5.1	4.3	12.6	15.8	11.2
3-5		9.6	8.6	10.7	36.7	34.7	30.7
5-7	Fe (kg ha⁻¹)	16.0	16.5	11.3	45.4	39.4	37.6
7-9		18.8	10.1	4.6	45.5	37.3	31.2
9-11		12.1	7.2	9.8	48.5	35.8	37.7
3-5		0.2	0.6	0.7	0.9	1.8	1.6
5-7	Cu (kg ha⁻¹)	0.6	0.8	0.7	1.2	1.6	1.6
7-9		0.2	1.1	0.8	0.7	1.9	1.8
9-11		0.2	0.7	0.4	0.9	1.3	1.5
3-5		0.2	0.3	0.6	2.1	2.0	3.2
5-7	Zn (kg ha⁻¹)	0.9	0.7	0.6	3.1	2.7	3.1
7-9		0.9	0.5	1.0	2.9	2.3	3.9
9-11		0.4	0.3	0.5	3.0	2.1	2.8