TIMBER GROWTH AND SUCCESSION IN THE MIXED EVERGREEN FORESTS OF THE SOUTHERN CAPE

by

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DECLARATION

I hereby declare that the thesis is my own work, both in concept and execution, and that apart from limited guidance from my supervisors, I have received no assistance except as stated below:

* The published papers were refereed by unidentified people. Many of their comments, as well as those by my colleagues, were incorporated in the text. Not one of the referees suggested any major changes in research approach, data analyses or text.

* The growth model was developed in collaboration with Dr Hank Shugart of the USA. He, together with some colleagues, developed the KIAMBRAM model that was used as the basis for the OUTENIQUA model. I spent three weeks with him, during which he explained his modelling approach to me and answered numerous questions. The KIAMBRAM model was written in FORTRAN IV and designed to run on a mainframe computer. Back in South Africa I altered the FORTRAN IV code to FORTRAN V and rearranged the entire model outlay to fit on an old-fashioned 16 bit Data General minicomputer with only 64 Kb memory available to each user. I did all the simulations, constructed the graphs and histograms and wrote the original draft paper.

* I initiated, designed and executed the tree dating study. Dr J C Vogel of the Division of Earth, Marine and Atmospheric Science and Technology, CSIR, assisted by Miss A Fuls, did the C^{14} dating of the wood samples. Dr Frans Malan of the CSIR Division of Forest Science and Technology did the radiation densitometric measurements, although I did

most of the sample preparation. I did all the data analyses, prepared the draft paper and incorporated the co-authors' comments into the final draft paper.

Signed by candidate

J C van Daalen

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ABSTRACT

A deterministic distance-independent individual tree model, called OUTENIQUA, was developed for a 44 ha southern Cape mixed evergreen forest compartment where the DBH's of all trees have been measured over a 15 year period. The central growth equation from another model for mixed forest was used and parameters adjusted to cater for the southern Cape forests. The developed model was then used to highlight research needs. Some of these research questions were addressed in this study.

Tree growth, mortality and recruitment rates were determined for the period 1972 to 1987 on the same forest stand as was used for the model development. Mean basal area for all species together changed from 32.7 m^2/ha in 1972, to 34.1 m^2/ha in 1978 and 35.3 m^2/ha in 1987. Net growth rates since 1942 have declined from 1.63 % per annum for the period 1942 to 1953 to only 0.35 % per annum for the period 1978 to 1987. Mortality rates of most species increased and for some species exceeded their recruitment rates. Gross volume growth rate for the stand since 1972 was very similar to that for unlogged tropical forests elsewhere in the world, i.e. about 2 m^3/ha per annum. Despite this relatively slow growth, recovery from disturbances was, nevertheless, relatively fast. Many aspects of the observed growth and mortality rates could be explained in terms of the development phases of the forest. The model of biomass accumulation by Bornmann and Likens (1979) was used as a vehicle for unravelling the development stage of the forest and it was concluded that it is in a late successional stage, close to its maximum timber carrying capacity.

Competition among trees was determined by locating the exact position (to the nearest 5 cm) of all trees on a 2.86 ha forest stand (i.e. 3970 trees), calculating all the distances among them by means of the Arcinfo Geographic Information System and correlating the distance between two neighbouring trees with the growth of the smaller one of the pair. Both inter- and intraspecific competition was evident between most of the chosen species combinations. The apparent more pioneer-like species, such as *Olea capensis* subsp. *macrocarpa*, *Ocotea bullata* and *Apodytes dimidiata*, showed weaker competitive abilities than later successional species such as *Podocarpus latifolius*, *Curtisia dentata* and *Pterocelastrus tricuspidatus*. Most of the southern Cape forest

trees are shade-tolerant and can grow in close proximity to other trees, but the growth rate of various species is retarded by competition. It was concluded that the harvesting of the weaker competitors strictly according to the numerical proportions by which they occur in the forest is unnecessary, that the more valuable timber species profit from the advanced development stage of the forest in that they are better late-successional competitors, that the role of the dominant forest tree, *Olea capensis* subsp. *macrocarpa*, is not fully understood and that the present management approach of harvesting trees that most likely die, is sound.

Diameter increment over a 13 year period for a range of forest tree species on the same 2.86 ha compartment was correlated with their crown position and form. It was found that both crown variables are useful for the selection of harvest trees of those species that occur in or above the canopy. The growth of subcanopy species was, in general, not related to the crowns' positions in the canopy. Crown form was, however, significantly correlated with growth of some subcanopy species. For all the tree species (mainly canopy species) for which increment was significantly correlated with both crown position and crown form, the crown position and form scores were significantly related. This confirmed the results of the competition study that the growth of these trees were influenced by competition.

The use of cambial electrical resistance readings for distinguishing trees with high from those with low growth rates, to detect trees with a reduced growth rate as a result of pathogen infection or to compare the vigour of indigenous versus alien trees proved to be of little value. Significant correlation coefficients between resistance readings and growth rates were obtained, but standard deviations were too high to be useful for indigenous management purposes.

Theoretically tree age is one of the more reliable methods for determining and predicting growth rates. In southern African hardwoods it is often very difficult, if at all possible, to determine this by tree ring counting. Different tree dating techniques were tested on *Pterocarpus angolensis*, a savanna hardwood. These were (a) C^{14} dating, (b) visual tree ring counting, (c) counting of rings on X-ray photographs taken from the transverse surfaces of samples cut from tree boles and (d) by using radiation densitometry. C^{14}

dating of some southern Cape forest trees of known ages provided accurate results. Therefore, the ages of the *Pterocarpus* trees determined in this way were accepted as correct. Visual ring counting and counting of rings on X-ray photographs is subjective and requires considerable experience to obtain reliable age estimates in these ways. C^{14} dating of trees is expensive and takes a few months to complete, but is the most reliable method for dating tropical trees where growth rings are absent or indistinct. For those tree species where the denser areas on the transverse surfaces of the wood samples correspond to annual growth, gamma ray densitometric measurements provide reliable age estimates. In the case of *Pterocarpus angolensis* the radiation densitometric system yielded poor results despite the fact that the wood of this species is semi-ring-porous and contains terminal parenchyma. However, alterations such as the use of the Fe^{55} isotopic source, which emits softer gamma rays that are better absorbed by wood, the use of thinner sections and measurements over smaller areas and intervals could improve the results considerably.

The modelling and follow-up approach followed in this study proved to be useful. It provided a framework for a systematic and logic sequence of studies on forest growth and succession, an approach that can be followed advantageously for research planning and motivations for funding. I recommended that the model should be rewritten using more modern software. The same modelling principles as were used for this study should be applied during the rewriting and improvement of the model. The incorporation of the results of this study can improve the model considerably and make it a useful management tool.

Research on the germination and establishment of forest tree seedlings and their development into saplings should receive priority. Little is known about this development stage of the forest and it is, in general, neglected by southern Cape forest managers.

ACKNOWLEDGEMENTS

Usually by the time a thesis is completed, one is so relieved and tired of the subject studied that the last thing one wants to do is to rewrite a conventional one-volume thesis into a number of papers suitable for publication. For this reason, and to save work, I prepared each chapter as a separate publication (in one instance as two shorter publications). A number of these have been published already and others are in the process of publication.

I want to thank Prof Eugene Moll, my original promoter, for allowing me to use this thesis format. His successor, Prof William Bond, kindly accepted this format. His input is much appreciated. Part of this study was funded by the Department of Water Affairs and Forestry (Forestry Branch). The final part of the study was done under contract with FORESTEK, CSIR. Both institutions are thanked for their support.

Finally, I am indebted to my wife, Hennie, and the children for their support and patience, especially during the final stages of the study and the thesis preparation. They had to forfeit many a family outing and other privileges because of me sitting in front of my computer.

Signed by candidate

Hans van Daalen.

SECTION 1

INTRODUCTION

INTRODUCTION

FOREST ECOLOGY AND LANDUSE

"It often is difficult to extract from the apparent tranquillity of a forest a sense of the actual dynamism of trees struggling over centuries to gain landscape for their species. To the human eye, a forest is a slowly changing ecosystem that superficially looks alike from one year to the next. Yet, this seeming quiet is, in fact, a balance between the tremendous proregenerative potential of trees and an equally tremendous mortality rate. A single tree can produce tens of millions and (in some species) hundreds of millions of potential offspring over its lifetime. This reproductive potential by far outstrips the reproductive rates of the vast majority of animals, and its makes the multiplicative powers of organisms such as rabbits and lemmings pale by comparison. When one couples a tree's reproductive potential with the fact that trees can grow to the most massive organisms on earth, then a notion of the ecological potential of trees begins to emerge." (Shugart, 1984).

These massive forces of increase must be counterbalanced by the forces of decrease, mortality and predation. The understanding of these forces, especially in the light of the longevity of trees, is very difficult. It is virtually impossible to collect complete data sets on the dynamics of natural forests. Typically one has bits of data from different points in time on certain aspects of forest dynamics. These bits of data are then put together like pieces of a huge jigsaw puzzle, and more than often many pieces are missing. To obtain additional pieces might take a lifetime of observations, but often one has no assurance that the new pieces will fit the old (Shugart, 1984).

Ecology, and in this case forest ecology, is more than a mere collection of facts. It is a way of assembling these facts into a logical whole (Oliver and Larson, 1990), and in many cases facts based on scientific inference. Because of this reliance on inference, mathematical simulations of forest dynamics offer verifiable expressions of the mechanisms that we think might be of importance in forest succession.

Seen in a broader context, mathematical models can be useful tools in developing rational land use policies that will result in a sensible balance between the transfer of land to other uses and its retention as forested land in perpetuity. At the end of 1980 the FAO estimated the total area of natural woody vegetation in the tropical regions of the world at 2.96×10^9 ha of which 1.2×10^9 ha was closed forest. It was estimated that 7.5 million ha of closed forest would be cleared per year between 1981 and 1985 for agricultural settlement, shifting agriculture, logging and other forms of landuse. Of this, shifting cultivation accounted for 45 %. An estimated 3.8 million ha of open tree formations in the tropical regions were also expected to be cleared each year. Thus the total area of forested land being cleared annually was estimated to be 11.3 million ha. This is an expected rate of clearing of 1.14 % per year. An additional 4.4 million ha of closed forests are logged every year but not cleared while considerable areas are being degraded because of repeated burning and overgrazing (particularly the open woodland), and excessive exploitation, especially for fuelwood (Lanly, 1983; Shepherd and Richter, 1985). In the light of such rapid loss and degradation of forest and woodland, the tools for proper resource management are of vital importance. With mathematical forest growth models long-term effects of certain management activities, such as the effect of a certain harvesting practice or the clearing of a forest patch, can be simulated and the implications assessed. Without modelling it might take 50 years and longer to obtain an answer.

SOUTHERN CAPE FORESTS

The southern Cape forests, also known as the Knysna forests (Phillips, 1931; Acocks 1953), form the largest forest complex in southern Africa (Anonymous, 1987). Forest type ranges from high to scrub forest (3 m to > 20 m in height). Both in composition and growth forms it resembles the Australian rain forests (Phillips, 1931; Von Breitenbach, 1974; Webb, 1978). It has a fragmented distribution on the seaward side of the coastal mountain ranges. The forests are evergreen and exhibit features typical for tropical oligotrophic ecosystems (Janzen, 1974; McKey *et al.*, 1978), such as sclerophylly, phenolic compounds in leaves, synchronised fruiting of trees at intervals of more than one year, and dense root mats on and in the surface soil layer (Van Daalen, 1984).

Since its discovery by European settlers during the middle of the 18th century it has been almost continuously and intensively utilised for timber (Phillips, 1963; Geldenhuys, 1982). Acocks (1953) suggested that much of the forested area from the Cape Peninsula to Port Elizabeth have been cleared since the arrival of European settlers to the Cape in 1652. The period of uncontrolled exploitation was followed by various harvest control systems, which finally resulted in the implementation of a single tree selection system in 1966 (Laughton 1937; Von Breitenbach, 1968; Geldenhuys, 1987). Since then the forest management system, or parts of it, have been modified and improved periodically (Geldenhuys, 1982; Seydack, 1982; Seydack *et al.*, 1982; Van Dijk, 1987; Seydack *et al.*, 1990). At present the forests are divided into five management classes. These are (percentage of forest area involved in parentheses) timber production (19.7 %), protection (55.8 %), nature reserves (23.0 %), recreation (0.4 %) and research (1.1 %) (Seydack *et al.*, 1990). High quality and much sought-after timber (*Ocotea bullata* (Burch.) E. Mey. is one of the world's most expensive timbers) is produced and despite the limited forest area used for timber production, it supports a well-known local furniture manufacturing industry.

The management policy for the southern Cape forests aims at sustained multiple resource utilisation, but subject to conservation constraints (Seydack *et al.*, 1982). Silvicultural treatments to increase timber production *per sé* are, therefore, not allowed. Timber is seen as one of the many assets of the forests and harvested in such a way as to simulate natural mortality as far as possible and to minimise the impact of harvesting. Under these conditions only the net timber volume growth can be realised. Thus the question arises: "Exactly how much timber can we harvest?" Under-utilisation of timber resources violates the principles of multipurpose management, which ensures maximum overall benefit. Over-utilisation, on the other hand, contradicts conservation aims and negates the principles of sustenance.

STUDY APPROACH

This study was aimed at providing the manager with a framework for determining and selecting the trees to be harvested. Such a framework should be general enough to be used under different management policies (for these can change overnight), but detailed enough to allow him to apply it to specific forest compartments. The research reported on here is, therefore, essentially applied.

The mathematical model that was developed served as a focal point of this study. In chapter 1 the model is described. During the model development certain assumptions on the growth rates of tree species and on the succession of the southern Cape forests were made. Logically, a study to validate or reject these assumptions received priority. Chapter 2 is about a forest growth case study on the same forest stand that was used for the model development. Chapter 3 discusses the effect of intra- and interspecific competition on timber growth. This study was conducted in a forest compartment adjoining the one used for the above-mentioned studies. The management system for the southern Cape forests requires that individual trees are selected for harvesting. Therefore, the management system is only as good as the accuracy with which these trees can be identified and selected in the forest. In the forest, frequently a suppressed tree cannot easily be distinguished from a tree with high vigour. For this reason variables that could serve as growth indicators were tested. These are discussed in chapter 4. Tree age should theoretically be one of the best growth indicators. Typically a tree reaches its fastest growth rate after establishment, when it reaches the crown, and before growth is retarded during the senility phase. Furthermore, individual trees can vary greatly in their growth rates due to factors such as competition, genetic variation, underlying soil and water availability. Conventional tree aging techniques, such as tree ring counting, are very difficult or impossible to apply to most southern African hardwoods (Van Daalen *et al.*, 1992). Possible alternatives are discussed in chapter 5. The techniques were tested on *Pterocarpus angolensis* DC., a savanna woodland tree occurring in northern and eastern Transvaal, but results can be applied equally to the southern Cape forest trees.

MODELLING FOREST GROWTH

Due to the variety of species composition, floristic structure, ecological situations and silvicultural practices possible in mixed forests a whole range of modelling strategies are possible. Four groups of models will be discussed briefly:

(1) Static yield functions.

Synnott (1980) calls this method "time-of-passage" calculations. This includes

(i) the calculation of average annual increments for each species and size class, and

(ii) the determination of growth of each tree through successive classes using average growth rates to predict sizes for a future date.

The principle feature of static functions is that time is included in the model as a total elapsed time from some reference point. This reference point can, for example, be the last harvesting operation or the last inventory (Alder, 1980).

As with other models site factors are included. In mixed forests environmental parameters form part of an effective model. In this way a type of site index is obtained (Alder, 1980).

Various methods can be used to predict variables, e.g. principal components analysis, multiple regression and others. However, a *priori* selection of selector variables in a relatively simple equation is generally preferable. This can be combined with a careful graphical analysis of residuals and preferably some commonsense relationship between the form of the function and the reality of the biological situation predicted (Alder, 1980).

Although these models are relatively straightforward to construct, three kinds of problems can be experienced (Alder, 1980):

(i) Implicitly the historical sequence of events to which the data set has been subjected, are part of the constructed model.

(ii) There is a problem of compatibility. If the volume is predicted, e.g. in three categories, viz. valuable, merchantable and useless species, the total of these three volumes does not equal the total volume, either from actual data or from a fourth function fitted directly to the volume.

(iii) Where only light selection fellings are carried out (as in the southern Cape forests) and the forest is a complex mixture of many species and ecological types, there may be no direct relationship discernible over time between yield, basal area and site class. In such cases growth prediction with a simple yield model is not possible.

(2) Transition matrix models

Where forecasts with transition matrix models are done, Markov chain transition probabilities are often used (Lloyd, 1974). This includes the following (Synnott, 1980):

(i) Calculate growth rates from each size class to the next larger.

(ii) Calculate the probability of any tree moving from one class to the next in a given time.

(iii) Apply these probabilities to each tree for successive intervals to predict size class distribution.

When a transition matrix is constructed from size class data only the following must be assumed (Alder, 1980):

(i) All ingrowth occurs into the lowest size class.

(ii) Outgrowth from one class can only occur into the next higher class.

(iii) The number of harvested stems in each class is known from an independent source or deduced from the treatment prescription.

To make the transition model for mixed forests workable, firstly, species must be grouped and separate matrices constructed for each group. The number of groups should not be too large, otherwise one may have too little data for many transitions. Secondly, data should be grouped into basal area classes for different forests to allow a different transition matrix to be used for different stand densities (Alder, 1980).

Markov models can display various features that are directly interpretable in terms of succession. For example, an extension of a Markov model will eventually lead to a stable state, analogous to the climax. Similarly, these models can display continuous succession and sequences similar to Connell and Slatyer's (1977) facilitation and tolerance pathways (Noble and Slatyer, 1981).

These models are suitable for fitting purposes (Lloyd, 1974) and can, therefore, be used for limited predictions and for testing ideas, like Horn (1975) has done. It is, however, only a fitting exercise. For prediction, transition matrices have various disadvantages (Alder, 1980; Synnott, 1980):

(i) It requires little insight in the mechanisms of dynamic vegetation changes and results are obtained exclusively by means of extrapolation of the data used to construct the model. Rare species often result in poor estimates of the transition probabilities with resulting poor extrapolations.

(ii) It is difficult and tedious to represent dynamic interactions. For each level of the controlling variable a separate interaction must be constructed.

(iii) The precision of a transition model is limited by the need to work with broadly defined classes (e.g. size classes), otherwise too many undefined transitions occur or the matrices become too large for easy computation.

(iv) Transition models are insufficient in terms of the number of parameters required to define a growth process. For example, a 9 x 9 matrix (81 parameters) might only correspond to a single variable growth equation. The addition of a second variable could increase the matrix size fourfold (18 x 18 matrix).

(3) Distance-independent individual tree models

A distance-independent individual tree model is one in which each tree in a stand is individually represented by a set of variables, e.g. tree species, DBH (diameter at breast height), height and crown condition. Tree position is not represented (Alder, 1980).

Mainly two types of models have been used:

(i) Models that do not necessarily require recurrent measurements: These are based on information of individual species characteristics such as maximum age, height, DBH, relationships of photosynthesis with light regime, climate and moisture, and data on environmental factors such as the influence of seed- and seedling-eaters, topography and climate. Examples of these models are FORET for north-eastern USA (Botkin *et al.*, 1972; Shugart and West, 1977), FOREST (Ek and Monserud, 1979) and KIAMBRAM (Shugart *et al.*, 1980).

(ii) Models that require recurrent measurements of trees on permanent sample plots: Here growth is correlated with size and other measured variables for each tree, for each species or group of species. A regression is derived from all the trees and is then applied to each tree individually to predict its increment from its size and status. Inevitably, the competitive status of each tree changes with time and its growth is influenced by different factors which cannot always be measured. A random element is, therefore, included in the model to allow for apparently random elements of growth such as the often poor correlation between growth rate and size, and the lack of measurements of status. This is a so-called stochastic model. Synnott's (1980) GROWTH model and the GROPE model of Alder *et al.* (1977) are examples of this approach.

With these distance-independent models competition can be represented in the form of stand density. The latter can be represented in a number of ways, e.g. as an absolute measure such as number of trees over a certain size limit, or as a relative measure such as basal area divided by the maximum basal area possible on that site, or it can be measured as total leaf biomass on a given area (Alder, 1980).

(4) Distance-dependent individual tree models

Although distance-independent models are generally much more economical in terms of computer resources than distance-dependent models, they give a less realistic and detailed representation of intertree competitive processes (Alder, 1980). For the distance-dependent models the growing space or competitive status of each tree can be defined from the sizes and distances from neighbours. This improves the value of stand projections and of the analyses of the effects of treatments on growth rates and production. When parameters such as tree heights and crown measurements are included increased definition of competition can be obtained (Synnott, 1977).

The deterministic distance-independent modelling approach was followed for this study because it allowed the use of an already derived growth equation, and it does not require the long term empirical growth data necessary for the stochastic model or the heavy database required for the distance-dependent modelling approach. Consequently it could be developed in much shorter time than would be needed for the other approaches.

FOREST GROWTH AND SUCCESSION

For the model developed in this study (called OUTENIQUA) many of the values of the underlying parameters of forest growth were assumed or estimated. For instance, does the central general growth function of the model reflect the growth rate of southern Cape forests accurately? Does succession happen as was assumed by this reductionistic model? Are the assumed phenological patterns correct? These were the type of questions asked after the model developing phase. Some of them are addressed in this study, others initiated other studies.

During 1972 the DBH's of a large number of trees in a compartment in the forest north of Knysna were measured, the points of measurement marked accurately and each tree was numbered with a unique number. Over the next 15 years all trees were remeasured twice, providing a growth data base of more than 26 000 trees. These data were used for a study on the growth, mortality and recruitment rates of southern Cape forest trees.

COMPETITION AMONG TREES

Odum (1971) described two broad types of ecosystem interaction, positive and negative. Positive interactions include mutualism (interaction favourable for both populations and obligatory), protocooperation (interaction favourable for both but not obligatory) and commensalism (population one, the commensal, benefits while two, the host, is not affected). Negative interactions include parasitism, predation, amensalism (one population inhibited and the other one not affected) and competition. In the broadest sense competition refers to the interaction of two organisms striving for the same thing. This could manifest, firstly, as competition for resources such as nutrients, water, space and sunlight (interference competition) (the use of the term competition is sometimes restricted to this meaning (Whittaker, 1975)) and, secondly, as the consumption or elimination of a resource item by one individual, making it unavailable for others (exploitation competition) (Miles, 1979; Murray, 1986; Rice, 1974).

With regard to inter- and intraspecific competition in the forest Botkin (1981) assumed that trees compete primarily for light, although some species grow much better in bright light than others, and the ones that grow well in bright light grow poorly in dim light. This distinction between shade-tolerant and shade-intolerant species was the primary mover in the interaction among species in the earlier versions of his JABOWA succession model. In a later version he added competition for soil nitrogen.

The purpose of the competition study reported in chapter 3 was to investigate the role of both inter- and intraspecific competition between trees in a mature southern Cape forest stand.

GROWTH INDICATORS

If size is not an indicator of the age and vigour of a tree, other criteria should be used, if available and practical. In the southern Cape senility indices, such as stem rotting, dying, damage and "agony" shoots (i.e shoots growing out of the main bole when the tree is under stress) are used to select trees for harvesting (Seydack *et al.*, 1990; Kobrie Vermeulen, personal communication, 1992). In this way an attempt is made to harvest as many as possible of the trees that will die in the period to the next harvest, i.e. mortality is as far possible pre-empted.

Apart from the senility indices, the position of the tree's crown in relation to the overall forest canopy and in relation to its neighbours' crowns (Synnott, 1979), the form of the crown (Dawkins, 1963 ex Synnott, 1979), crown size (Oliver and Larson, 1990) and the cambial electrical resistance (Davis *et al.*, 1981) have been used as indications of growth rates and vigour. Of these, crown size is the only parameter which is too difficult to determine in the forest to be of practical use (chapter 4). Crowns intermingle to such an extent that the distinction of a specific crown is difficult, let alone measuring its dimensions.

DATING OF TREES

Theoretically tree age remains one of the more reliable methods for predicting growth rates. In southern African hardwoods, however, it is often impossible to determine this in the conventional way, i.e. with tree ring counting. Lilly (1977) rated a large number of indigenous trees according to their dendrochronological potential. Only a few species, such as the *Podocarpus* species, obtained high ratings.

Four dating methods were compared, viz. visual growth ring counting, C^{14} dating, counting of rings on X-ray photographs taken from the transverse surfaces of samples cut from tree boles, and counting rings by using radiation densitometry (chapter 5). The study was done on a savanna timber tree, *Pterocarpus angolensis*. Samples from three southern Cape forest trees of known age were sent for C^{14} dating. This method provided accurate results. Therefore, the ages of the *Pterocarpus* trees determined in this way were accepted as correct. Results from the other dating techniques were compared with the C^{14} dating results.

SECTION 2

RESEARCH FINDINGS

CHAPTER 1

MODELLING FOREST SUCCESSION

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OUTENIQUA – A computer model to simulate succession in the mixed evergreen forests of the southern Cape, South Africa

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Abstract

A succession model for mixed evergreen forests of the southern Cape, South Africa, called OUTENIQUA, was developed based on one for subtropical rain forest in New South Wales, Australia. The model simulates the regeneration, growth and mortality on a 0.04 ha plot using an individual-tree based modeling approach to forest succession. The OUTENIQUA model was tested on its ability to simulate species dynamics of the forest stand used for its development, as well as on independent data from a neighboring stand and not used for the model derivation. The model is used as a research tool to summarize published and unpublished knowledge on the southern Cape forests and to highlight aspects where knowledge is insufficient. The development of the model represents a test of an individual-tree gap model as a simulation tool for use in management and directing research in subtropical and tropical forests.

Introduction

The simulation of diverse, mixed-aged stands of trees would seem difficult given the effort required to develop simulators of much simpler (mono species, even-aged) plantations (see reviews by Munro 1974; Shugart and West 1980; Dale *et al.* 1985). Nevertheless, mixed-aged and mixed-species forests are characteristic of the world forest reserves.

We feel that the development of forest simulators which can interface with forest management is essential to any realistic attempts at managing tropical forest. Hence, the junior author and several Australian colleagues developed the KIAMBRAM simulation model of Australian subtropical rain forest (Shugart *et al.* 1980). This model was derived from a well tested family of forest simulators and tested for the complex notophyll vine forest. Although the model could be improved by the addition of species-specific growth equations, only very basic information is needed to develop a KIAMBRAM-type model (Shugart *et al.* 1980).

In this paper, we investigate this applicability of this approach by developing and testing a model of the mixed-species forest of the southern Cape of Africa with a relatively minimal calibration. The resultant model will be used to synthesize information in South Africa prior to further research on functioning of southern Cape forests. In a more general context, we are documenting a modeling protocol that, based on data sets that could the developed in a research program conducted by a developing nation, can provide a usable and tested mixed-species, mixed-aged forest model suitable for management applications. In developing this protocol, we use forest inventory data on tree growth and the understanding of tree species natural history based on the experience of local foresters

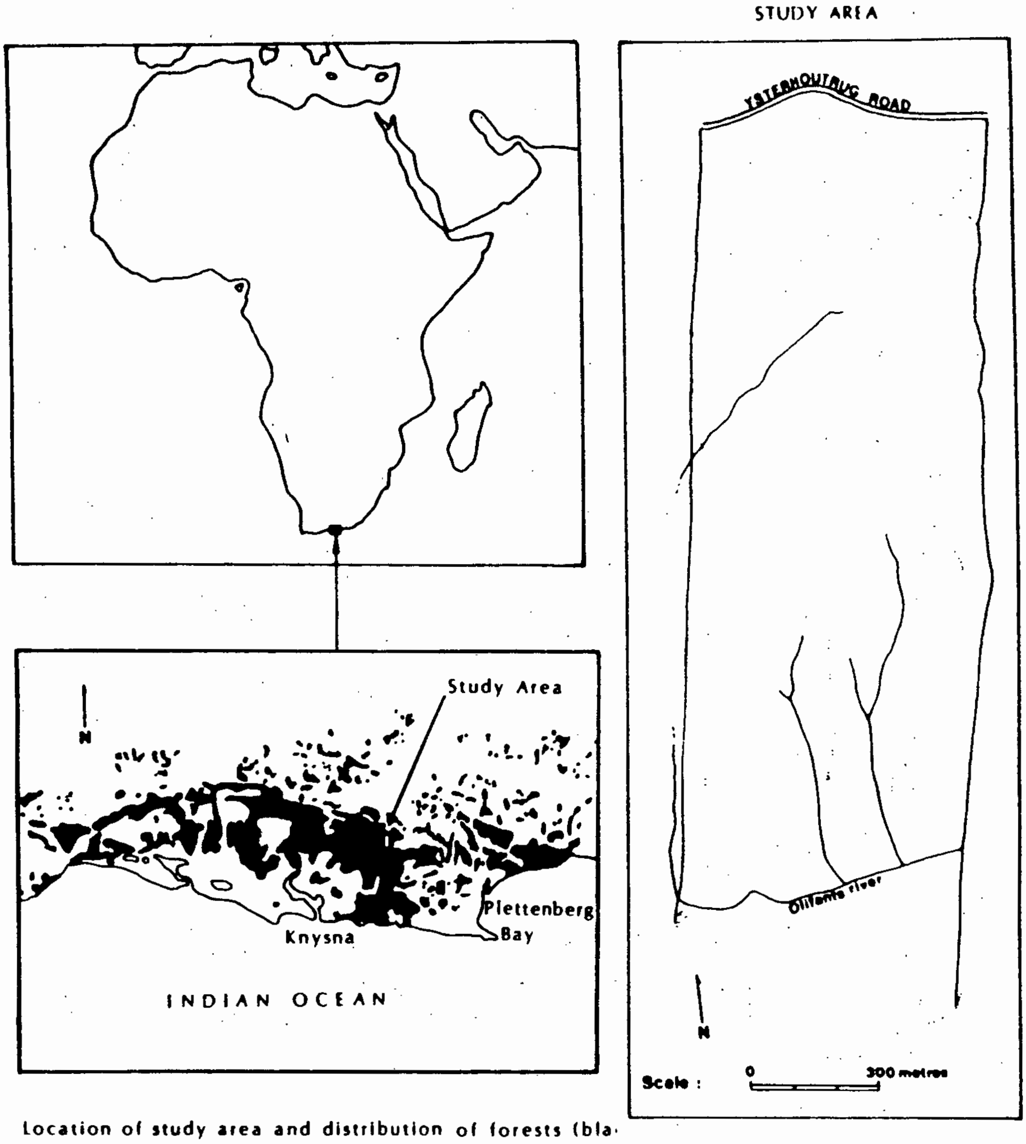

Fig. 1. Location of the study site. a. Location of the study area on the African continent. b. Location of the study area on the southern Cape. Dark areas are forested. c. Map of the study area showing trails and the Olifants River. Survey sites north of the Olifants River are used for model verification; those south of the river are used for model validtion.

to implement a modified version of the KIAMBRAM model. We then test the reliability of the resultant model against independent data.

The forest of the southern Cape

The southern Cape forests occur as an archipelago in a narrow belt 16 to 32 km wide between the Indian Ocean on the south and the Outeniqua Mountains on the north (Fig. 1). The geological formations affect the type of forest growing on it, but do not affect the distribution of forests. Soils are nutritionally poor, with phosphate being very deficient (Van Daalen 1984). Distinguishing features of the forest species are evergreenness, a high occurrence of sclerophylly, high levels of phenolics and other secondary compounds, fruiting intervals of more than one year and dense root mats on and in the surface soil layer (Van Daalen 1984).

Based on species composition, the forests are subdidived into three major types:

1. The wet mountain forests are typically Afromontane forests (White 1978). Canopy height ranges from 12 to 30 m. *Cunonia capensis* and *Ocotea bullata* form the main canopy. The tree fern *Cyathea capensis* is characteristic.

2. The forests of the coastal escarpment or the steep slopes of river valleys are generally scrub or dry forest with high species richness, including many Tongaland-Pongoland forest (*i.e.*, the northeastern forests of South Africa) species (Moll and White 1978). Canopy height varies between 9 and 18 m. Most of the species of the coastal platform forest also occur in these forests.

3. The coastal platform forest, for which this computer model was developed, include mostly Afromontane and transgressor species, the latter occurring with abundance in both the Afromontane and the Tongaland-Pondoland forests. Canopy height varies between 16 and 30 m. The main canopy species are *Olea capensis*, subsp. *macrocarpa*, *Podocarpus latifolis*, *P. falcatus*, *Pterocelastrus tricuspidatus*, *Apodytes dimidiate*, *Curtisia dentata*, *Rapanea melanophloeos*, *Canthium obovatum*, *Nuxia floribunda* and *Olinia ventosa* (Geldenhuys 1987).

Due to their basically tropical features (Phillips 1931; Webb 1959; Dawson 1962; Donald and Theron 1983), their floristic richness (119 tree and woody shrub species, Geldenhuys 1979), multistoried structure, and similarity to forests used to develop the Australian model (Shugart *et al.* 1980), the southern Cape forests represent a logical extension as a subject for testing the general utility of the existing KIAMBRAM model for subtropical rain forests in Australia.

The model

The KIAMBRAM model developed by Shugart *et al.* (1980) for the subtropical rain forest at Wiangaree State Forest, New South Wales, was chosen as the basis for the present model, which we will call the OUTENIQUA model. Outeniqua refers to the mountain range that forms the northern boundary of the narrow belt of indigenous forests in the southern Cape. These mountains cause the orographic rain and mist that enable the forests to grow and survive. The model is implemented as FORTRAN V code that has been modified where appropriate to run on a 16 bit Data General minicomputer with 64 K byte memory available to each user.

OUTENIQUA retains the stochastic features of the KIAMBRAM succession model. Essentially, it simulates the birth, diameter growth and death of each tree in a forest gap created by the death of a large tree or by clearing. This gap is assumed to be within an intact forest. All species are assumed to have an adequate seed source. The model simulates the tree populations on a 0.04 ha plot, the standard plot size used in the southern Cape for forest surveys (Geldenhuys 1982) and within a recommended plot size (Mueller-Dombois and Ellenberg 1974). In the present model, the LUMBER subroutine of KIAMBRAM has been excluded. Similarly, provisions for strangler figs (*Ficus* sp.) from the KIAMBRAM model are omitted since this life form does not occur in the southern Cape.

Model parameters were obtained from tree growth studies on a 45 ha forest compartment (Fig. 1), a study of Geldenhuys (1975) on *Podocarpus falcatus*, and unpublished information and experience of local researchers. Estimated values must eventually be verified, but the best estimates of experienced forest researchers was essential to make the model a useful synthesis of knowledge of these forests, much of which is unpublished. Model parameters derived from expert opinion deal with the silvicultural attributes of the species and are be identified explicitly below.

The growth function used (Botkin *et al.* 1972; Shugart and West 1977; Shugart *et al.* 1980) reflects the currently debated reductionists view of succession (Finigan 1982; Innis 1976; Levins and Lewontin 1982). The OUTENIQUA model and related models are useful for testing the different hypotheses about tree growth and succession. For management purposes, the model should be useful for examining the long-term effects of human activities on stand development (Dale and Hemstrom 1984).

The OUTENIQUA model includes the 28 tree species encountered on the study area (Table 1).

Table 1. Species list and species specific parameters used in the OUTENIQUA model.

	B2	B3	AGE (MX)	HMAX	G	TOL	P1	P2	FELL	SPRT	DEC	SEED	Switches					
													1	2	3	4	5	6
Podocarpus falcatus (Thunb.) R.Br. ex Mirb.	29.09	.048	1463	4500	27	2	2	4	3	2	1	3	T	F	T	F	T	F
Podocarpus latifolius (Thunb.) R.Br. ex Mirb.	44.84	.149	437	3500	70	1	1	2	3	2	1	2	T	F	T	F	T	F
Ocotoa bullata (Burch.) E.Mey.	67.26	.336	289	3500	106	2	2	2	1	1	1	1	T	F	T	F	F	F
Platylophus trifoliatus (L.f.) D.Don	71.57	.447	252	3000	104	2	2	2	1	1	1	1	F	T	F	F	F	T
Lachnostylis hirta (L.f.) Muell. Arg.	105.02	1.167	295	2500	74	3	2	3	1	2	2	3	F	T	F	F	T	F
Ilex mitis (L.) Radlk.	56.05	.234	403	3500	76	2	2	2	2	2	1	3	T	F	T	T	F	F
Maytenus peduncularis (Sond.) Loes.	71.57	.447	401	3000	65	2	1	2	2	1	1	1	T	F	T	F	F	F
Pterocelastrus tricuspidates (Lam.) Sond.	81.80	.584	243	3000	108	2	2	3	3	2	1	3	T	F	T	F	F	F
Cassine eucliformis (Eckl. & Zeyh.) Kurtze	94.52	.945	244	2500	89	1	2	3	3	2	1	2	T	F	T	F	F	F
Cassine peraqua L.	94.52	.945	349	2500	63	2	2	3	3	2	1	2	T	F	T	T	F	F
Cassine papillosa (Hechst.) Kuntze	72.71	.559	264	2500	84	1	1	4	3	2	1	1	T	F	T	T	F	F
Apodytes dimidiata E. Mey. ex Arn	84.07	.525	395	3500	77	2	2	3	2	1	2	3	T	F	T	T	F	F
Rhamnus prinoides L'Herit	136.30	3.407	139	1500	94	3	1	2	3	3	1	2	T	F	T	T	T	F
Ochna arborea Burch ex DC	60.58	.673	619	1500	22	1	2	3	3	2	2	1	T	F	T	F	F	F
Kiggelaria africana L.	95.43	.795	297	3000	88	3	2	3	2	2	3	1	T	F	T	T	T	F
Curtisia dentata (Burm.f.) C.A. Sm	96.09	.686	250	3500	121	2	2	4	3	2	1	3	T	F	T	T	F	F
Rapanea melanophloes (L.) Mez	96.09	.686	299	3500	101	3	2	3	3	1	1	3	T	F	T	T	F	F
Diospyros dichrophylla (Sand.) De Wint.	93.15	1.164	201	2000	88	3	2	4	2	2	2	2	T	F	T	T	T	F
Diospyros whyteana (Hiern) F. White	82.80	.920	223	2000	80	1	2	4	2	2	1	3	T	F	T	T	T	F
Chionanthus foveolatus (E. Mey.) Stearn	105.02	1.167	296	2500	73	2	2	4	3	2	1	2	T	F	T	T	F	F
Olea capensis subsp. *L. macrocarpa* (C.N. Wr.) Verd	56.05	.234	186	3500	165	1	2	4	3	3	1	3	T		F	T		T
Olea capensis subsp. L. capensis	72.71	.559	340	2500	65	3	1	4	2	1	1	1	T	F	T	T	F	F
Nuxia floribunda Benth.	71.57	.447	161	3000	163	1	2	1	2	1	2	3	F	T	F	F	F	F
Conioma kamassi E. Mey.	82.80	.920	271	2000	65	2	1	2	2	1	1	1	F	T	F	F	F	F
Halleria lucida L.	85.93	.781	465	2500	47	3	2	2	2	2	2	2	T	F	T	T	F	F
Burchellia bubalina (L.F.) Sims	109.04	2.181	425	1500	31	2	1	2	3	2	1	1	T	F	T	T	F	F
Canthium mundianum Cham & Schlechtd.	93.15	1.164	207	2000	85	3	2	3	3	2	3	2	T	F	T	T	F	F
Canthium obovatum Klotzsch	84.07	.525	335	3500	91	2	2	3	3	2	1	2	T	F	T	T	F	F

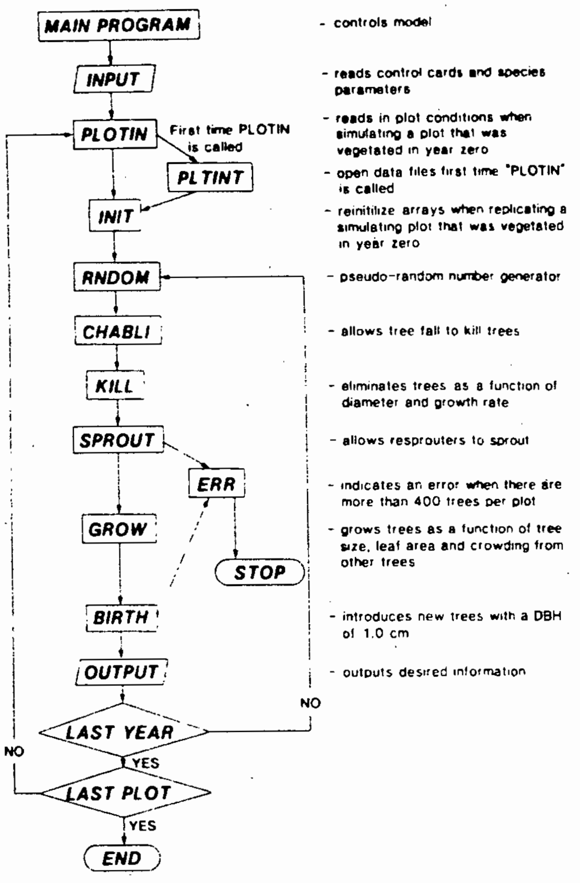

Fig. 2. Flow diagram for calls to subroutines in the OUTENIQUA model.

B2 and B3 are form factors derived from AGE (MX) (in years) and H_{max} (in meters) and used to calculate the height of trees (Shugart *et al.* 1980. AGE(MX) is the age that a tree under optimal conditions should attain the maximum height. G is a growth form parameter calculated from the maximum known annual increment for the species. TOL is shade-tolerance (1 = shade-tolerant; 2 = intermediate; 3 = shade-intolerant). P1 is the seed phenology (1 = regular; 2 = irregular). P2 is the seed longevity (1 for > 6 weeks but < 3 months; 3 for > 3 months but < 1 year; 4 for > 1 year). FELL is the species' resprouting ability when felled, and SPRT its resprouting ability when the tree has fallen over (1 = strong resprouter; 2 = intermediate; 3 = does not resprout). DEC indicates deciduousness (1 = evergreen; 2 = semi-deciduous, 3 = deciduous). SEED is the amount of viable seed produced (1 = small amounts; 2 = medium amounts; 3 = large amounts). SWITCHES 1 to 6 are categories of dispersal and germination site requirements of each species.

A simplified flow diagram is given in Fig. 2. Annual model projections can start from a bare or vegetated plot. Normally a vegetated plot would be the starting point since completely devegetated gaps of size 0,04 ha seldom occur in the southern Cape forests. For each year of simulation trees can die, regeneration and stump resprouting can occur, and trees can grow.

Oldeman (1978) refers to 'fall of a tree, its impact on the forest, the fallen tree itself, and the resulting destruction all together' as a 'chablis' or a negative sylvigenesis (Oldeman 1978). Two parts of chablis are simulated:

1. The crown gap that consists of the area that is directly under a fallen canopy tree. This area has relatively little physical destruction, but has an increased ambient light level due to the removal of the fallen tree's crown.

2. The site at which the crown of the tree falls. At this site, there may be a larger number of trees killed, the mineral soil may be exposed, and the fallen branches may provide shade and protection for regeneration against browsing by bushbuck.

The first part of the chablis is simulated by actually computing light levels as a function of leaf area. Thus when a canopy tree dies, the forest floor light level is increased. The second part of the chablis is simulated by a stochastic decision with a probability of 0.006 (as opposed to 0.003 for the Australian forests where tree fall gaps are common) whether or not a canopy crown from an adjacent plot has fallen onto the simulated plot during a given year. In a year in which there is such a crown fall, each tree on the plot has an increased probability of mortality as might be associated with the impact of the fall. In computing the effects of the chablis, the direction of fall is not taken into account. This feature might be important in plots on steep slopes. However, no quantitative data on this effect is available at this time.

In the current version of the OUTENIQUA model, only trees are included. However, an understory shrub, *Trichocladus crinitus*, locally called 'onderbos' is abundant in the southern Cape forests. These onderbos stems probably compete directly with tree regeneration. To simulate this competition 2.75% of all stems below 5 cm are eliminated each year before trees are subjected to other sources of mortality.

The probability of mortality of each individual tree is determined as a stochastic function. Each tree is assumed to have an intrinsic mortality rate such that, under normal conditions, 1% of the individuals in a cohort could be expected to live long enough (AGEMX, Table 1) to attain their maximum height and diameter (H_{max} and D_{max}, respectively; Table 1). Thus the probability of mortality is:

$$P_m = 1 - \exp(-4.605/AGEMX),$$

where P_m is the intrinsic probability of mortality, and AGEMX is the age at which one would expect 1% of a cohort to be alive and, by assumption, the age at which one might expect an individual to reach its maximum size.

The growth rates of the southern Cape forest trees are relatively slow (the greatest diameter increment measured on the study site was 2.26 mm/yr). Therefore, trees with a minimum diameter increment of only 0.25 mm/yr (compared to 1 mm for KIAMBRAM) are subjected to additional mortality,

$$P_s = 0.368,$$

where P_s is the probability of survival of a suppressed (due to shade or other factors) individual. This has the effect of allowing only 1% of a suppressed cohort to survive 10 years.

In the event of a chablis, each tree is subjected to a probability of mortality. Each tree is then checked for its resprouting ability (Table 1). When it belongs to a strong resprouting species, the tree is eliminated, but the resprout is tallied. When it belongs to an intermediate resprouter, only half the resprouts are tallied. In the case of a non-sprouting species, the tree is simply eliminated.

OUTENIQUA simulates the resprouting of trees. Sprouts grow on stumps with established root systems and tend to grow faster than seedlings, at least initially. Therefore, they enter the plot with an average DBH of 2.0 cm, as compared with 1.0 cm for seedlings. Computationally, this gives them a competitive advantage over seedlings. Sprouts are planted with a DBH of 2 cm plu or minus a small error term designed to give the sprout a unique size.

The central assumption in formulating the diameter increment equation is that growth in trees is the consequence of two opposite processes. The positive part of rate of volume accumulation is assumed under optimal conditions to increase as a positive linear function of the leaf area of the tree (presumably the realization of the net photosynthesis rate). There is a counter-balancing negative rate that is associated with respiration and other energy losses. This latter term is proportional to the volume of living tissue. As a tree increases in size, the respiration costs increase, and the rate of growth of the tree slows and stops.

The following equation is solved for each tree for each year of the simulation using annual calculation steps:

$$\frac{dD}{dt} = \frac{G.D(1 - D.H/D_{max}\,H_{max}) \cdot S(BAR) \cdot r(AL)}{(274 + 3b_2D - 4b_3D_2)}$$

where:

D = diameter of tree (D_{max} = maximum possible diameter)
H = height of tree (H_{max} = maximum possible height)
S(BAR) = stand basal area affecting nutrient competition
r(AL) = reduction of photosynthetic rate due to shading
G = growth parameter derived from maximum known increment for species (Table 1).

For a derivation of this general growth equation, see Botkin *et al.* 1972 and Shugart 1984.

All species are assumed to have an adequate seed source. The success of these seeds establishing on the plot is modified as follows:

1. Seed phenology: Some tree species produce seed regularly; others do not. Species with irregular seed set are allowed to have a seed source every 2.5 years.

2. Seed longevity: Each species' seed is classified according to its longevity (Table 1), which is used to compute the proportion of time a mature tree might provide seed to a site. Ignoring seed predation, the longevity of seeds with similar phenology should be an index of the probability of a species having a viable supply of seeds when conditions favor germination.

3. Amount of viable seed produced: The number of seeds produced is classified as: small, medium and large (Table 1). In the case of small amounts, the number of saplings eligible for establishing on a plot is halved, whereas a large numbers of seed doubles the number of eligible saplings.

When a species is eligible to germinate at a site, its dispersal mechanisms and germination site requirements are (Table 1) used to check whether a species' establishment requirements are met at the site during particular year.

When the species is bird- or bat-dispersed, the probability of seeds establishing on a plot is increased by 50%. Birds tend to use specific perches, concentrating seed in their droppings. In the case of wind-dispersed species, both the phenology and longevity restrictions are lifted. Wind-dispersed species are assumed to be able to establish on any plot whenever the seed is produced in the forest. Gravity dispersed species drop all their seed below the parent. Therefore, the establishment probability is doubled. Mammals that distribute seed sometimes have a slight tendency to concentrate seed. Therefore, the probability of seed establishment is increased 20% for mammal-dispersed species. When the species is dioecious, establishment probability is halved. Dioecious trees on average need two trees to produce seed. Those species requiring mineral soil for germination can only establish after a chablis, when the simulation starts with a bare plot, or when the total leaf area is less than 1.0 m^2/m^2.

After 'filtering' (*sensu* Harper 1977) the species regeneration requirements against the site conditions and computing the outcome of the probabilistic factos mentioned above, species selected to be planted in a given model year are determined. A species is selected at random from this list of possible species and between 1 and 10 individuals are planted under normal forest conditions (between 1 and 46 when the total leaf area is less than 1.0 m^2/m^2). This process is repeated between 1 and 32 times per year (according to a selected uniform random number). All saplings have a DBH of at least 1.0 cm when planted. These stochastic levels of regeneration were found to approximate the patterns of regeneration noted in the southern Cape forests.

The model simulates seedling establishment as a stochastic process (or set of processes) with mild deterministic constraints on the total spectrum of possibilities that might occur in any year's regeneration at any given site. This reflects the concept of Webb *et al.* (1972) that rain forest regeneration of this spatial scale consists of a series of patches composed of species which occur probabilistically. According to Webb *et al.* (1972), the species composition of plots such as those simulated by the OUTENIQUA model should vary in space and time, and if the trees on such a plot are destroyed or become overmature, they would probably be replaced by a new mixture of species out of many possible configurations. Others have also noted this stochastic pattern in species composition which is a recurrent theme in discussions of rain forest regeneration beginning with the classic papers of Aubreville (1933, 1938).

Model parameter estimation

The parameter estimation procedures used in this implementation of the OUTENIQUA model provide insight as to how useful the gap modeling approach might be in applications to forests in which the species silvics are reasonably well known (even if this knowledge is not codified into publications) and in which there is some information on the growth rates. This is a minimal set of information that would be necessary to develop any individual-tree-based, forest-growth simulator. Parameters in the OUTENIQUA model are either species specific parameters (*e.g.*, growth rates, life history attributes) or system level parameters (*e.g.*, rate of light extinction through the canopy). System level parameters in the OUTENQUA model are unchanged from the KIAMBRAM model (Shugart *et al.* 1980) or indicated in the section above. With the exception of the 'G' parameters, species level parameters (Table 1) were estimated from a study of Geldenhuys (1975) on *Podocarpus falcatus*, and unpublished information and experience of local researchers and the senior author. These parameters were all estimated *a priori* to the development and implementation of the OUTENIQUA model. The parameters encode the major silvicultural features of the species and are essentially free of modification (*e.g.*, if a species is bat-dispersed, it is inappropriate to declare it otherwise; the maximum diameter of a species does not take on arbitrary values.).

The 'G' parameter for the growth equation is directly related to the maximum increment of a species (see Botkin *et al.* (1972) for the derivation of this relationship). We estimated the 'G' parameter for all species (Table 1) by determining the magnitude of the 95th percentile of increments recorded for trees of each species from the study plot north of the Olifants River (Fig. 1). This automated the parameter estimation procedure and hopefully eliminated possible bias from arbitrary parameter fitting. The 95th percentile was used to protect the parameter estimation procedure from statistical outliers in the remeasurement data set.

Model testing

It is desirable to conduct model tests under conditions in which the parameters are estimated *a priori* and in which the parameters in the model are realistic (Shugart 1984). Both the model structure and the emphasis on species natural history in gap models make it appropriate to have a high level of realism in the model parameters. Mankin *et al.* (1977) and Shugart (1984) divide model testing into verification and validation, and see model application as a measure of a model's usefulness. The model verified on its consistancy with some set of observations. The OUTENIQUA model is verified by its ability to capture the broad compositional patterns of the subject forest and to reproduce the observed changes in DBH distributions (both for the entire forest and for the populations of tree species making up the forest). A model is validated on its agreement with a set of observations *independent* of those observations used to structure the model and estimate its parameters. The OUTENIQUA test used the data from the study site south of the Olifants River (Fig. 1). These tests focus on the detailed structure and dynamics of forests.

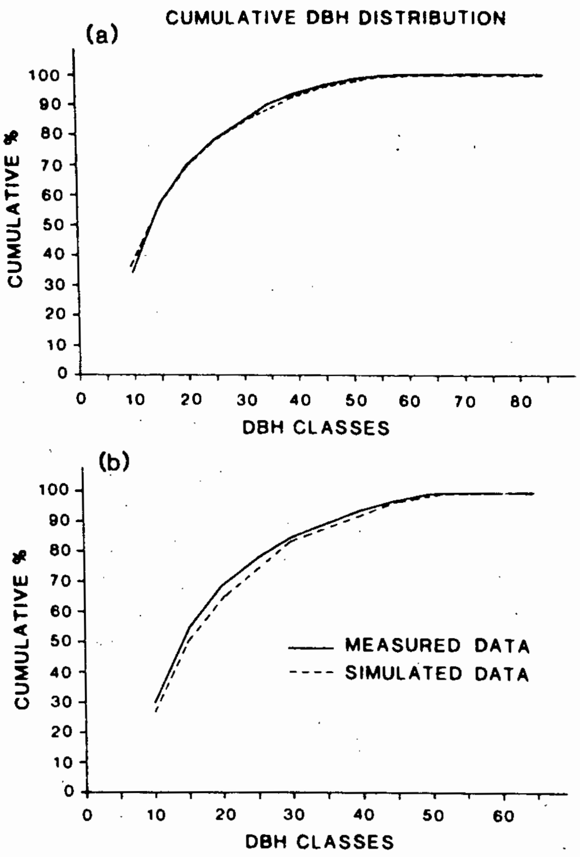

Fig. 3. Comparison of cumulative percentages of diameter distributions between actual observations in 1983 and model simulations initialized with 1972 inventory data and projected to 1983. a. Comparison based on the data from 63 .04 ha inventory plots located north of the Olifants River. These data were used to estimate the growth rates of trees species (see text for details). b. Comparison based on data from 13 .04 ha inventory plots south of the Olifants River and independent of any of the model parameter estimation.

The OUTENIQUA model was verified (*sensu* Shugart 1984) on its ability to reproduce dynamics of diameter distributions over a 13 year period. Percentage cumulative DBH distribution projected by the model were plotted against the actual remeasurement data (Fig. 3a) from the part of the forest

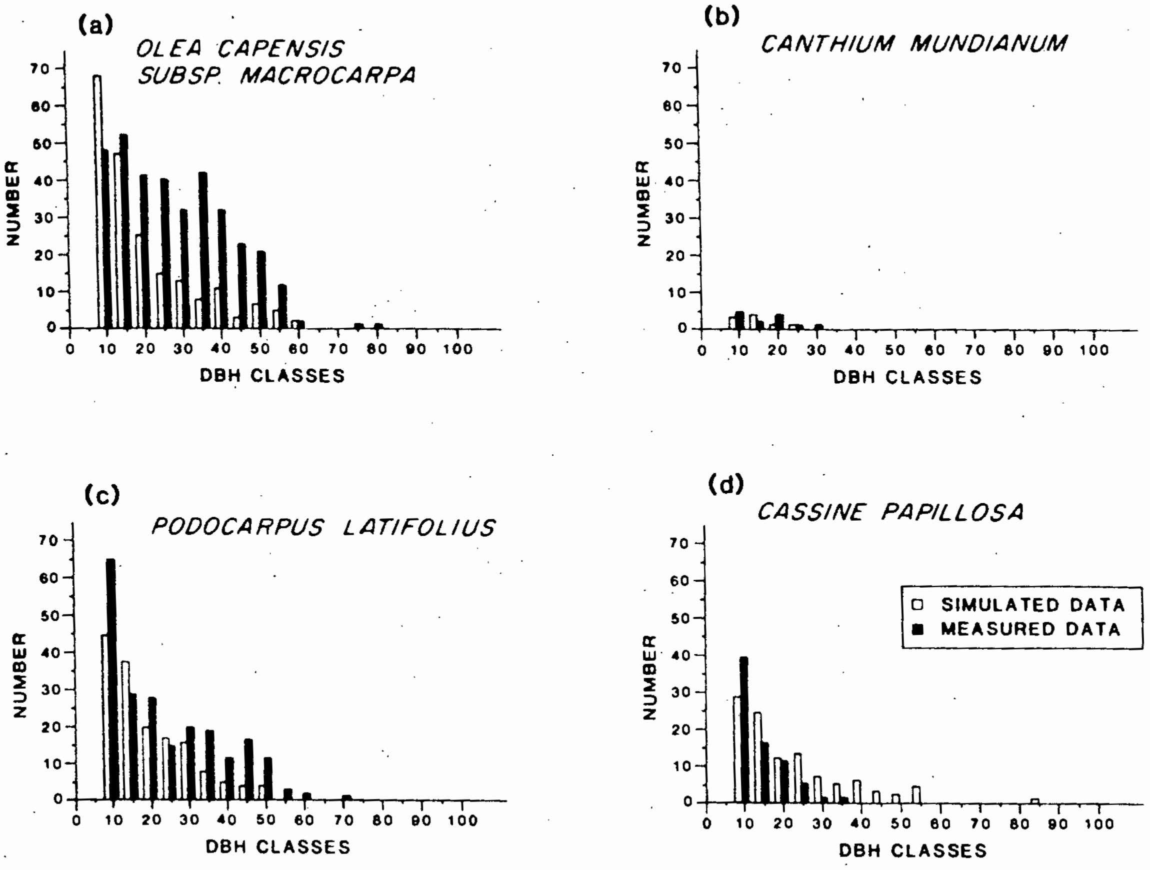

Fig. 4. Comparisons between numbers of stems in 5 cm diameter intervals measured on 63 0.04 ha inventory plots (in 1983) from the part of the study area north of the Olifants River and the results obtained by initializing the model with data from 1972 and projecting the stand dynamics forward for 11 years. a. *Olea capensis* subsp. *macrocarpa*. b. *Canthium mundianum*. c. *Podocarpus latifolius*. d. *Cassine papillosa*.

north of the Olifants River (Fig. 1) (*i.e.*, the stand used for the model development). This comparison (Fig. 3a) is based on the mean of 63 simulated plots, initialized with the plot data collected at the time of first detailed measurement (1972) and compared with the last remeasurement 11 years later (1983). As is indicated in Fig. 3, a high level of agreement between the actual forest and the simulation results was obtained. The model was not 'fitted' to match the diameter distribution (Fig. 3). The nature of the dependency between the model and data was in the use of the data to obtain the 95% confidence limit on diameter increment.

Species-level and more detailed model verifications involved using the model to develop histograms of the frequency of trees per DBH class, totaled over all 63 plots for each species. This latter procedure is more sensitive to differences between the remeasurement data and the values simulated by the model. For example, larger diameter classes of *Olea capensis* subsp. *macrocarpa*, the most abundant tree of the southern Cape forests are underestimated (Fig. 4a). *Canthium mundianum*, a reasonably rare species on the study area is closely simulated (Fig. 4b). The larger diameter classes of *Podocarpus latifolius* (Fig. 4c) are slightly underestimated, while those of *Cassine papillosa* (Fig. 4d) are slightly overestimated.

A similar graph (Fig. 3b) and similar histograms were developed for the 13 plots south of the Olifants River for the validation (*sensu* Shugart 1984) of the model. Although a slight underestimate in the percentage cumultive DBH curve (Fig. 3b) is apparent, the simulation appears satis-

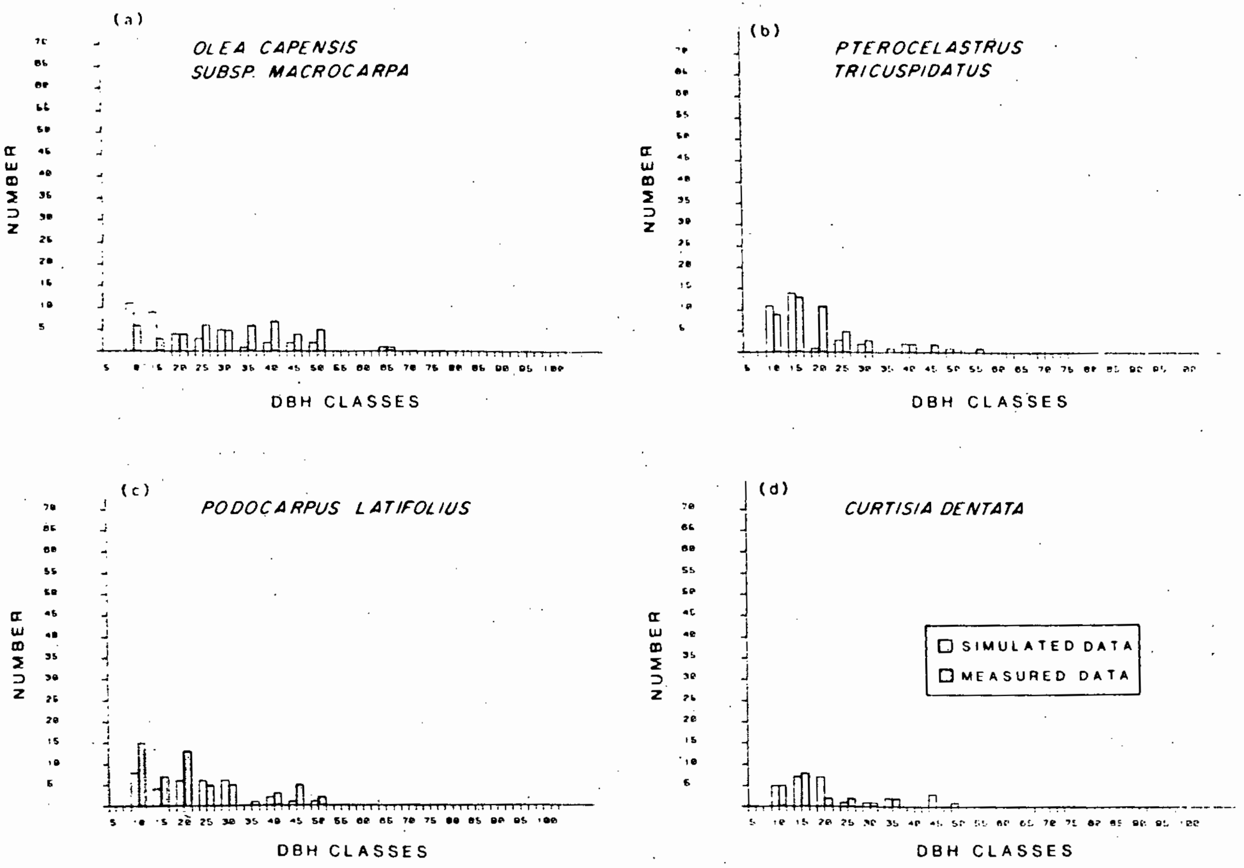

Fig. 5. Comparisons between numbers of stems in 5 cm diameter intervals measured on 63 0.04 ha inventory plots (in 1983) from the part of the study area south of the Olifants River and the results obtained by initializing the model with data from 1972 and projecting the stand dynamics forward for 11 years. a. *Olea capensis* subsp. *macrocarpa*. b. *Pterocelastrus tricuspidatus*. c. *Podocarpus latifolius*. d. Curtisia dentata.

factory. Explanations of the slight deterioration of the model's ability to duplicate these independent diameter frequency distributions include the change in sample size (allowing for more variability) and slight differences in soils and topography between plots used to calibrate and validate the model. Nevertheless, the agreement between the two curves (Fig. 3b) is within the range of variation one would expect in replicate samples of the same forest. Similarly, histograms of individual species diameter distributions are within the range of variation shown in the verification case (Figs 4 and 5).

The forests have been logged prior to 1955, which might have affected the diameter distributions of some species. Data are being collected in a virgin forest in the southern Cape, to eventually test the degree to which management has affected diameter distributions.

The advantage of using comparisons between subsequent cumulative diameter curves such as Fig. 3 is that birth, growth and death rates are tested simultaneously across all species. The modeled curves can differ from the observed due to several causes. If the model simulates too little regeneration, the initial size classes will be too low. If there is too much regeneration, they will be too high. Errors in simulated tree growth rates can distort the rate at which the curve changes, as can errors in the simulated mortality rates. Slow growth and/or high mortality can cause the diameter curve to drop away too rapidly in the larger diameter classes. The effect of growth suppression associated with high

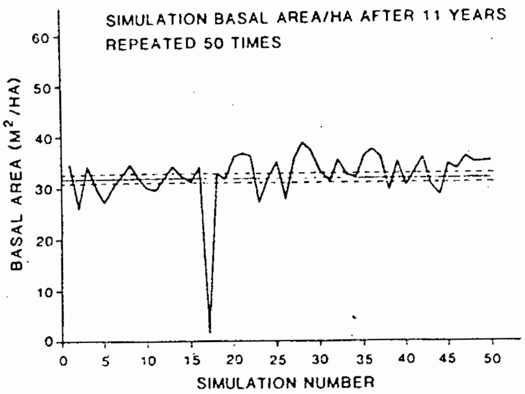

Fig. 6. Variation in total basal area in replicate simulations initialized with a single inventory plot and simulated 11 years for 50 cases using different random number sequences in each case.

mortality shapes the parts of the curve associated with the smallest and largest diameter classes. This is because diameter growth is slower in large trees and because the likelihood of competition causing growth suppression is highest in small trees. Thus verifications of models such as these can be used to develop specific hypotheses about the species silvics that can be used to guide future studies.

A vegetated plot was simulated with 50 replicates for 11 years to determine repeatability. The total basal area on the plot (in m^2/ha) at the end of each simulation is plotted in Fig. 6. Mean simulated basal was 32.3 m^2/ha (compared to 33 m^2/ha measured) with a 95% confidence interval of ± 1,5 m^2/ha. The simulation varied between 26 and 36 m^2/ha, except where a chablis occurred. In the gap resulting from this chablis, the basal area dropped to 3 m^2/ha. For management purposes, the mean simulation would provide a fair representation of the growth that could be expected in the plot.

Discussion

The OUTENIQUA model is presently a research tool directed to summarizing existing information and identifying inadequacies. Research on the indigenous forest in the southern Cape is aimed at better understanding system dynamics to ease the solution of management problems. A succession model can be very useful for exploring the long-term effects of certain management activities such as the effect of a certain harvesting practice which may only be apparent in 50 years time.

The model has been used to identify future research topics and to provide a context for studies on the forest biology of the southern Cape forests. Quantitative information is needed, for example, on mortality rates of different species, the influence of *Trichocladus crinitus* on regeneration, the influence of the method and time of seed production and distribution on the establishment of species, and the influence of mature trees on the establishment of different species (competition, allelopathy etc.). It is also important to know when diameter growth of different species decreases, and the influence of site on growth. As this information becomes available, it can be incorporated in the model. Functions used can be refined, or be replaced by more empirically-derived functions.

The reductionist approach to succession, which this model reflects, seems to represent the forest dynamics reasonably well, although this approach has certain shortcomings of its own (Finigan 1984). The model can be modified to reflect another succession theory, and results can be compared with observed data. In this way, the model can be useful vehicle in the present succession debate.

It is important to remember that this, or any other type of succession model, can only represent a limited part of the processes and dynamics of a forest. Referring to a Markov model for the Princeton Forest, Horn (1981) cautioned that 'even where the model works, it is intended only to be sufficient as a caricature of reality, rather than necessary as a mechanistic explanation'. This caution is equally true for other types of succession models as well. In the case of the present study, the KIAMBRAM model was moved to simulate forests on a different continent from that on which it was developed. This was accomplished by parameterizing and in some cases reformulating the model as indicated by the silvics of the individual species, and estimating the growth parameters of the model in an automated fashion from standard inventory data. The relative success in using the model to predict growth of the forest over 11-year periods and the utility of the model in identifying future studies indicate that this modeling approach appears effective in applications involving subtropical and tropical forest investigations and management.

Acknowledgments

This research forms part of the conservation research program of the Forestry Branch, Department of Environment Affairs in South Africa. Part of the work was funded by the United States National Science Foundation grant BSR 8510099 to the University of Virginia. We want to express our gratitude to both institutions. Thanks are due to Mr. C.J. Geldenhuys of the Saasveld Forestry Research Centre at George, South Africa, for making available much unpublished information on the southern Cape forests, to personnel of the Planning Section of the Directorate of Forestry in Knysna, South Africa, for constructive discussions, to Mrs. Peggy Gilbert of Science Applications, Inc. of Oak Ridge, Tennessee, who did much of the FORTRAN programming, and to J.F. Franklin of the University of Washington on his very helpful comments on an earlier draft of this manuscript.

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CHAPTER 2

FOREST GROWTH

Forest Growth: A 35-Year Southern Cape Case Study

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SYNOPSIS

1. Tree growth, mortality and recruitment rates were determined on a 44 ha evergreen mixed forest stand in the southern Cape, South Africa, for the period 1972 to 1987. All trees with a DBH > 10 cm on the study area were marked and the DBHs measured in 1972, 1978 and 1987.
2. Up to 1954 experimental thinnings were executed. Since then (i.e. more than 30 years) no timber has been extracted.
3. Mean basal area for all species together changed from 32,7 m^2/ha in 1972, to 34,1 m^2/ha in 1978 and 35,3 m^2/ha in 1987. Net growth rates since 1942 have declined from 1,63 % per annum for 1942 to 1953 to only 0,35 % per annum for the period 1978 to 1987. Mortality rates of most species increased, and for some species exceeded their recruitment rates.
4. Gross volume growth rate for the stand since 1972 is very similar to that for unlogged tropical forests elsewhere in the world, i.e. about 2 m^3/ha per annum. Recovery from disturbances was, nevertheless relatively fast.
5. Many aspects of the observed growth and mortality rates could be explained in terms of the development phases of the forest. It was concluded that the forest could be close to its maximum timber carrying capacity.

INTRODUCTION

The processes of growth, mortality and recruitment in forests are influenced by disturbances, which can operate on a wide variety of temporal and spatial scales (White and Pickett, 1985). The death of a single canopy tree will have a very local and relatively brief influence on the forest dynamics. A lightning fire can burn for several weeks and destroy considerable parts of the forest (C.J. Geldenhuys, personal communication, 1984) which will take many years to regrow. Bormann and Likens (1979) distinguished between endogenous and exogenous disturbances, the former being a disturbance that occurs within the scope of normal plant succession (for example the death of a canopy tree), and the latter being one that will deflect the autogenic pattern (for example in the case of a lightning fire destroying a considerable part of a forest).

Many forests are subjected to relatively frequent large-scale exogenous disturbances, such as fires and cyclonic winds (Loucks, 1970; Frissell, 1973; Heinselman, 1973; Henry and Swan, 1974). Others, such as the northern hardwood forests of the White Mountains of New England in the north-eastern United States of America, are seldom subjected to large-scale disturbances (Bormann and Likens, 1979) where severe logging and shifting cultivation is practised. Where ecosystems are sufficiently free of exogenous disturbances, progression to a steady state would be possible. Woodwill and Sparrow (1965, in Bormann and Likens, 1979) defined the steady state as "a condition in which there is no net change in total biomass over time, with annual ecosystem respiration approximately equalling annual gross primary production".

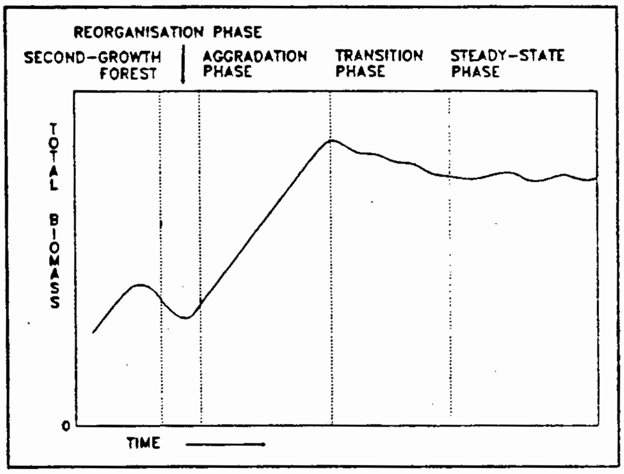


FIGURE 1. Bormann and Likens's (1979) model of biomass accumulation. The model delineates four phases of biomass decline and recovery, with a sharp drop in the reorganisation phase and maximum accumulation of biomass occurring prior to the steady state.

Bormann and Likens (1979) proposed a theoretical biomass accumulation model for ecosystem development (*Figure 1*). They hypothesised that a severe disturbance of a forest would be followed by a reorganisation phase of biomass decline, an aggradation phase of bio-mass build-up, a transition phase of erratic biomass decline and finally a steady-state phase. A stabilisation in the amount of living biomass could be achieved only several centuries after the severe disturbance. When the disturbance is less severe the actual shape of the curve will differ, and the steady-state achieved in a shorter period. The steady-state concept should, however, be considered at best approximate. "In a strict sense there can be no absolute steady state but only a system undergoing slow long-term changes" (Bormann and Likens, 1979).

After a severe disturbance, such as clear-cutting, numerous small trees, each with relatively small living biomass, grow up together with short-lived herbs and shrubs. During the reorganisation phase the short-lived plants die off, decreasing the total biomass. The aggradation phase is characterised by a steady increase in biomass and an even-aged condition is imposed on the ecosystem. As time passes thinning occurs and fewer larger dominants occur. At the end of this phase maximum living biomass for the entire developmental sequence is attained. Forest structure at this stage might be considered similar to a plantation where spacing has been adjusted to maximise living biomass accumulation. This biomass peak is followed by a period of biomass decline (the transition phase) which results as even-aged dominants die out and are replaced by patches of young vegetation. This results in a drop of total living biomass of the forest. The steady state is achieved after the progressive elimination of these even-aged dominants and with the development of dominants of all ages. Although the total living biomass for the whole forest will remain more or less constant with time, the fall of a large tree may create a gap where the living biomass will be locally reduced. In this way a mosaic of locally varying biomasses is created. This dynamic but relatively unchanging condition is termed the shifting-mosaic steady state (Bormann and Likens, 1979).

Diameter increment rates of the southern Cape forest trees have been measured since the early thirties (Phillips, 1931; Laughton, 1938), but no data on mortality or recruitment rates were available. In this paper I report on the observed diameter increment, mortality and recruitment rates of trees on a 44 ha study area. The following questions are addressed:

1. How do the observed rates relate to the developmental phases of the forest?
2. How do the observed rates in the southern Cape forests compare to those in tropical forests elsewhere in the world?

STUDY AREA

The study was carried out in a forest stand on the Diepwalle State Forest (33°56'S, 23° 09'E), 20 km north of Knysna, in the mixed evergreen subtropical (Phillips, 1931; Webb, 1959) Afromontane (White, 1978) forests of the southern Cape (*Figure 2*). It is representative of the stands from which timber is extracted (Von Breitenbach, 1974; Van Dijk, 1987). The main canopy is 18 to 22

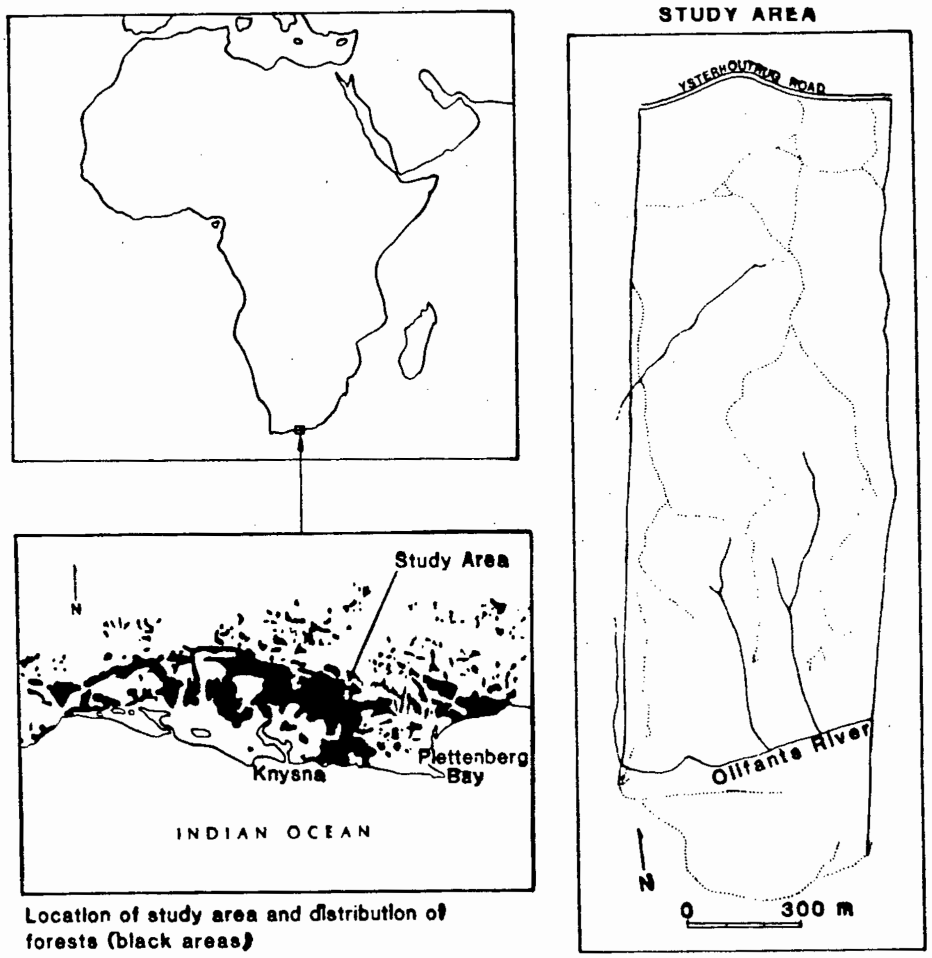


FIGURE 2. Location and map of the 44,4 ha *forest stand on the Diepwalle State Forest used for this study.*

m high. A dense shrub layer, composed mainly of *Trichocladus crinitus* (Thunb.) Pers., grows up to 4 m tall. Ground vegetation is relatively abundant.

The climate is warm temperate subhumid to humid (Poynton, 1971; Schultze and McGee, 1978). Mean annual rainfall is about 1 200 mm with a more or less even distribution throughout the year (Weather Bureau, 1986).

Most of the study area faces south to south-west, except for the lower portion south of the Olifants River, which is a level floodplain continuing into a moderate northern slope. Soils are heavy, with a gravelly (silcrete) or stony subsoil. On the small floodplain deep, moist alluvial soils are present. The whole area is underlain by fine to coarse-grained brownish sandstone of the Goudini formation (former Tchando formation) (Toerien, 1979) of the Table Mountain group (SACS, 1980).

The area has been used for testing an experimental management system since 1937. The whole area was divided into 27 parallel plots each some 1.5 to 2.5 ha in size. Plots were allocated at random to three different thinning treatments. In 1954 all treatments were terminated. The effect of the treatments are today still detectable in so far as there is a significant difference in the present standing timber stock among the plots subjected to different treatments.

METHODS

In 1972 the DBH (diameter at breast height, i.e. 1.3 m above ground level) of all trees with a DBH > 10 cm was measured. A unique number was painted on each tree and the exact point of measurement was marked. In 1978 and 1987 the measurements were repeated. In this way the individual growth rates of more than 26 000 trees were determined. Dead trees, or trees recorded in 1972 and absent in 1987, were recorded as mortality. Trees with a DBH of between 10 and 20 cm added to the record in 1987 were taken as recruitment. In 1983 the 27 plots, as indicated on old maps and marked in the forest, were mapped in detail and the area of each plot determined accurately.

I calculated Pearson product-moment correlation coefficients (SAS Institute Inc., 1985) for the mean rate of increment and total basal area of the standing stock in 1972 (i.e. the stock at the beginning of the study period, the base line data) for the recruitment rate and total basal area, and for the mortality rate and total basal area. This I did for individual species and for all species together. Basal area of a tree is the area of a disc cut from the tree bole at the same point at which the DBH measurement was taken. This is used as an indication of timber volume without having to measure all the variables needed for volume calculation.

For comparison of mortality rates of different species (*Table 1*) I calculated the number of stems that died during a particular period as a percentage of the number of living stems at the beginning of that period. This I did for 10 cm size classes (*Figures 6* and *9*) and for all trees of a species, regardless of size (*Figure 8*).

I chose to use timber volume instead of basal area for the comparison of growth rates with those of tropical forests elsewhere in the world. Normally canopy height, and implicitly bole length, remains fairly constant within a particular forest. This allows one to use basal area as a volume indication. However, owing to the differences in

TABLE 1. Percentage mortality and the change in number of stems for selected species on the Diepwalle study site for the period 1972 to 1987

Species	*% Mortality*	*1972 Stock*	*Change 1972 – 1987*	*% Change*
Olinia ventosa	20.4	63	+2	+3,17
Ocotea bullata	14.0	553	**-14**	**-0,03**
Olea capensis subsp. *macrocarpa*	12.3	6 985	**-263**	**-377**
Apodytes dimidiata	10.2	2 243	-58	-0,03
Curtisia dentata	8.5	2 744	+168	+6,12
Gonioma kamassi	8.5	3 133	+479	+15,29
Pterocelastrus tricuspidatus	7.0	2 767	+347	+12,54
Cassine papillosa	5.5	1 099	+217	+19,75
Podocarpus latifolius	5.1	4 315	+281	+6,51
All species together	**110,6**	**29 049**	**+1 459**	**+5,02**

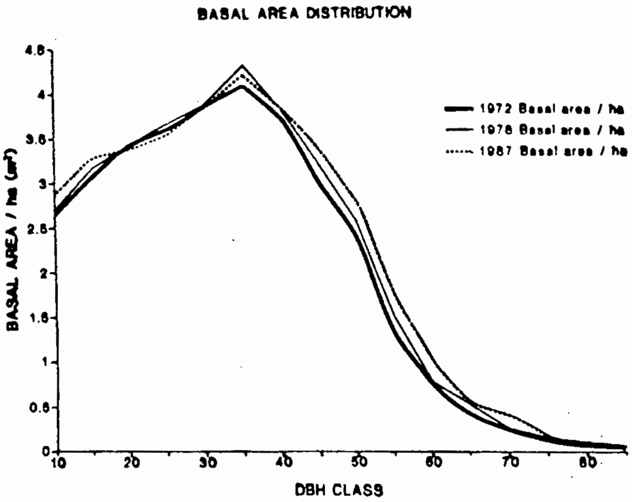


FIGURE 3. Total basal area distributions for 1972, 1978 and 1987 on the Diepwalle study site.

canopy height among forests of the world, basal area figures are not comparable. Volumes were calculated using separate regression equations for different species based on the following function (Van Laar and Geldenhuys, 1975):

log Volume (in dm^3) + b_0 + b_1 × log DBH (over bark, in cm)

where b_0 and b_1 are empirically defined partial regression coefficients.

For comparison, species were selected to cover the assumed spectrum of successional tree species. Included were *Olinia ventosa (L.) Cufod.*, being one of the most light demanding (i.e. pioneer) species and *Podocarpus latifolius* (Thunb.) R. Br. ex Mirb., one of the shade tolerant later successional species, as well as emergents (*Olea capensis* L. subsp. *macrocarpa* (C.H. Wr.) Verdoorn), subcanopy species (*Gonioma kamassi* E. Mey.) and the most valuable timber species in the forest (*Ocotea bullata* E. Mey.) (*Tables 1* and *2*).

RESULTS

Increment, recruitment and mortality rates

The mean basal area for the total growing stock (all species together) on the study area increased from 32.703 m^2/ha in 1972 to 34.105 m^2/ha in 1978 and 35.251 m^2/ha in 1987, i.e. 0.234 m^2/ha per annum from 1972 to 1978 and 0.127 m^2/ha per annum for 1978 to 1987. In 1987, however, the growing stock for the size classes 20 to 35 cm DBH was below that of 1972 and 1978 (*Figure 3*).

Net basal area growth rates (allowing for recruitment and mortality) since 1942 are available for 12 of the 27 plots on the study area (C.J. Geldenhuys, unpublished data). For the period 1942 to 1953 the mean annual rate was 1.63 %. This dropped to 1.42 % between 1954 and 1972, to 0.55 % for the six years between 1972 and 1978, and to only 0.35 % between 1978 and 1987.

The number of stems of *Olinia ventosa*, *Ocotea bullata*, *Olea capensis* subsp. *macrocarpa* and *Apodytes dimidiata* E. Mey. ex Arn. decreased or increased at a lower rate than the 5.02 % increase for the total number of stems (*Table 1*).

Increment and mortality rates for all the species together were positively correlated with the total basal area of the 1972 standing stock. This was not true for individual species.

Mean mortality of all species for the 15-year period 1972 to 1987 amounted to 10,6 % of the 1972 standing stock (*Table 1*). *Olinea ventosa*, *Ocotea bullata*, *Olea capensis* subsp. *macrocarpa* and *Apodytes dimidiata* had mean mortality rates higher than the overall mean for all species. Recruitment was insufficient to make up for the high mortality rates of these species. Even the increase of 3,17 % of the number of stems of *Olinia ventosa* means a relative decrease when compared to an overall increase of 5.02 % in the standing stock since 1972. The reduction in stems was limited largely to the 15 to 30 cm DBH classes (*Figure 4*). Species with below average mortality increased their number of stems across all size classes (*Figure 5*).

The mortality rates of most of the species listed in *Table 1* and *2* increased more or less constantly from 1972 to 1987 (*Figure 6*). However, for *Ocotea bullata* the rate of increase was much higher for the period 1978 to 1987 than for 1972 to 1978. For *Cassine papillosa* (Hochst.) Kuntze the mortality rate remained constant. The order of mortality rates was very similar to the order of diameter growth rates in an artificially re-established forest stand on the Diepwalle State Forest (*Figure 7*).

Mortality rates for both *Olinia ventosa* and *Ocotea bullata* have a decreasing tendency from the smaller to the larger size classes (*Figure 8*). This is not true for *Curtisia dentata* (Burm.f.) C.A. Sm., *Podocarpus latifolius* and for the mean mortality rate of all trees, regardless of species.

When the mortality rate per size class for all species together is simulated by fitting a polynomial (*Figure 9*), a U-shaped trend becomes apparent.

TABLE 2. Timber volume growth for selected tree species on the Diepwalle study site for the period 1972 to 1987

Species	***True growth (m^3/ha per annum)***	***Net growth (m^3/ha per annum)***
Olinia ventosa	0.017	0.014
Ocotea bullata	0.038	**-0.011**
Olea capensis subsp. *macrocarpa*	0.845	0.360
Apodytes dimidiata	0.117	0.049
Curtisia dentata	0.121	0.078
Gonioma kamassi	0.050	0.071
Pterocelastrus tricuspidatus	0.225	0.194
Cassine papillosa	0.033	0.030
Podocarpus latifolius	0.411	0.274
All species together	**2.065**	**1.124**

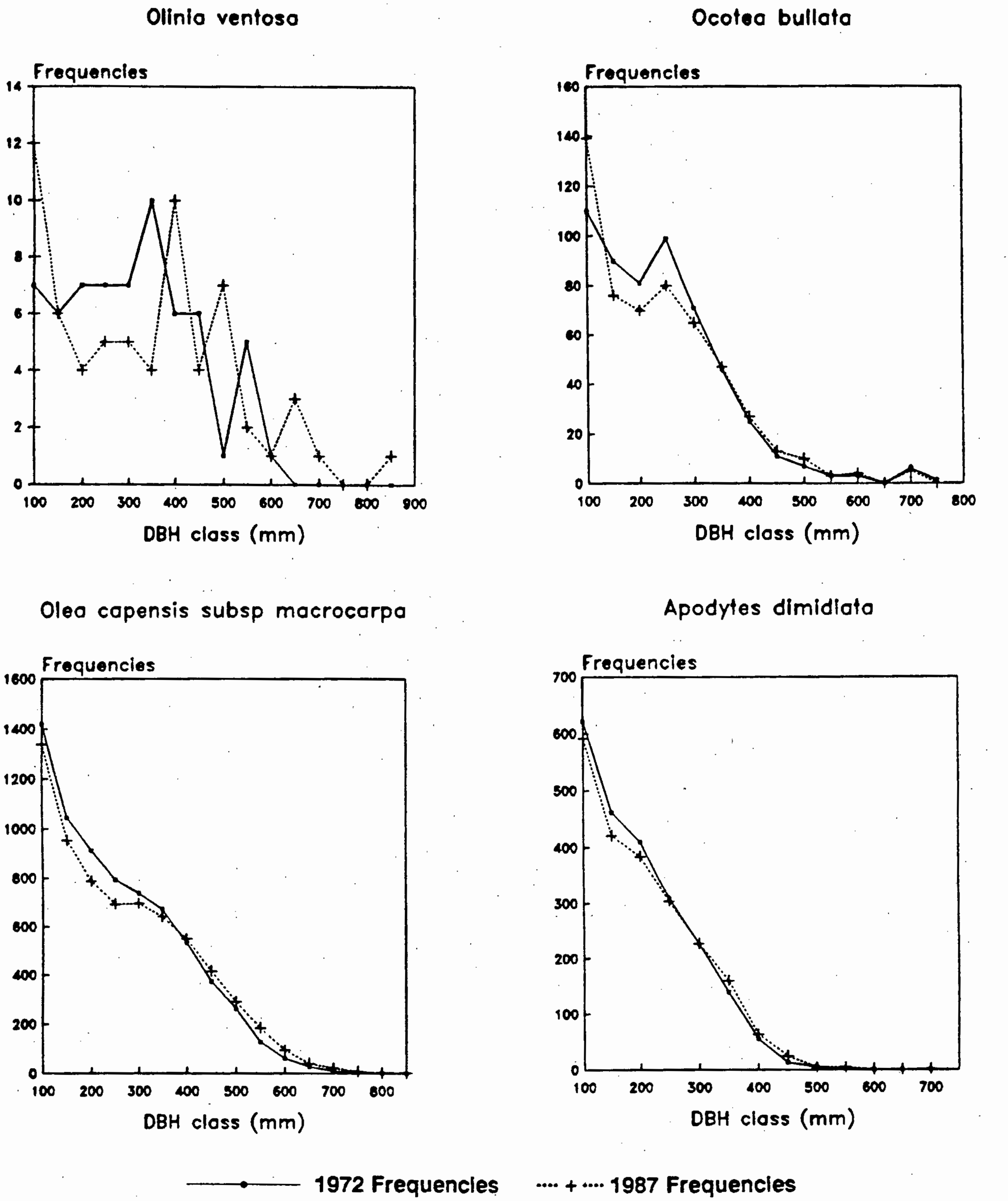
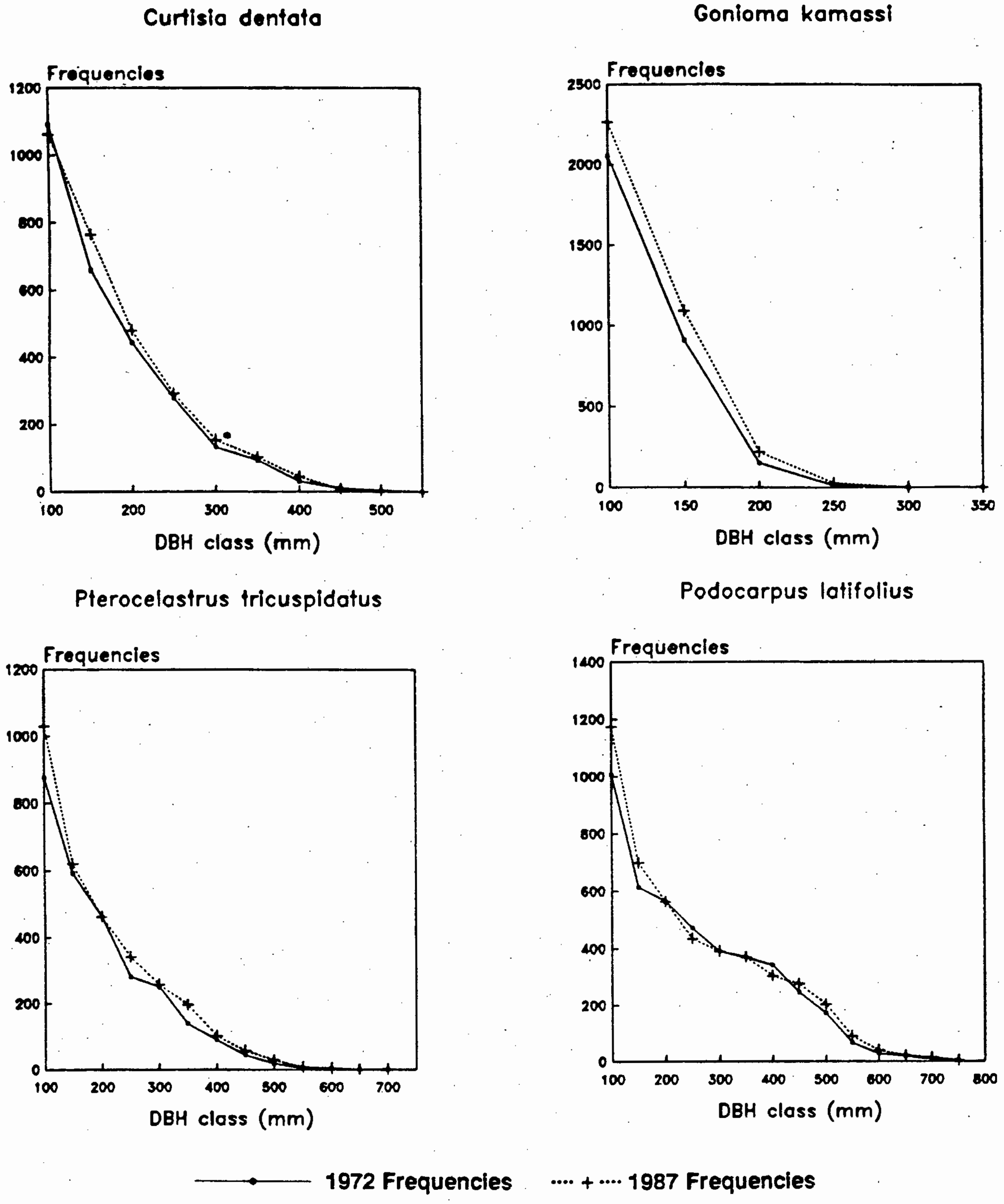


FIGURE 4. 1972 and 1987 frequency distributions for selected species with mortality rates higher than that for all tree species together.



Curtisia dentata

Goníoma kamassi

Pterocelastrus tricuspidatus

Podocarpus latifolius

FIGURE 5. 1972 and 1987 frequency distributions for selected species with mortality rates lower than that for all tree species together.

Rates of volume growth

The gross annual timber volume increment (*Table 2*) for all species together amounted to 2,065 m^3/ha for the period 1972 to 1987, whereas the net increment (after accounting for recruitment and mortality) was only half of that, i.e. 1,124 m^3/ha.

DISCUSSION

Increment, recruitment and mortality rates

Both the net basal area growth rate for the total area since 1972 and the net growth rate for 12 plots since 1942 show a considerable decline over time. This, together with the positive correlation between both the increment and mortality rates and the total standing stock, indicates stagnation and suggests that trees are competing for space and other resources (Franklin *et al.*, 1987). At present, this competition manifests itself in the smaller size classes of some species (*Figures 3, 4* and *5*). These are the species that experienced a relative reduction in their number of stems (*Table 1*). With time, the competition might become apparent in the larger size classes. Only 30 years has elapsed since the cessation of timber extraction from the area, and assuming that smaller trees do not compete with larger trees (Connell *et al.*, 1984), the competitive effect of recruitment since then will only become visible among the larger size classes at a later stage.

Geldenhuys (1975) regarded *Cassine papillosa*, *Podocarpus latifolius* and *Olea capensis* subsp. *macrocarpa* as more slow-growing and shade-tolerant (less pioneer-like) than some other species, such as *Cunonia capensis* L. and *Olinia ventosa*. The faster growing, more pioneer-like species had higher mortality rates (compare the observed mortality rates in *Figure 6* with diameter growth rates reported by Geldenhuys (1975) (*Figure 7*)). The only exception is *Ocotea bullata*. This species coppices, especially after being cut, and the high mortality rate from 1978 to 1987 could be partly due to severe competition among coppice shoots, which were recorded as separate stems during the surveys.

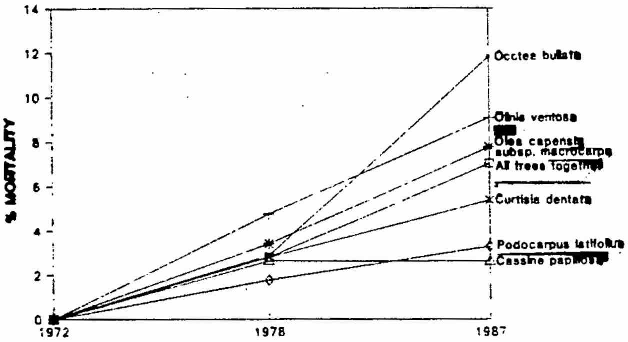


FIGURE 6. Mean mortality rates of selected species for the period 1972 to 1978 and 1978 to 1987.

Franklin *et al.* (1987) came to the conclusion that mortality rates in coniferous forests of the Pacific Northwest region of the United States of America decline as succession proceeds. This is contradictory to the patterns observed for the hardwood forest on the study area (*Figure 7*). The only species for which the mortality rate stabilised was *Cassine papillosa*, according to Geldenhuys (1975) one of the least pioneer-like species. Assuming that mortality rates will eventually decline as for coniferous forests, this suggests that the forest is still in a developmental phase.

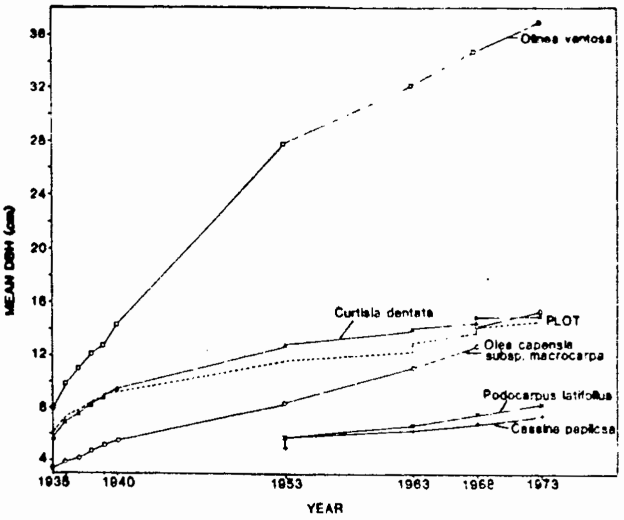


FIGURE 7. Mean DBHs of an artificially established forest stand on the Diepwalle State Forest for the period 1935 to 1973. (Geldenhuys 1975, reproduced with permission from author.)

According to Bormann and Likens's (1979) model of biomass accumulation, the southern Cape forest stand would be near the end of the aggradation phase or the start of the transition phase. Biomass (i.e. standing stock) increased at a declining rate during the study period, whereas mortality rates for the light-demanding pioneer-like species increased considerably, but stabilised for the tolerant, less pioneer-like species.

Van Valen (1975) suggested that a decreasing risk of death with increasing size (or age) is the most common pattern among all organisms. This seems to be true for *Olinia ventosa* and *Ocotea bullata* (*Figure 8*). The former is a shade-intolerant species, implying that competition for light would be fierce among small trees. Once they reach the canopy, and often emerge above it, this competition decreases among the few remaining individuals. For even-aged stands a simple monotonic decline in death rate with increasing diameter might be expected (Goff and West, 1975). In these stands the vertical structure and interaction between overstorey and understorey are not causing variation in growth and mortality as is the case in all-aged forests. In the latter a U-shaped mortality curve could be expected. In these stands vigorous overstorey trees should experience lower mortality than young competing trees and old trees which become more vulnerable to mortality factors such as disease and windthrow. This U-shaped curve is commonly applied in models predicting mortality (Lorimer, 1983; Shugart, 1984). Both *Curtisia dentata* and *Podocarpus latifolius* have a more or less constant mortality rate for diameters of 10 cm and more (*Figure 8*). The mortality rate for all species together exhibits the U-shaped curve (*Figure 9*). One can expect to find high-

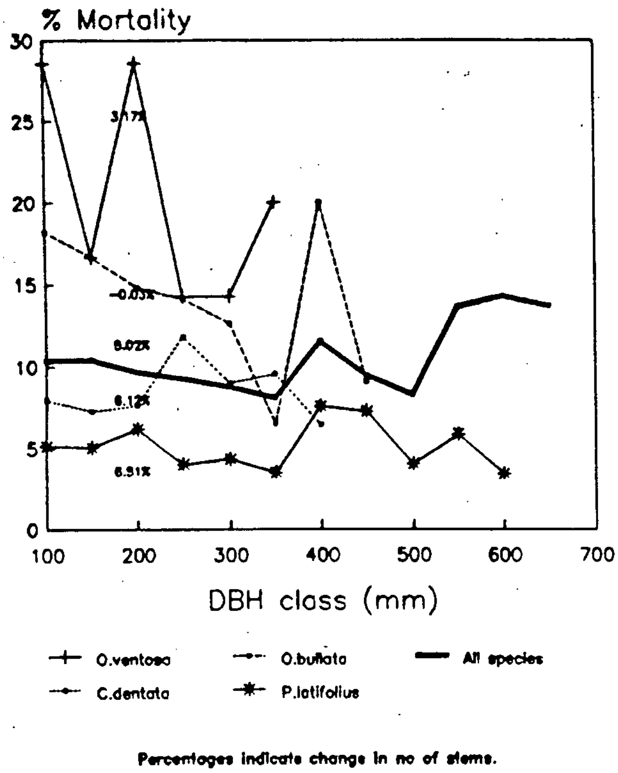


FIGURE 8. Mortality rates per size classes for selected species for the period 1972 to 1987. The X-axis denotes the 1972 size class distribution. The curve of "all species" include the data for all the species found on the study site. It is not the total of the data for the four species illustrated in the figure.

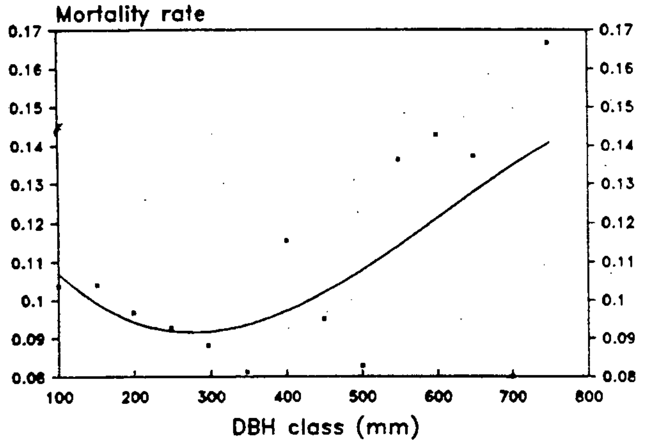


FIGURE 9. Total mortality rate for all tree species for the period 1972 to 1987. The X-axis denotes the 1972 size class distribution.

er mortality rates for the size classes below 10 cm DBH (Lieberman *et al.*. 1985). These will then change the horizontal lines for *Curtisia dentata* and *Podocarpus latifolius* into the negative exponential mortality curve described by Van Valen (1975).

Rates of volume growth

I concluded above that in terms of Bormann and Likens's (1979) model of biomass accumulation the forest stand on the study area is close to its maximum biomass carrying capacity. Therefore, the gross volume growth for all species together could be compared to the growth of unlogged forests elsewhere in the world.

Wyatt-Smith (1987) stated that tropical moist forests yield up to 2 m^3/ha per annum. Maitre (1987) reported that unlogged tropical forests in the Ivory Coast produced 0,7 to 1,8 m^3/ha per annum utilisable timber, whereas logged forests yielded about 2,5 m^3/ha per annum. Leslie (1987) wrote that the mean annual increment of 3 m^3/ha that he used for an economic feasibility study of natural management of tropical forests is near the upper volume growth limit for dipterocarps and well above the average reported for tropical forests. Thus, a yield of 2 m^3/ha per annum, which is similar to the volume growth for the study area, seems to be the universal timber production potential for unlogged mixed evergreen tropical and subtropical forests. Selective thinning treatments can, however, increase this figure up to 6 m^3/ha per annum (Wyatt-Smith, 1987).

CONCLUSIONS

Although the forest growth observed in the southern Cape is slow compared to for example that of *Pinus radiata* D. Don plantations (with a mean annual increment of about 15 m^3/ha) in the same area, the gross rate of 2 m^3/ha per annum is comparable to those of tropical and subtropical forests elsewhere in the world. Despite this slow growth, recovery from the disturbances up to 1955 was relatively fast. The thinnings executed at the time were described as "disturbingly heavy" and "clearfelling" (letters on file R3790/219 B:2 of the then Department of Forestry). Thirty-two years later the same stand is close to its maximum timber-carrying capacity.

In the southern Cape the management policy excludes silvicultural treatments, such as selective thinnings, to increase timber production *per sé*. Seydack et al. (1982) wrote: "The realisation of this policy entails the optimal utilisation of resources with overriding regard to the maintenance of natural diversity and the protective and aesthetic value of the indigenous forests." Timber is seen as one of many assets of the forests and is harvested in such a way as to simulate natural mortality as far as possible and to minimise the impact of harvesting. Under these conditions only the net timber volume growth can be realised.

The high mortality rate of *Ocotea bullata* (*Figure* 6) is notable. The reason could be competition between coppice shoots with a DBH of 15 to 35 cm (*Figure 6*), although Lübbe (1989) did not detect such a phenomenon in his autecological study of *Ocotea bullata*. He did find group die-back of *Ocotea bullata* on areas that are poorly drained and temporarily waterlogged. These diebacks are often associated with the presence of the root pathogen *Phytopthora cinnamomi* Rands, which seem to attack trees that are under stress (Von Broembson *et al.*, 1986). The development of this species on the study area should be observed closely and the hypothesis of competition among shoots tested.

Many aspects of the observed growth and mortality rates could be explained in terms of the developmental phases of the forest as described by Bormann and Likens's (1979) model of biomass accumulation. Growth rates are declining and mortality rates are increasing, indicating competition for space and other resources. Some species, such as *Curtisia dentata*, *Gonioma kamassi*, *Pterocelastrus tricuspidatus* (Lam.) Sond., *Podocarpus latifolius* and *Cassine papillosa*, are favoured by this situation and are increasing their numbers relative to other species, whereas recruitment rates of *Olinia ventosa*, *Ocotea bullata*, *Olea capensis* subsp. *macrocarpa* and *Apodytes dimidiata* are less than their mortality rates (*Table 1*).

Some species exhibit a U-shaped curve (although often only slightly) described by Van Valen (1975) for all-aged forests. *Olinia ventosa* and *Ocotea bullata* showed a simple monotonic decline in death rate with increasing diameter typical of even-aged forests.

Data on volume growth rates for tropical and subtropical mixed, all-aged forests are very scanty. If, however, it could be proved that growth rates for these forests are globally fairly constant, as seem to be indicated by the little data available, it could be a unique opportunity for the refinement and standardisation of forest succession models, such as the KIAMBRAM model developed by Shugart *et al.* (1980) and the OUTENIQUA model for the southern Cape forests (Van Daalen and Shugart, 1989). These models can then be applied on a much wider scale with much less laborious and time-consuming calibration than at present.

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CHAPTER 3

COMPETITION IN THE FOREST

THE EFFECT OF COMPETITION ON TIMBER GROWTH IN A MIXED EVERGREEN FOREST STAND

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SYNOPSIS

Competition among trees of the southern Cape forests was determined by calculating the distances among all trees on a 2.86 ha forest stand and correlating the distance between two neighbouring trees with the growth rate of the smaller one of the pair. Both inter- and intraspecific competition was evident between most of the chosen species combinations. The apparent more pioneer-like species, such as *Olea capensis* subsp. *macrocarpa*, *Ocotea bullata* and *Apodytes dimidiata*, showed weaker competitive abilities than later successional species such as *Podocarpus latifolius*, *Curtisia dentata* and *Pterocelastrus tricuspidatus*. Most of the southern Cape forest trees are shade-tolerant and can grow in close proximity to other trees, but the growth rate of various species is retarded by competition. It was concluded that the harvesting of the weaker competitors strictly according to the numerical proportions by which they occur in the forest is unnecessary, that the more valuable timber species profit from the advanced development stage of the forest in that they are better late-successional competitors, that the role of the dominant forest tree, *Olea capensis* subsp. *macrocarpa*, is not fully understood and that the present management approach of harvesting trees that will most likely die, is sound.

INTRODUCTION

Competition as such was seldom, if ever, mentioned as a factor to consider during the management of the southern Cape mixed, evergreen indigenous forests. In their management proposals Seydack *et al.* (1982) mentioned that during the marking of the trees to be harvested the operator should concentrate on dying and diseased trees or those prone to windthrow. This

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implies that they select the competitively inferior trees. In subsequent alterations to the management system (Seydack *et al.*, 1990; Kobrie Vermeulen, personal communication, 1992) emphasis has been placed increasingly on selecting trees according to certain senility criteria. Competition, however, remains an underlying controlling factor.

During the past decade the role of competition has been controversial. Despite various extensive reviews (e.g. those by Connel, 1983, Schoener, 1983 and Strong *et al.*, 1984), the matter is still far from resolved. Competition for resources such as nutrients, water, space and sunlight may involve outright fighting (interference competition), or could be the consumption of a resource item by one individual, making that item unavailable for others (exploitation competition) (Murray, 1986). The consequences of failing to find and obtain adequate resources would be increased probabilities of dying, decreased probabilities of breeding, or both. Therefore, in forests, any tree that starts at a competitive disadvantage will almost certainly die (Peet & Christensen, 1987). For example, a tree seed that falls and germinates in the immediate vicinity of a larger tree, occupying the soil around it by its root system, will barely have a chance of survival. Generally, competitive exclusion will proceed faster where the available resource base is greater (Huston, 1979). Thus, the resource base, or factors affecting the resource base, such as mycorrhiza, will influence the outcome of competition.

Zeide (1972 & 1975, ex Franco & Harper, 1988; 1985) studying natural forests in the U.S.S.R. observed that a dominant tree is usually surrounded by a ring of suppressed trees. In turn, trees in the next concentric ring act as dominants and so on. The overall effect is one of a 'density wave' that damps down with distance, propagating in all directions from dominant trees. The strength of the symmetrical wave propagation is obscured by waves from other dominants, resulting in asymmetrical waves. The asymmetry of the waves makes the unambiguous demonstration of especially interspecific competition very difficult, as has been shown by Connell's (1983) survey. For this reason the use of observations on species distributions and abundances, which are essentially static observations, to infer information about the dynamic processes of competition in natural communities is often not very successful (Hastings, 1987; Strong *et al.*, 1984). Furthermore, the suppression of trees might vary among different forest types. In the southern Cape large trees are often surrounded by a ring of young trees as a result of seed dispersal by birds, dropping the seed in the vicinity of the source tree after eating the softer outer parts of the fruit. Much more successful is the use of experimental manipulations to detect competition (Hastings, 1987; Schoener, 1983). Where this is not possible, as in the case of the southern Cape forests, the use of distance dependent competition indices often provide a satisfactory alternative. In the forestry environment the measurement of the proximity of competitors and their size (or change in size over time, such as diameter increment) have been shown to have high predictive value (Daniels, 1976; Lorimer, 1983; Monserud, 1976; Smith & Goodman, 1986; Weiner, 1984).

Nearest-neighbour data is relatively easy to obtain and to analyse. It must, however, be remembered that although the plant's performance is considered as a function of the conditions of its neighbours (Weiner, 1984), the period over which this performance is measured in the case of trees, is normally short relative to the tree's life-span. The performance is, therefore, apart from being a function of the proximity of the trees' neighbours, related to the successional stage of the forest stand.

The purposes of this study was to investigate the role of inter- and intraspecific competition between trees in a mature southern Cape forest stand and to provide guidelines for harvest selection. Competition was defined as the negative influence of one tree on another's diameter growth. The stand is representative of forest used for harvesting furniture timbers. The following null hypotheses were tested:

(1) Interspecific competition does not affect tree growth in the southern Cape indigenous forests.
(2) Intraspecific competition plays no significant role in these forests.
(3) Spacing of trees need not be considered during the selection of trees for felling.

STUDY AREA

The study was done in a forest stand on the Diepwalle State Forest (33°56'S, 23°09'E), 20 km north of Knysna, in mixed evergreen subtropical (Phillips, 1931; Webb, 1959) Afromontane (White, 1978) forests of the southern Cape (*Figure 1*). It is representative of the stands from which timber is extracted (Von Breitenbach, 1974; Van Dijk, 1987). The main canopy is 18 to 22 m high. A dense shrub layer, composed mainly of *Trichocladus crinitus* (Thunb.) Pers. grows up to 4 m tall. Ground vegetation is relatively abundant.

The climate is warm temperate subhumid to humid (Poynton, 1971; Schultze & McGee, 1978). Mean annual rainfall is about 1200 mm with a more or less even distribution throughout the year (Weather Bureau, 1986).

The study area forms part of a larger compartment lying partly on a gentle northern and partly on a gentle southern slope. The compartment, together with other adjoining compartments, has been used for testing experimental management systems since 1937. The whole compartment was divided into 48 oblong plots, 0.8 to 1.4 ha in size (*Figure 1*). In 1954 all treatments were terminated.

The specific area used for this study is more or less level. Soils are heavy, with a gravelly (silcrete) subsoil. The area is underlain by fine to coarse-grained brownish sandstone of the Goudini formation (former Tchando formation) (Toerien, 1979) of the Table Mountain group (SACS, 1980).

METHODS

In 1974 the DBH (diameter at breast height, i.e. 1.3 m above ground level) of all trees on the whole compartment with a DBH ≥ 10 cm were measured. A unique number was painted on each tree and the exact point of measurement was marked. In 1987, three adjacent plots, totalling 2.86 ha and lying in a homogenous part of the compartment were selected for remeasurement (*Figure 1*). These selected plots (called main plot from now onwards) included 3970 trees with a DBH ≥ 10 cm. The main plot was subdivided into 286 10x10 m subplots, and each subplot was further subdivided into 25 2x2 m sub-subplots. The boundaries of the latter were demarcated with white nylon rope and the position of each tree within these sub-subplots estimated to the nearest 5 cm. At the same time the DBH of each tree was measured on the exact same point as

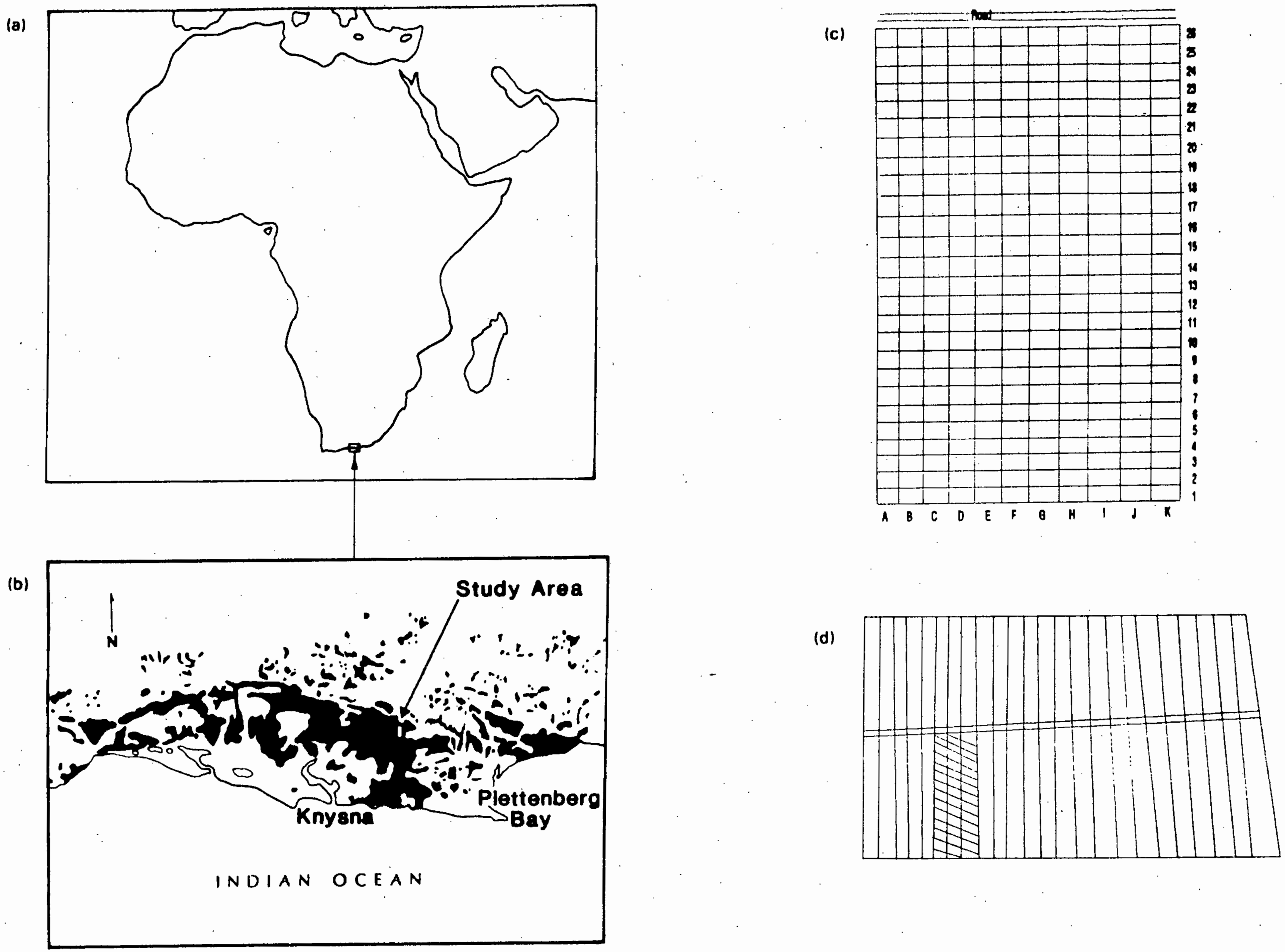

FIGURE 1. *Location of the study area in the southern Cape mixed evergreen forest (black areas) South Africa (a & b). The study site (c), which was subdivided into 10 x 10 m subplots, formed part of a larger forest growth study area (d).*

was done in 1974. The data were recorded for the 10x10 m subplots, not for the sub-subplots. The purpose of the sub-subplots was purely to facilitate the determination of the trees' relative co-ordinates.

The relative tree co-ordinates were used to calculate all the intertree distances using the Arcinfo Geographic Information System. These distances were then correlated with the measured growth for the period 1974 to 1987 for selected species and selected trees within species. The Arcinfo output files tend to be very large and to some extent the size of files that could be handled on the available computer hardware influenced the choice of the species combinations chosen for correlation analysis.

In line with the approach followed by Connell *et al.* (1984) I considered a tree a neighbour that will influence a specific tree's growth only if it was equal or greater in size than the tree under consideration. Lorimer (1983), studying 35 to 50 year old shade-tolerant hardwoods whose growth potential is probably not strongly affected by competition from dominant trees, obtained higher correlations when competitors were defined as trees of equal or higher height classes than the subject tree, than when he considered all trees as competitors. However, Mugasha (1989), found that for predicting competition between *Pinus banksiana* Lamb. (jack pine) and *Populus tremuloides* Michs. (trembling aspen) in Ontario, Canada, better results were obtained when all trees were considered competitors. In this case the jack pine was only eight years old, the stands were pure jack pine/trembling aspen mixtures and only dominant or codominant subject trees were selected. The forest type considered here bares closer resemblance to those studied by Connell *et al.* and Lorimer than the plantation studied by Mugasha. The former two authors' approach has therefore been adopted.

The non-parametric Spearman correlation coefficient was used for the correlation analysis. Various authors (e.g. Lorimer, 1983; Mugasha, 1988; Weldon *et al.*, 1988) used regression analysis for the detection and prediction of competition among trees and shrubs. Others (such as Smith & Goodman, 1986) concentrated on correlation analysis. Weldon *et al.* (1988) found that although competition among trees and shrubs in the semi-arid Colorado was present, the intensity (i.e. the regression slope) of competition within different species combinations did not differ significantly. I was more interested in the detection of competition than in the prediction of the extent of competition and decided on correlation analysis.

When using the nearest-neighbour method, many of the distance values are duplicates, since paired neighbours (which have each other as nearest neighbours) make up a significant portion (up to 62%) of the total population (Clark & Evans, 1955; Hamming & Gilbert, 1954, ex Cottam & Curtis, 1956). This problem was avoided by the restriction that competitors could only be trees of equal or greater size than the subject (smaller) tree.

When the subject tree is close to the plot boundary there is always a degree of uncertainty about the nearest neighbour's position (Connell *et al.*, 1984). The real nearest-neighbour could be outside the plot, but because it does not form part of the dataset it will not be known. This edge effect was limited by eliminating from the dataset the subject trees occurring in the outer row of subplots. This meant that subject trees were at least 10 m away from the boundary of the main plot.

I adopted Connell's (1983) operational definition in deciding whether competition was affecting a species. "If there was a statistically significant response in the opposite direction in the species being studied, ... competition was judged to be occurring". In other words, if the distances between neighbours were positively correlated with diameter growth (i.e. the greater the distance the faster the growth rate) competition was considered to be limiting tree growth.

For each species combination frequency tables of the number of smaller nearest trees according to 5 m distance classes away from the larger trees (which were divided into 5 cm DBH classes) were calculated. For example, for the *Olea capensis* L. subsp. *macrocarpa* (C.H.Wr.) Verdoorn trees within the 20 to 25 cm DBH class the number of smaller nearest *Curtisia dentata* (Burm.f.) C.A. Sm.

trees were listed according to 5 m distance classes away from the *Olea* (*Table 1a*). For this specific example smaller *Curtisia* occurred 22 times within 5 m from an *Olea* with a DBH of 20 to 25 cm, 18 times between 5 and 10 m away from an *Olea* in this size class, 16 times between 10 and 15 m and so on. The information for each of these DBH classes of the larger trees was then further subdivided into tables of the number of smaller trees in 5 cm DBH classes at 5 m distance classes from the larger tree (*Table 1b*). In this way the distribution of smaller trees around a larger tree for a specific species combination could be assessed.

RESULTS

The results are summarised in *Table 2*. Interspecific competition was present between all chosen species combinations except for the mutual influence between *Pterocelastrus tricuspidatus* (Lam.) Sond. on *Apodytes dimidiata* E. Mey. ex Arn. and for the influence of *Olea capensis* subsp. *macrocarpa* on *Ocotea bullata* E. Mey. The influence of larger *Curtisia dentata* on smaller *Podocarpus falcatus* (Thunb.) R.Br. ex Mirb. became significant only when the latter was surrounded by four or more trees. The influence of *Curtisia dentata* on *Pterocelastrus tricuspidatus* was very weak too. The more larger *Curtisia* trees surrounded smaller *Pterocelastrus* trees, the weaker the influence became.

Intraspecific competition was evident for *Curtisia dentata* and *Apodytes dimidiata*, but not for *Ocotea bullata*. For *Ocotea* the presence of other larger trees of the same species enhanced the growth of the subject tree.

From the frequency tables (e.g. *Table 1a*) the relative close proximity of trees to each other becomes apparent (*Table 2*). Of the species combinations studied between 29% and 100% (on average 71%) of the trees occurred within 15 m from each other. The subdivisions of the frequency tables (e.g *Table 1b*) just showed the obvious, i.e. that the closest trees of a subject species to a larger (competing) tree of another or the same species were the smallest trees. Larger trees were, with a few exceptions, spaced further apart than the smaller trees. No difference in pattern between competing and non-competing species could be detected.

TABLE 1a. Number of smaller *Curtisia dentata* (in body of table) per 5 m distances away from larger *Olea capensis* subsp. *macrocarpa* trees, divided into 5 cm DBH classes.

Distance class -> Size class	0 to < 5 m	5 to < 10 m	10 to < 15 m	15 to < 20 m	20 to < 25 m	25 to < 30 m	Total
10 to < 15 cm	36	45	38	7	5	2	133
15 to < 20 cm	24	34	24	5	2	1	90
20 to < 25 cm	22	18	16	3	1	2	62
25 to < 30 cm	23	24	9	5	1	2	64
30 to < 35 cm	15	20	7	0	2	0	44
35 to < 40 cm	16	12	10	2	0	0	40
40 to < 45 cm	18	17	6	3	0	0	44
45 to < 50 cm	9	11	3	1	1	0	25
50 to < 55 cm	8	10	4	2	0	0	24
55 to < 60 cm	8	9	5	0	0	0	22
60 to < 65 cm	4	6	2	0	0	0	12
65 to < 70 cm	2	3	0	0	0	0	5
75 to < 80 cm	1	0	0	0	0	0	1
Total	186	209	124	28	12	7	566

TABLE 1b. Number of smaller *Curtisia dentata* trees (divided into 5 cm DBH classes) per 5 m distance classes away from *Olea capensis* subsp. *macrocarpa* trees with a DBH of 20 to less than 25 cm.

Size class -> Distance class	5 to < 10 cm	10 to < 15 cm	15 to < 20 cm	20 to < 25 cm	25 to < 30 cm	30 to < 35 cm	35 to < 40 cm	Total
0 to < 5 m	12	5	5	0	0	0	0	22
5 to < 10 m	11	3	3	1	0	0	0	18
10 to < 15 m	11	5	0	0	0	0	0	16
15 to < 20 m	1	0	2	0	0	0	0	3
20 to < 25 m	1	0	0	0	0	0	0	1
25 to < 30 m	1	0	1	0	0	0	0	2
Total	37	13	11	1	0	0	0	62

the stronger competitors in terms of diameter growth under the present circumstances.

Despite the evidence that *Olea capensis* subsp. *macrocarpa* is one of the weaker competitors, that its mortality rate is relatively high (Van Daalen 1991) and that it is a weak "gap-filler" (Cameron, in preparation) it is by far the most abundant tree in the forest, both in areas that have been harvested and in unharvested areas (Cameron, in preparation; Geldenhuys, 1980). The reasons for this contradiction are not clear. There must be other trades which enables it to maintain dominance. Possibly one should measure competition in terms of crown size and/or volume, and one could look at its seed dispersal pattern and its growth development during the sapling stage.

Van Daalen (1991) suggested that there might be strong competition among coppice shoots of *Ocotea bullata*. The stump of this species often coppices prolifically after the felling of the bole. Of these shoots only a few survive. With a few exceptions all the *Ocotea* trees measured on the study site were single-stemmed trees and Van Daalen's suggestion could not be tested. It is, however, clear that the close proximity of other trees of this species (88% of the trees occurred within 15 m from each other despite the fact that there were only 60 on the whole study site - see *Table 2*) is beneficial to the tree. Exactly why is not clear. The species does tend to occur in clumps (Lübbe, 1989). If intraspecific competition within this species was prevalent, clumping would probably not have occurred.

Until recently harvesting of different tree species from the forests was done strictly according to the relative proportion of each species in the forest (Seydack *et al.* 1982; 1990). Even when a species was not utilisable, the same proportion of the growing stock of that species was removed from a production compartment as was removed from the utilisable species' stock. With the latest adjustment to the management system this requirement has effectively been dropped (Kobrie Vermeulen, personal communication, 1992). For the weak competitors this proportionality during harvesting would not have been necessary. These species' numbers would have been kept down by competition from the strong competitors.

To a certain extent the close proximity of the smaller trees to the larger ones is an artifact of the abundance of smaller trees of several species on the study site (*Table 2*). This is confirmed by a significant Spearman correlation coefficient (P = 0.024) for the number of smaller trees within 15 m from the larger trees for each species combination.

The similarity of the average distances between competing and non-competing species could be the result of the stocking density of the forest. Most of the trees in the southern Cape forests are shade-tolerant and can grow in close proximity to other trees, despite the fact that the growth rate of various species is retarded by competition. This could in part explain why trees of equal size in natural forests can have vastly different ages.

In the light of the above, spacing of trees (hypothesis 3) must be taken into account for those species that are influenced by competition. This implies that the forest manager must know which species combinations will influence each others growth. For example, *Ocotea bullata* can grow in the immediate proximity of *Olea capensis* subsp. *macrocarpa* without any effect on its growth rate, but both *Podocarpus* species' growth will be hampered by a larger *Olea* close by. On the other hand, a smaller *Olea* tree will not affect a *Podocarpus* tree's growth significantly. The opposite would rather happen.

In summary, the following practical conclusions for the forest manager can be made:

- There is no danger of decreasing the numbers of the *Podocarpus* species during normal harvesting levels. To the contrary, these species seem to have the ability to increase their numbers.

- There is no evidence that *Olea capensis* subsp. *macrocarpa* affects the growth of *Ocotea bullata* and they need not be "freed" from *Olea* trees.

- The more pioneer-like species appear to be the weaker competitors in the present successional stage of the forest. This confirms Van Daalen's (1991) conclusion that the southern Cape forests are in an advanced successional stage. To increase the growth rates of selected more pioneer-like tree species the standing stock will have to be reduced substantially to push the forest into an earlier successional stage favourable for the growth and development of these species. Although the principle of substantial growth stock reduction to accelerate growth is/has been applied in various tropical forests of the world (Maitre, 1987) the present policy for the southern Cape forests does not allow this (Seydack *et al.*, 1982). Furthermore, the results of this study and those reported by Van Daalen (1991) suggest that such a stock reduction will be detrimental to the growth rate of the two most valuable species, viz *Ocotea bullata* and *Podocarpus latifolius*.

* The role of *Olea capensis* subsp. *macrocarpa* is not yet fully understood and should be the subject of further study. Why is it so abundant? How does it maintain its abundance in the light of the results of this and Cameron's (in preparation) studies? What will be the effect of the removal of dominants of this species out of a compartment used for harvesting timber?

* The emphasis placed on mortality pre-emption during the harvest selection in the forest appears to be sound. Suppressed trees will have a greater chance of dying than healthy trees with enough growing space. These suppressed trees will be those selected for felling first, provided the selection criteria accurately reflect signs of suppression.

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CHAPTER 4

TREE GROWTH INDICATORS

THE VALUE OF CROWN POSITION AND FORM AS GROWTH INDICATORS IN MIXED EVERGREEN FOREST

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SYNOPSIS

Diameter increment over a 13 year period was correlated with crown position and crown form scores for a range of southern Cape forest tree species. It was found that both crown position and form are useful variables for the selection of harvest trees of the canopy species. The growth of subcanopy species was, in general, not related to the crowns' positions in the canopy. Crown form was, however, significantly correlated with the growth of some subcanopy species. For all the tree species (mainly canopy species) for which increment was significantly correlated with both crown position and crown form, the crown position and crown form scores were significantly related. This indicates that the exposed crowns had better forms, implying that competition does have a significant influence on the growth of these trees.

INTRODUCTION

The management of the mixed evergreen southern Cape forests is based on a system where single trees are selected for harvesting. These trees are selected in such a way that mortality is as far as possible pre-empted. For this purpose senility indices, such as stem rotting, dying, damage and agony shoots, are used (Seydack *et al.*, 1990; Kobrie Vermeulen, personal communication, 1992). However, frequently a suppressed tree cannot be distinguished from a tree with high vigour on the basis of the above-mentioned senility criteria and further indicators are needed.

The position of a tree's crown in the canopy and in relation to its neighbours' crowns, irrespective of the size of its bole, can serve as an

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index of dominance, competitive status or canopy exposure. Studies in plantations and homogeneous natural stands have shown that subdominant or concealed (overshadowed by larger trees) trees generally are growing more slowly than exposed or dominant trees. A similar correlation between a tree's crown position and the rate of increment can be expected in mixed forests. An index of crown position is regarded as most important for reliable timber growth models (Synnott, 1979). Dawkins (1963, ex Synnott, 1979) found that crown position scores were better correlated with increment than other measures of the environment and was the only significant environmental variable in his regression equations.

Trees growing in the shade of others will react in various ways, such as reduced height growth (Oliver and Larson, 1990), altered crown architecture (Hallé, 1976; Waring and Schlesinger, 1985) and crown volumes (Brunig, 1983), the development of asymmetric crowns (Young and Hubbell, 1991) and in extreme cases of suppression, the loss of conducting tissue, little taper in tree stems, reduced root growth, reduced seed production, low carbohydrate reserves and a resultant susceptibility to wind and snow damage (Waring, 1987).

Height growth can be reduced significantly. Various authors have shown that understorey trees often exhibit periodic slowdowns and accelerations of height growth as they are released by thinnings and later suppressed again by the reclosing overstorey (Jaeck *et al.* 1984; Oliver and Larson, 1990). In (sub)tropical forests reduced height growth of trees will result in their shading by others, which in turn will affect their crown shapes. Shade on the side of a crown affects the growth of the shaded branches (Oliver and Larson, 1990). Each branch must photosynthesize enough to maintain its growth and survive. Where shade limits photosynthesis on a side of a crown, lateral shoot growth is reduced (Cochrane and Ford, 1978) and the symmetry of the crown affected. Trees tend to lean away from the shade. This could be the result of the trees actually growing towards the sunlight or the heavier portion of the crown on the more sunny side of the tree pulling it away from the shade (Oliver and Larson, 1990). Young and Hubbell (1991) have shown that crown asymmetry affects the direction and frequency of treefalls in the Barro Colorado tropical forest in Panama. They suggested that by incorporating crown asymmetry and the neighbourhood relations that cause it, treefalls will become more predictable. Dawkins (1963, ex Synnott, 1979) described his crown form score "as an index of quality, its value being dependent on past history and perhaps indicating future potential".

Crown size is often proportional to tree height, especially in trees with strong epinastic control, as is usually the case with conifers. In trees growing without competition height is, therefore, correlated with foliage area and total tree volume increment. This explains why the height of dominant trees in even-aged stands is an expression of site index (Oliver and Larson, 1990). Epinastic control in tropical forest trees is often weak, and the relation between crown size and height growth can be expected to be weaker than in the case of conifers. However, the shading of trees will no doubt affect the crown size and height growth of suppressed trees.

Crown size is very difficult and time consuming to measure in the mixed (sub)tropical forests, such as the southern Cape forests. Crowns intermingle to such an extent that the distinction of a specific crown is difficult, let alone measuring its dimensions.

Crown position and crown form are quick and easy to assess, and the value of these two parameters as growth indicators were evaluated in this study. The following hypotheses were tested for a mixed evergreen subtropical (Phillips, 1931; Webb, 1959) Afromontane (White, 1978) forest stand in the southern Cape:

1. Diameter increment of trees growing in full sunlight is faster than trees growing in the shade of others.

2. Diameter increment and crown form are positively related, i.e. the closer the crown conforms to a complete circle, the better diameter growth can be expected.

In addition, the relation between crown position and crown form of a tree was tested.

STUDY AREA

The study was done in forest stand on the Diepwalle State Forest (33°56'S, 23°09'E), 20 km north of Knysna (*Figure 1*). It is representative of the stands from which timber is extracted (Von Breitenbach, 1974; Van Dijk, 1987). The main canopy is 18 to 22 m high. A dense shrub layer, composed mainly of *Trichocladus crinitus* (Thunb.) Pers. grows up to 4 m tall. Ground vegetation is relatively abundant. Since 1954 no timber was extracted from this stand.

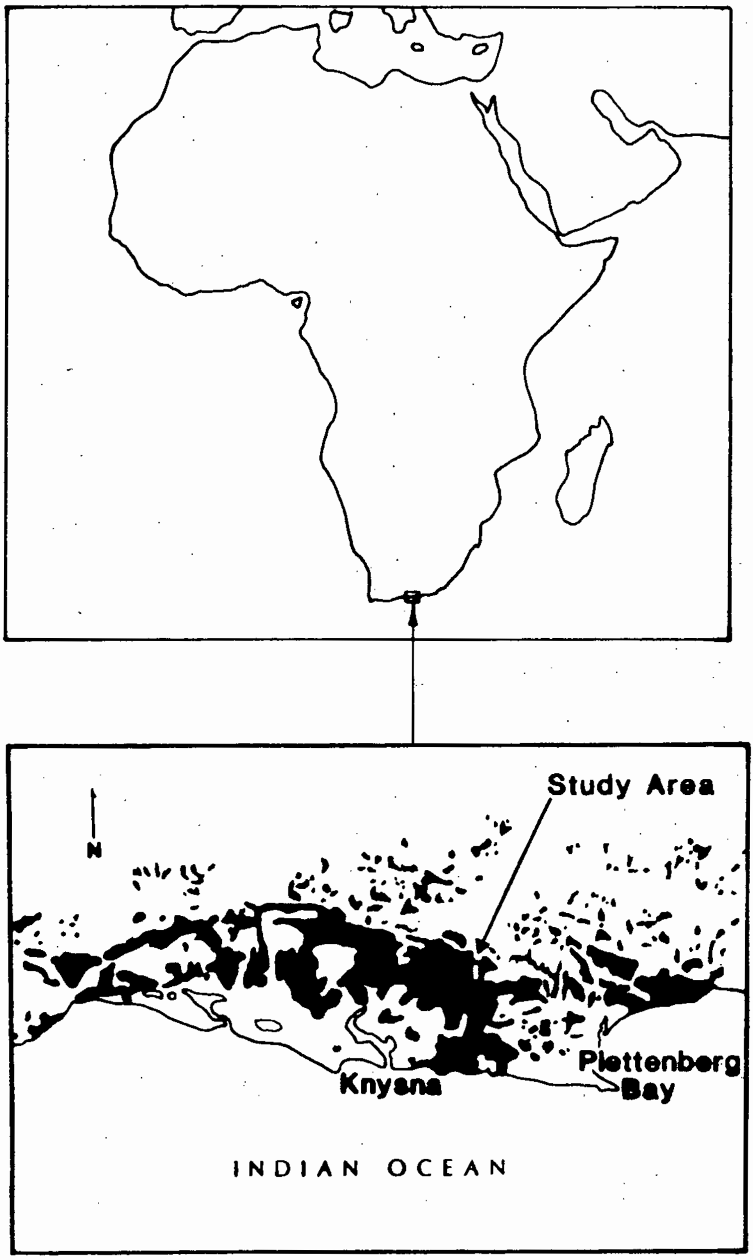

FIGURE 1. Location of study area within the mixed evergreen forest (black areas) north of Knysna, South Africa.

The climate is warm temperate subhumid to humid (Poynton, 1971; Schultze & McGee, 1978; Walter, 1979). Mean annual rainfall is about 1200 mm with a more or less even distribution throughout the year (Weather Bureau, 1986).

The specific area used for this study is more or less level. Soils are heavy, with a gravelly (silcrete) subsoil. The area is underlain by fine to coarse-grained brownish sandstone of the Goudini formation (former Tchando formation) (Toerien, 1979) of the Table Mountain group (SACS, 1980).

METHODS

In 1974 the DBH (diameter at breast height, i.e. 1.3 m above ground level) of all trees on the whole forest compartment with a DBH ≥ 10 cm were measured. A unique number was painted on each tree and the exact point of measurement was marked. In 1987 a 2.86 ha plot was selected and the DBH's remeasured on the marked points. At the same time the crown position and crown form of each tree was assessed according to Dawkins' scores as reproduced in Synnott (1979) (*Figures 2a & 2b*).

The measured diameter increment for each tree species with ten or more specimens on the plot was correlated with its crown position and crown form scores by means of the non-parametric Spearman rank correlation coefficients. The same method was used to calculate the correlation between each species' crown position and form scores (*Table 1*).

TABLE 1. Spearman correlation coefficients between DBH increment and crown position, DBH increment and crown form, and between crown position and crown form. The correlation coefficients are indicated by "r", "P" indicates probability > |r| under $H_0: \rho=0$ and "n" represents the sample size. The median and range values are for the crown position and crown form scores. The probabilities for significant correlation coefficients are shaded. For significance level of 1% or less the probabilities are printed in bold. The species are arranged in descending order according the median crown position and crown form values.

Species	n	Increment x crown position			Increment x crown form			Crown position x crown form	
		r	P	Median (range)	r	P	Median (range)	r	P
Olinia ventosa	16	0.5258	0.0365	4 (2-5)	0.1175	0.6647	3 (2-5)	0.5927	0.0155
Olea capensis subsp. *macrocarpa*	585	0.4972	**0.0001**	3 (1-5)	0.4256	**0.0001**	3 (1-5)	0.5385	**0.0001**
Podocarpus latifolius	316	0.2092	**0.0002**	3 (1-5)	0.3116	**0.0001**	3 (1-5)	0.1873	**0.0010**
Psydrax obovata	51	03872	**0.0050**	3 (1-5)	03785	**0.0062**	3 (1-5)	0.3925	**0.0044**
Ocotea bullata	27	0.2327	0.2428	3 (1-5)	0.7087	**0.0001**	2 (1-4)	0.5478	**0.0031**
Apodytes dimidiata	98	0.2940	**0.0033**	2 (1-5)	0.4343	**0.0001**	3 (1-4)	0.4049	**0.0001**
Curtisa dentata	174	0.2360	**0.0020**	2 (1-5)	0.2483	**0.0010**	3 (1-4)	0.1917	0.0133
Podocarpus falcatus	19	0.8097	**0.0001**	2 (1-5)	0.5450	0.0158	3 (2-5)	0.5746	**0.0080**
Canthium mundianum	32	0.2872	0.1109	2 (1-4)	0.2346	0.1961	3 (1-4)	0.2794	0.1215
Cassine papillosa	114	0.0702	0.4577	2 (1-4)	0.1705	0.0697	3 (1-4)	0.2386	0.0106
Nuxia floribunda	33	0.2649	0.1362	2 (1-5)	0.5299	**0.0015**	2 (1-4)	0.2669	0.1332
Pterocelastrus tricuspidatus	92	0.2069	0.0478	1.5 (1-4)	0.2006	0.0552	2 (1-5)	0.2841	**0.0081**
Cassine eucleiformis	13	-0.4261	0.1466	1 (1-2)	0.4309	0.1416	4 (1-5)	0.0441	0.8861
Gonioma kamassi	269	0.0976	0.1104	1 (1-4)	0.1792	**0.0032**	3 (1-5)	0.1072	0.0792
Diospyros whyteana	47	0.2212	0.1351	1 (1-4)	0.3170	0.0289	3 (1-4)	0.3014	0.0385
Lachnostylis hirta	46	-0.1334	0.3769	1 (1-4)	0.4194	**0.0037**	2 (1-4)	0.3163	0.0322
Maytenus peduncularis	56	0.1554	0.2529	1 (1-5)	0.2910	0.0296	2 (1-4)	0.3575	**0.0088**
Ochna arborea	50	-0.3005	0.0340	1 (1-4)	0.2150	0.1339	2 (1-4)	-0.0182	0.9002
Olea capensis subsp. *capensis*	21	-0.0308	0.8946	1 (1-4)	0.0302	0.8965	2 (1-3)	0.3032	0.1816
Burchellia bubalina	18	0.2464	0.3244	1 (1-2)	0.2056	0.4130	2 (1-4)	0.6708	**0.0023**

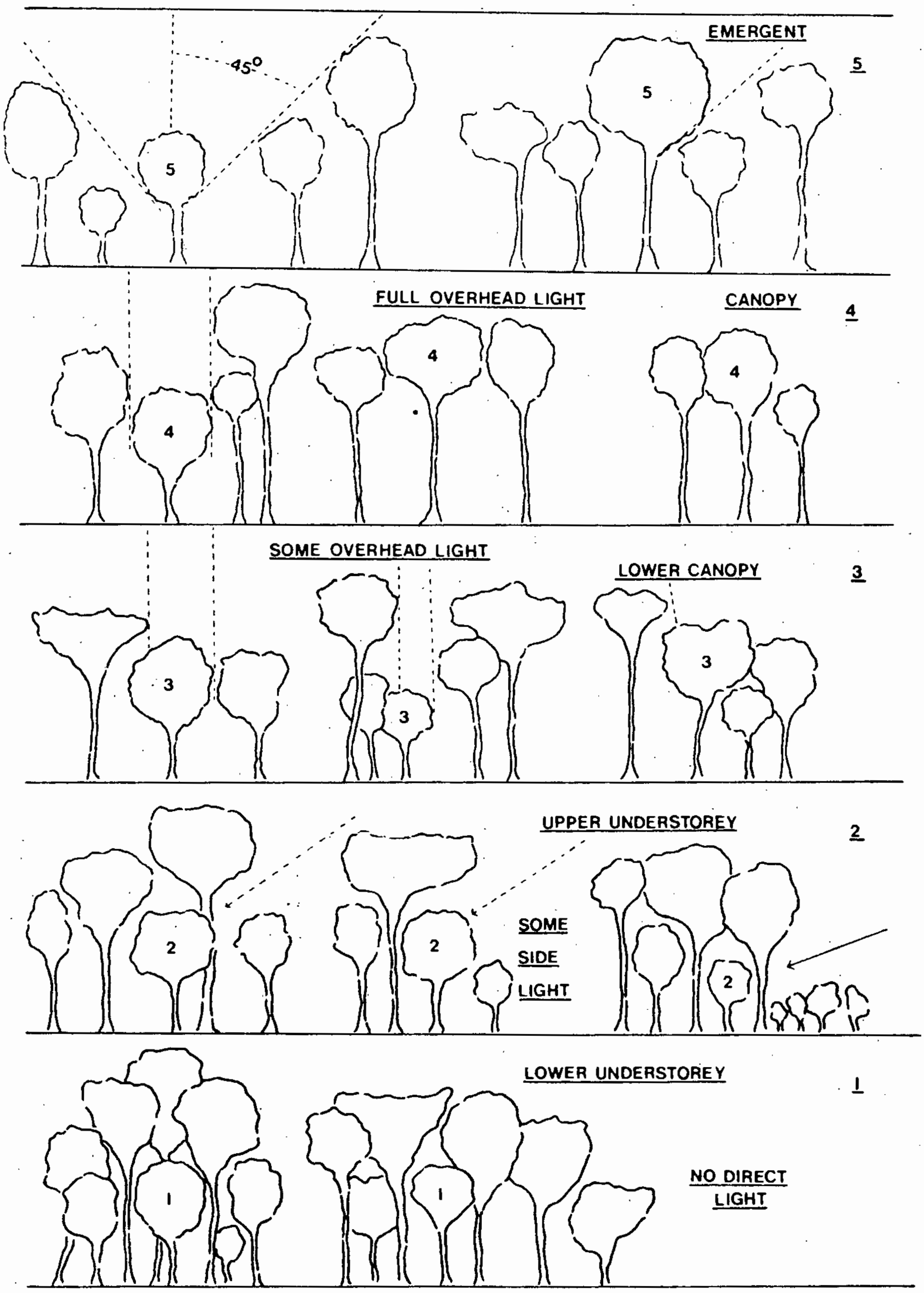

FIGURE 2a. Crown position scores (reproduced from Synnott, 1979).

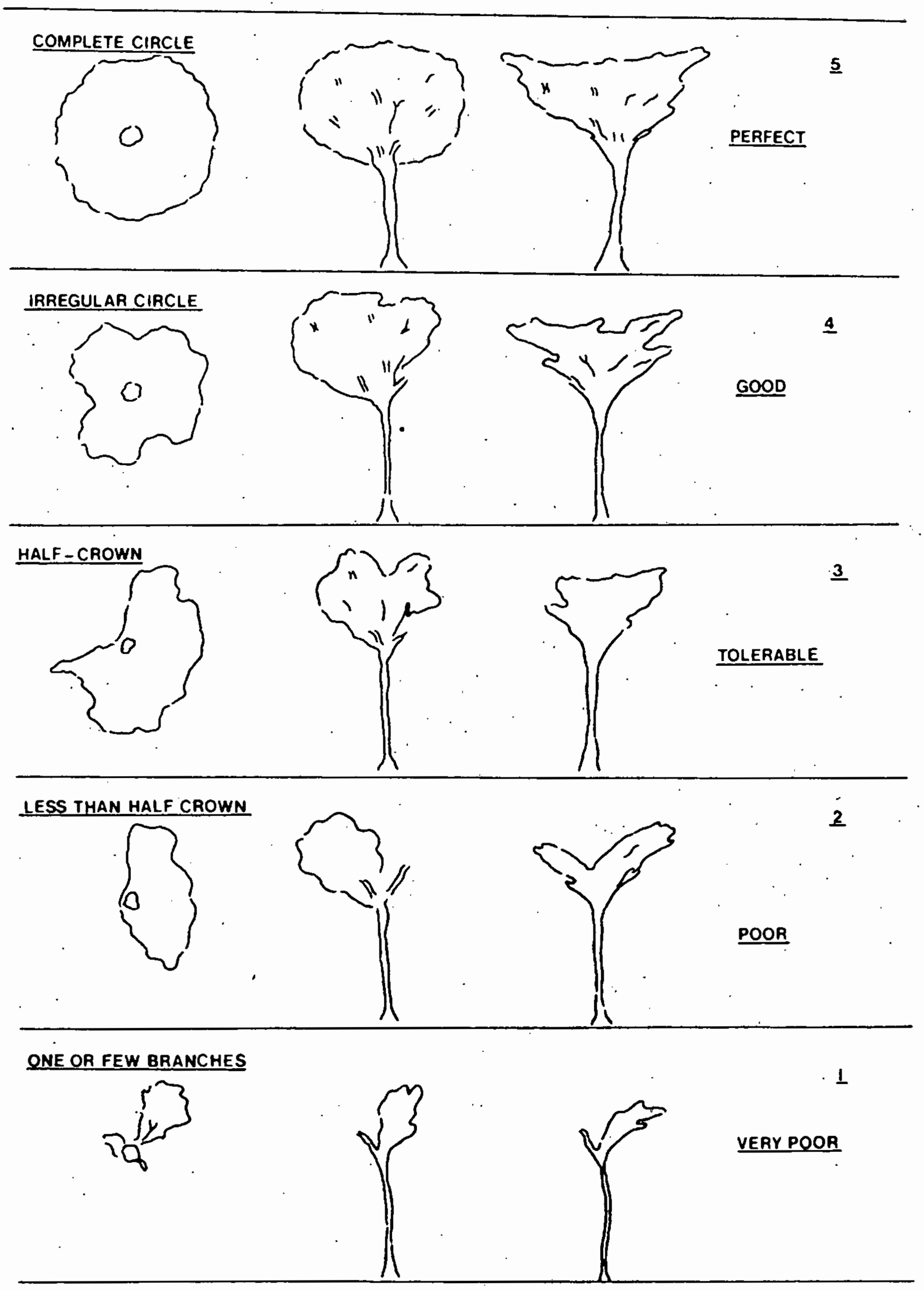

FIGURE 2b. Crown form scores (reproduced from Synnott, 1979).

RESULTS

Significant correlation coefficients were more common among the species with the higher crown position and crown form scores. For the majority of species the crown position and crown form scores were significantly correlated. Note that for all the species with significant correlation coefficients for increment x crown position the upper limit of the crown position score was 5, i.e. emergents in terms of the scores used (*Figure 2a*). The only exceptions were *Pterocelastrus tricuspidatus* (Lam.) Sond. and *Ochna arborea* Burch. ex DC. Despite the occurrence of scores of 5, the majority of crown position scores were very low for these two species (median values of 1.5 and 1 respectively). The same tendency can be observed for the crown form scores, although not as conspicuous as for the crown position scores. All the species with significant correlation coefficients for increment x crown form had upper crown form scores of 4 or 5.

DISCUSSION

Both crown position and crown form seem to be factors controlling the diameter growth rate of a variety of forest tree species in the southern Cape. This confirms Van Daalen's (in preparation) results of the significant roles of inter- and intraspecific competition in the forest. Although many of the species can survive shading for considerable periods, release into full sunlight accelerate the growth rates. Due to the positive relation between crown position and crown form such a release will probably improve the crown form too.

The lack of any relation between DBH increment and crown position for *Ocotea bullata* (Burch.) E. Mey. emphasizes its ability to grow beneath other trees (Van Daalen, in preparation). Although it does reach the canopy or can grow in the open (the maximum crown position score was 5), it is not dependent on full sunlight for its growth. For this reason it cannot be classified as a true subcanopy tree, as can be done with species such as *Cassine eucleiformis* (Eckl. & Zeyh.) Kuntze, *Gonioma kamassi* E. Mey., *Diospyros whyteana* (Hiern) F. White, *Lachnostylis hirta* (L.f.) Muell. Arg., *Ochna arborea* Burch. ex DC., *Olea capensis* L. subsp. *capensis* and *Burchellia bubalina* (l.f.) Sims. All the subcanopy species have median crown scores of 1 and no significant correlation between DBH increment and crown position, except for *Ochna arborea*. This latter species' growth was actually enhanced by shading (the significant correlation was negative). Several of these subcanopy species had, however, significant positive correlation coefficients between increment and crown form scores. This indicates that, although the tree can grow in the shade of others, it still needs a good crown form, and implicitly enough foliage, to grow well.

The hypotheses of dependence of diameter growth on crown position and crown form must be accepted for the canopy emergents. Exceptions are *Olinia ventosa* (L.) Cufod. and *Ocotea bullata*. *Olinia ventosa* is the fastest growing, shade-intolerant, pioneer-like species (Van Daalen, 1991) for which full sunlight is of utmost importance for its growth and survival. For *Ocotea bullata* a good crown form and enough foliage are much more important than its position in the canopy.

For the subcanopy species the first hypothesis (of a positive relation between increment and crown position) can, in general, be rejected. The second hypothesis (of a positive relation between increment and crown form) can be accepted for certain subcanopy species and rejected for others.

Thus, crown position and crown form can be used during the harvest selection process for those species that are normally part of the main canopy, keeping in mind the special cases of *Olinia ventosa* and *Ocotea bullata*. There is no single criterion for selection and the better the manager knows the dynamics of the forest under his control, the better he will be able to manage.

In the light of the above the selective opening of the canopy (e.g. during selective harvesting of trees) will be beneficial for the canopy species, except for *Ocotea bullata*. This confirms Van Daalen's (in preparation) conclusion that *Ocotea bullata* need not be "freed" from *Olea capensis* L. subsp. *macrocarpa* (C.H. Wr.) Verdoorn. The latter species tends to form heavy crowns and due to its abundance in the forest (Geldenhuys, 1980) often dominates the crown. Therefore, the "freeing" of the more valuable (in terms of timber) canopy species could increase production without disturbing the forest ecology, provided it is done in a conservative way. Stock reduction to the point where the growth of pioneer-like species such as *Olinia ventosa* L. (Cufod.) is enhanced will be detrimental to the growth of some of the valuable timber species such as *Podocarpus latifolius* (Thunb.) R. Br. ex Mirb. (Van Daalen, in preparation).

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Research note

Cambial Electrical Resistance as an Indicator of Tree Growth in the Southern Cape Indigenous Forests

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SYNOPSIS

The usefulness of cambial electrical resistance readings, measured with a Shigometer, to indicate growth rates of indigenous forest trees, to detect trees with a reduced growth rate as a result of pathogen infection, and to compare tree vigour of indigenous and alien trees was tested. Although significant correlation coefficients between resistance readings and growth rates were obtained, standard deviations were too high to be useful for indigenous forest management purposes.

INTRODUCTION

Owing to the multiple use and limited area of indigenous forests in South Africa, over-exploitation of timber can cause untold damage to these forests. Underutilisation, on the other hand, will result in loss of the limited and extremely valuable indigenous timber. The backbone of the intensive management of those indigenous forests in the southern Cape used for timber production (Seydeck *et al.*, 1982) is the proper marking of trees for removal. No matter how good a management system is, if the marking process fails the whole system fails.

Frequently, a suppressed tree in the indigenous forest cannot be distinguished from a tree with high growth vigour. Therefore, during forest management for timber production, trees are marked for removal according to their size and, where possible, according to other silvicultural criteria, like apparent competition, health condition etc.

In order to try to quantify the selection of trees, an instrument to measure the cambial resistance of trees, called a Shigometer (after Dr Alex Shigo, its inventor) was tested*.

Fungal pathogens can affect a tree's vigour in the same way as when it is suppressed. Therefore, electrical resistances of healthy and *Phytophthora cinnamomi* affected *Ocotea bullata* trees were measured to determine whether the affected trees could be separated from healthy trees on this basis.

In the eastern Cape resistance readings on *Rapanea melanophloeos* under alien trees were compared with readings on *R. melanophloeos* trees in forest. Resistance readings on two alien species growing together were also compared.

Analyses indicated high standard deviations for resistance readings for different rates of diameter growth. In an attempt to explain this, experimental errors for increment measurements were determined.

In summary then, the following was tested:

1. Do cambial electrical resistance readings (measured with a Shigometer) indicate growth rates of forest trees reliably?
2. Can reduced vigour in pathogen affected forest trees be detected with a Shigometer?
3. Assuming (1) above to be true, how do alien trees affect tree vigour of indigenous trees?
4. Does the vigour of two (related) alien tree species growing on the same site differ?
5. Are relationships (if any) between resistance readings and tree increment rates affected significantly by errors in tree diameter and resistance measurements?

TECHNICAL DESCRIPTION OF THE SHIGOMETER

The following is a summary of an information sheet on the Shigometer by OSMOSE, the manufacturers in the United States of America:

"The Shigometer is a battery powered, portable field instrument that delivers a pulsed current through a probe to wood tissues and measures the resistance of the tissues to the current. The condition of the wood at the tip of the probe is deter-

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For the purpose of the study a Shigometer was provided by the local agents, Holley Marketing (Pty) Ltd, Pietermaritzburg.

mined by the pattern of measurement displayed on the digital meter. In sound wood only slight changes occur as the probe is inserted. When the probe tip passes from sound wood to discolored or decayed tissue, ... an abrupt change occurs in the digital reading. The magnitude of change in the readings indicate the degree of tissue deterioration."

"The principle ... revolves around the cations ... that concentrate in decayed wood and the decreased resistance that results. To measure these changes a probe of two twisted copper wires is inserted into holes drilled in the wood. The probe, attached to the Shigometer by a length of flexible cable, is entirely insulated except for the tips, which are curved into a bell shape. When the exposed probe tips enter the drill hole their sides press against the walls of the hole, so that the pulsed current is passed from the meter through one wire into decayed or healthy wood. The current then returns to the meter through the other wire. Readings are made in 1 000-ohms."

"The primary use of the Shigometer is to locate decay accurately in standing utility poles and piling by using the patented twisted wire probes in the groundline area."

"Using the needle probe in the cambial zone trees with relatively high vitality can be separated from trees with relatively low vitality. Trees are accurately selected for thinning, and forest stands can be indexed for growth rate. In addition, mortality can be predicted using the needle probe." This aspect was tested and will be reported on.

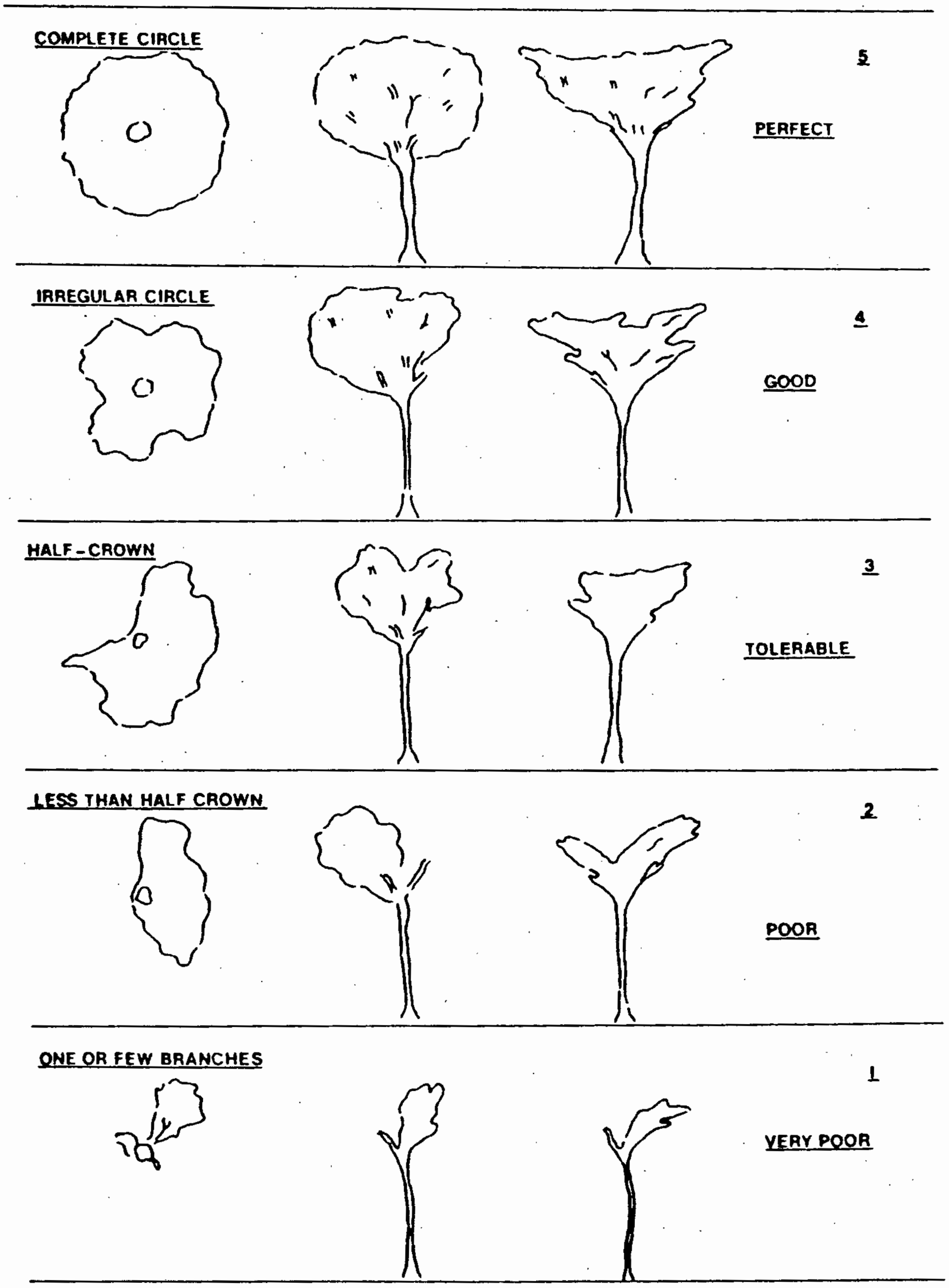

FIGURE 1. Crown form scores (reproduced from Synnott, 1979).

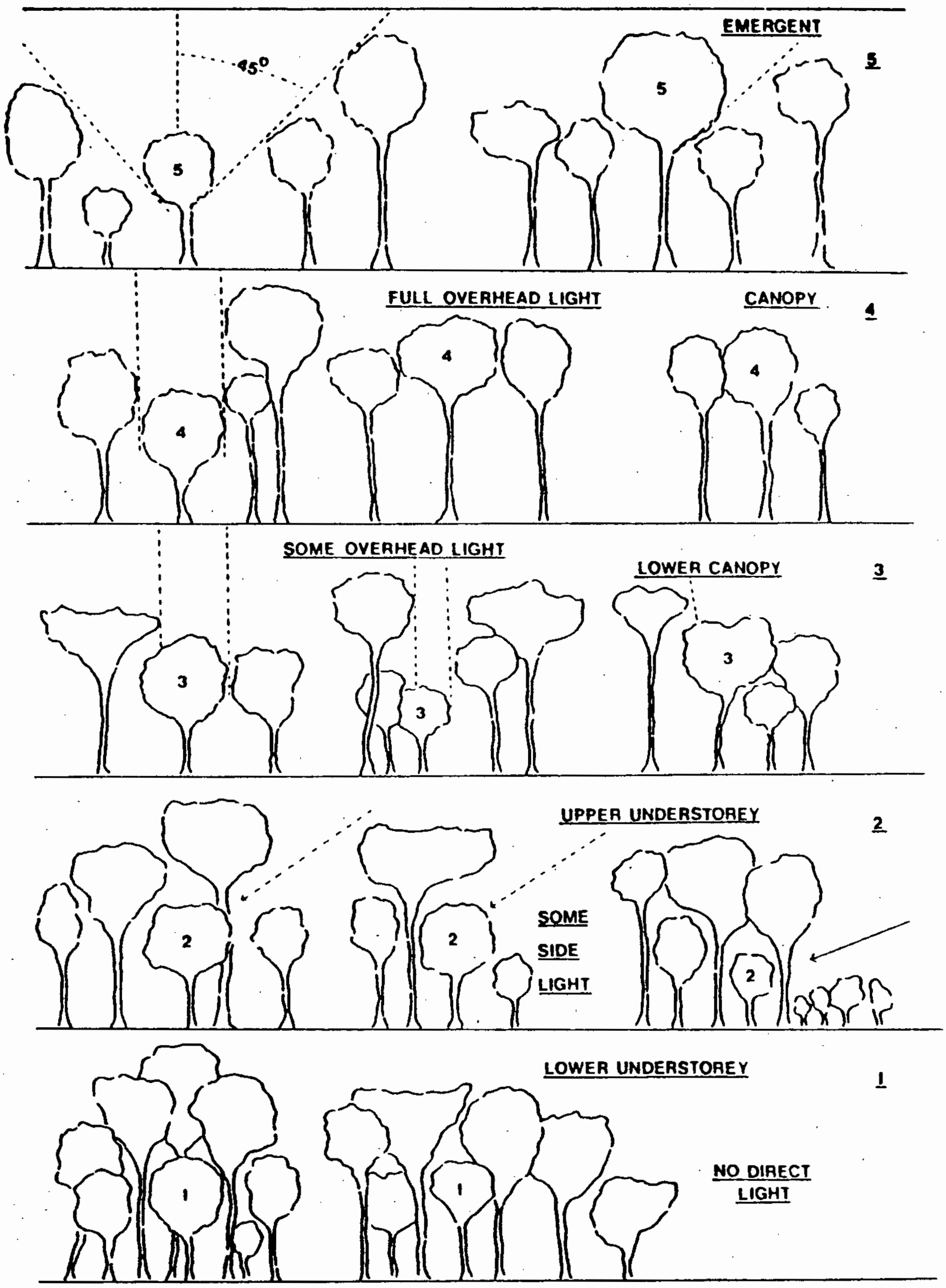

FIGURE 2. Crown position scores (reproduced from Synnott, 1979).

METHODS

On an increment study site at the Diepwalle State Forest, north of Knysna, detailed increment measurements were made in 1972, 1978 and 1983. Tree diameter was measured at marked (1,3 m high) points on 76 permanent sample plots and each tree numbered permanently. Four species, *Podocarpus latifolius, Ocotea bullata, Apodytes dimidiata* and *Olea capensis* subsp. *macrocarpa* were selected for testing the Shigometer. Of each species, trees were selected to cover the complete range of increments. Four measurements of the cambial resistance (in the four wind directions) at the point at which the diameter measurements were taken, were made.

These readings were correlated (data were tested for normality and a Pearson correlation was used) with

1. the mean diameter increment from 1972 to 1983 and 1978 to 1983; and
2. mean tree basal area increment from 1972 to 1983 and 1978 to 1983;

Spearman rank correlations were used (data included categorical variables) to determine the relationship between resistance readings and crown form (*Figure 1*), crown position (*Figure 2*) and diameter.

Four cambial resistance measurements (in the four wind directions) were made on 295 *Ocotea bullata* trees on a study site at the Witelsbos State Forest in the Tsitsikamma: 202 trees in a forest stand infested with the root pathogen *Phytophthora cinnamomi* and 93 trees in a control, apparently pathogen free, stand. The diameter and crown form of these trees were known (subproject 1/03/02/06/04). The crown position of each tree was estimated according to the scale in *Figure 2*. Spearman rank correlations were calculated between resistance readings and the different measured and estimated variables. The difference between the mean resistance readings for the *P. cinnamomi* infested and the control stand was tested by means of analysis of variance.

At Hogsback, in the eastern Cape, cambial resistance readings were made on *Rapanea melanophloeos* trees in the forest and under alien trees, mainly *Acacia mearnsii* and *Rachospermae melanoxylon* (= *Acacia melanoxylon*), and on *A. mearnsii* and *R. melanoxylon* trees growing together. Resistance readings were plotted against measured diameters and estimated crown positions.

To determine the sampling error in increment measurements in indigenous forest the diameter of five trees of each of four species mentioned above, representing three bark types, were measured 25 times at a marked point. To avoid bias a group of people were used to measure the trees. Care was taken not to let the same person measure the same trees in any fixed order. Variances were determined and sample sizes calculated using the following equation (Snedecor and Cochran, 1974):

$$N_{.05} = 4\sigma^2/L^2$$

where

N_{05} = sample size needed for a ($P \leq {}_{0.05}$) required level of accuracy

σ^2 = variance

L = maximum allowable sampling error (one direction).

RESULTS

The correlations between the cambial electrical resistance and the increment figures, and their levels of significance are listed in *Table 1*. With the exception of those for *Apodytes dimidiata*, all the correlations were significant. However, standard deviations were very high, up to 100 % of the mean.

The Spearman rank correlation coefficients between the resistance readings and diameter, crown form and crown position for trees at the Diepwalle and Witelsbos study sites are given in Table 2. The correlations between resistance and crown condition were much weaker (half of them were insignificant) than those between resistance and diameter, and between resistance and crown position.

Although the mean resistance readings for the control area at Witelsbos was slightly lower than that for the infested area (15,09 and 17,26 Kohm respectively), the difference was insignificant.

Results from the resistance measurements on *Rapanea melanophloeos, Acacia mearnsii* and *Rachospermae melanoxylon* are illustrated in *Figures 3* to *6*.

DISCUSSION

Although many of the correlation coefficients between cambial electrical resistance and increment (*Table 1*) were highly significant, the standard deviations were too high to use the relationships for predictive and management purposes.

Possible reasons for the unreliable relationships, whereas workers elsewhere obtained much better results (Davis *et al.*, 1981; Shigo and Shigo, 1974), are the following:

1. Increment is measured over a long period, whereas the resistance reading is taken at one point in time. Trees with relatively high increment rates might have lost their vigour shortly before measurement and *vice versa*.
2. Mean annual diameter increment rates for forests in the Knysna area range from 0,3 mm to 2,2 mm (J.C.

TABLE 1. Pearson correlation coefficients between cambial electrical resistance and basal area and diameter increment

Species	Sample size	Cambial electrical resistance versus			
		DBH increment 1972–1983	DBH increment 1972–1983	Basal area increment 1972–1983	Basal area increment 1972–1983
Podocarpus latifolius	74	−0,569**	−0,567**	−0,540**	−0,541**
Ocotea bullata	25	−0,383	−0,406*	−0,492*	−0,453*
Apodytes dimidiata	55	−0,076	−0,054	−0,410*	−0,211
Olea capensis subsp. *macrocarpa*	104	−0,555**	−0,385**	−0,583**	−0,503**

* significant at 5 per cent level of probability

** significant at 1 per cent level of probability

TABLE 2. Spearman rank correlation coefficients between cambial electrical resistance and diameter, crown form and crown position of trees at the Diepwalle and Witelsbos State Forests. The latter site was divided into a forest stand infested with the root pathogen, ***Phytophthora cinnamomi****, and a control, apparently pathogen free, stand*

Species	Location	Cambial electrical resistance versus DBH	Crown form	Crown position
Podocarpus latifolius	Diepwalle State Forest	−0,473** (74)	−0,483** (73)	−0,600** (73)
Ocotea bullata		−0,807** (25)	−0,239 (25)	−0,547** (25)
Apodytes dimidiata		−0,822** (55)	−0,221 (55)	−0,506** (55)
Olea capensis subsp. *macrocarpa*		−0,655** (104)	−0,565** (103)	−0,605** (103)
O. bullata – control area	Witelsbos State Forest	−0,935** (93)	0,212* (93)	−0,801** (93)
O. bullata – infested area		−0,925** (202)	0,116 (202)	−0,843** (202)

* significant at 5 per cent level of probability
** significant at 1 per cent level of probability

Numbers in brackets are sample sizes.

van Daalen, unpublished data). These slow growth rates can result in large sampling errors in diameter measurements (causing large standard deviations). This is shown in *Table 3*. On average 21 measurements are necessary to obtain a 1 mm accuracy (significant at 5 per cent level of probability) for diameter measurements. The normal way to overcome this problem is to measure a large number of trees, making mean values reliable. However, the predictive values for individual trees will remain low.

Contrary to the above the negative relationships between resistance readings and DBH and between resistance and crown position, both at Diepwalle and Witelsbos, were highly significant and reliable (*Table 2*). DBH readings are several orders larger than increment readings and are much less affected by sampling errors. The negative relationships indicate that taller trees with more exposed crowns yield lower resistance readings than smaller trees with sheltered crowns, indicating faster growth of taller trees (Davis *et al.*, 1981). This does not indicate the decreasing growth of old (senescing) trees (Phillips, 1931; Laughton, 1938; J.C. van Daalen, unpublished data), but the reason is not clear.

It was not possible to separate the apparent pathogen infested *Ocotea bullata* trees at Witelsbos from the healthy ones on the basis of the resistance readings. The slightly higher mean resistance for the infested trees can be attributed to chance. The difference is too small to attribute it to assumed slower growth of infested trees. No independent measure of the health of the trees besides the area in which they were growing, was available. Therefore, vigorous trees in the pathogen infested stand could obscure differences in mean resistance readings that

TABLE 3. Sample sizes needed for different accuracies of DBH measurements for different species (see text for equation used)

Species	Bark roughness*	Maximum allowable error (one-directional) 1 mm	2 mm	3 mm	4 mm	5 mm	6 mm
Podocarpus latifolius	medium	14	4	2	1		
Ocotea bullata	coarse	33	9	4	3	2	1
Apodytes dimidiata	smooth	16	4	2	1		
Olea capensis subsp *macrocarpa*	medium	20	5	3	2	1	
Mean		21	6	3	2	1	

* The bark roughness indicated applies to the measured trees only, e.g. although *O. bullata* bark is normally smooth, the specimens in the sample had coarse bark.

might have been significant if infested and healthy trees could have been separated individually.

As expected, resistance readings did indicate faster growth for *Rapanea melanophloeos* trees in forest than those among alien trees (*Figure 3*) whereas resistance readings for *Acacia mearnsii* and *Rachospermae melanoxylon* were in the same range (*Figure 5*), indicating similar growth rates. Similar graphs for resistance reading versus crown position (*Figures 4* and *6*) indicate higher growth rates for trees receiving more sunlight.

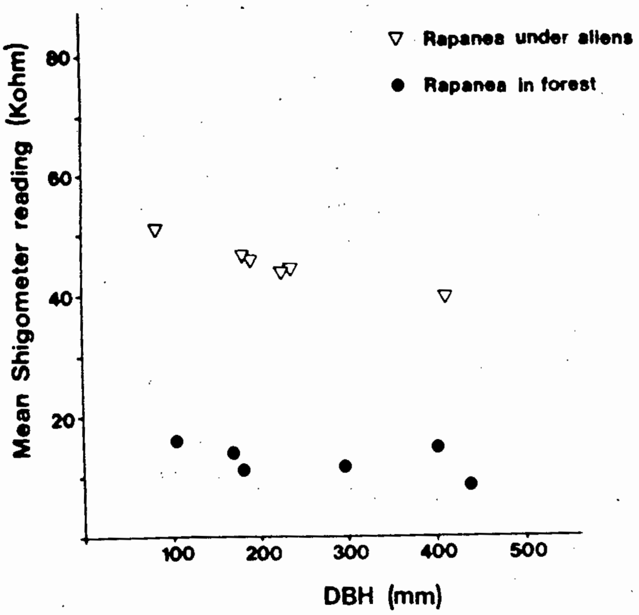

FIGURE 3. Scatter diagram of electrical resistance readings (measured with a Shigometer) versus DBH of Rapanea melanophloeos *trees in forest and under alien trees at Hogsback, eastern Cape.*

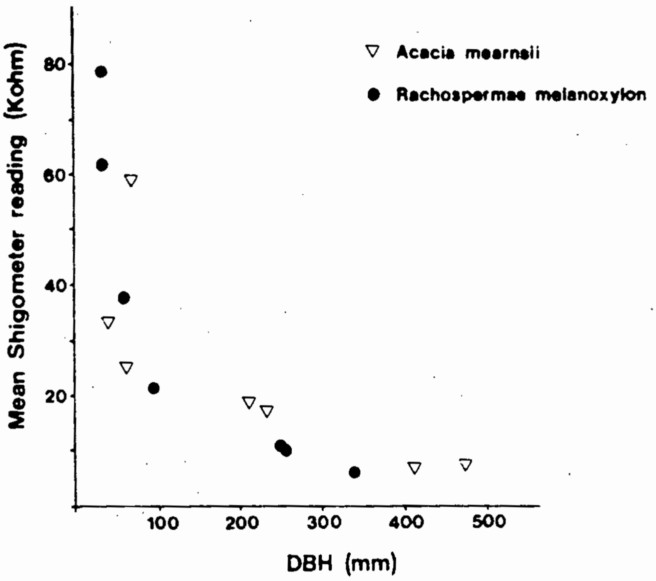

FIGURE 5. Scatter diagram of electrical resistance readings (measured with a Shigometer) versus DBH of Acacia mearnsii *and* Rachospermae melanoxylon *trees at Hogsback, eastern Cape.*

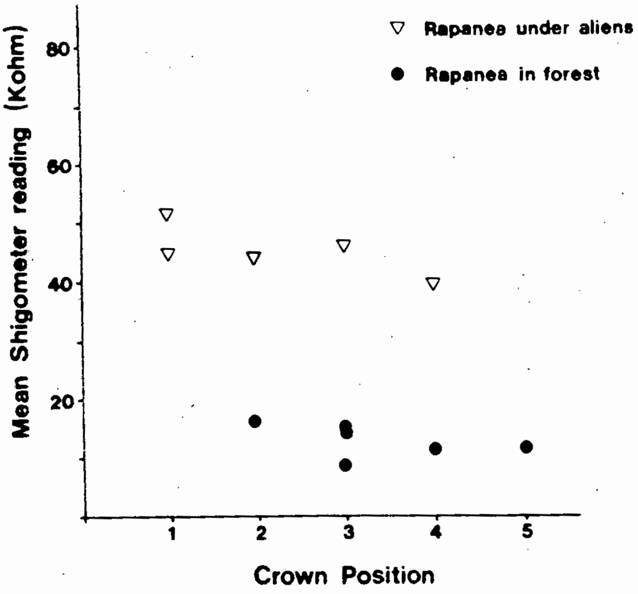

FIGURE 4. Scatter diagram of electrical resistance readings (measured with a Shigometer) versus crown position of Rapanea melanophloeos *trees in forest and under alien trees at Hogsback, eastern Cape.*

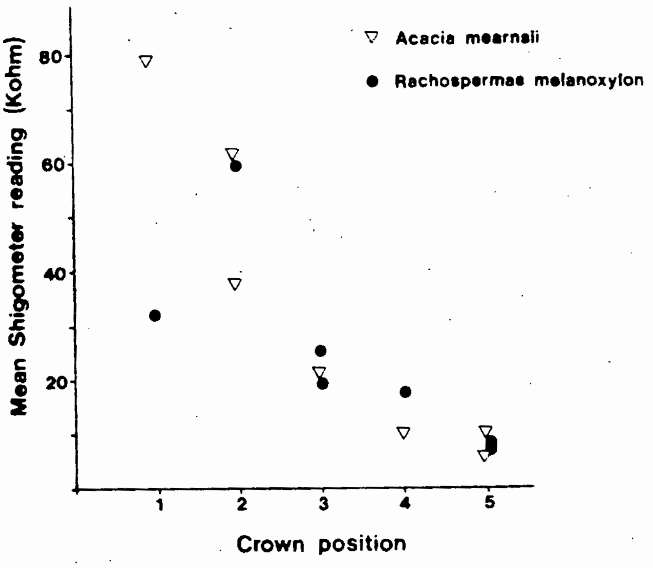

FIGURE 6. Scatter diagram of electrical resistance readings (measured with a Shigometer) versus crown position of Acacia mearnsii *and* Rachospermae melanoxylon *trees at Hogsback, eastern Cape.*

CONCLUSIONS

Given the problems with measuring growth and determining the pathogen infestation of individual trees, I could not prove that cambial electrical resistance readings could indicate growth rates of forests trees reliably (question 1); and that these readings could indicate which trees are affected by the root pathogen

CHAPTER 5

DATING OF TREES

Scientific Paper

Dating of *Pterocarpus angolensis* Trees

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SYNOPSIS

Samples of *Pterocarpus angolensis* collected in KaNgwane were dated by means of (a) the C^{14} dating method, (b) visual ring counting, (c) counting of rings on X-ray photographs taken from the transverse surfaces of samples cut from tree boles, and (d) by using radiation densitometry. C^{14} dating of some forest trees of known age provided accurate results. Therefore, the ages of the *Pterocarpus* trees determined in this way were accepted as correct. Visual ring counting and counting of rings on X-ray photographs is subjective and experience is necessary to provide reliable age estimates in these ways. C^{14} dating of trees is expensive and takes a few months to complete, but it is the most reliable method for dating tropical trees where growth rings are absent or indistinct. For those tree species where the denser areas on the transverse surfaces of the wood samples correspond to annual growth, gamma ray densitometric measurements provide reliable age estimates. In the case of *Pterocarpus angolensis*, the radiation densitometric system yielded poor results despite the fact that the wood of this species is semi-ring-porous and contains terminal parenchyma. However, alterations such as the use of a Fe^{55} isotopic source, which emits softer gamma rays that are better absorbed by wood, the use of thinner sections and measurements over smaller areas and intervals could improve the reliability of results considerably.

INTRODUCTION

Pterocarpus angolensis is one of the best-known, most generally used and most valuable savanna trees in tropical southern Africa. Its mechanical properties and attractive figure and colour make it one of the world's most sought-after timbers for furniture, building and high-class joinery (Vermeulen, 1990).

Under natural conditions successful germination appears to depend on fire (Edwards, 1981) and sufficient rain soon after seedfall (Van Daalen, 1991). Early survival of seedlings seems to be dependent on soil conditions and absence of fire for the first few years (Edwards, 1981). Personal observations suggest that grazing pressures can be very detrimental to the survival of seedlings. During later years frequent and hot fires can be beneficial to the fire resistant *Pterocarpus angolensis* saplings in that competition is removed by killing off the less resistant trees (Boaler, 1966). Most of these conditions are typical of shifting cultivation – areas with favourable soil conditions are cleared, fire and grazing are prevented and after the cessation of cultivation, grasses tend to grow temporarily more strongly than in the surrounding savanna, resulting in hot fires. These are the reasons for the belief that *Pterocarpus angolensis* is a weed of shifting cultivation (Von Breitenbach, 1973; Edwards, 1981). The present distribution of this species in South Africa in general is patchy, lacks a healthy size class distribution and regeneration is poor or absent (Van Daalen, 1991; personal observations). This could be the result of the cessation of shifting cultivation and the protection of natural areas. If tree ages can be determined, historical records on the agricultural practices could explain aspects of the present state of *Pterocarpus angolensis* in South Africa and provide clues to the sound management of this important timber species. Furthermore, if growth rates are known, harvest levels can be prescribed.

Boaler (1966) found that apparently no correlation exists between diameter and age, and that there is a great variability in the growth rates of individual trees. Diameter growth rate estimates vary from 10,69 mm/a for some trees in Zimbabwe (Groome *et al.*, 1957) to 5,4 mm/a in northern Namibia (Lückhoff, 1969), 5,28 mm/a at Gwaai in Zimbabwe (Groome *et al.*, 1957), 3,07 mm/a in Transvaal (Lückhoff, 1969), and 3,03 and 1,5 mm/a in Tanzania (Groome *et al.*, 1957).

The diameter growth rate estimates can be done either by remeasurements over long periods (e.g. the above-mentioned growth rate of 10,69 mm/a in Zimbabwe was determined over a 33-year period) or by dividing the DBH (diameter at breast height) by the estimated age. In most cases these age estimates were based on growth ring counts. According to Pierce (1982) *ex* Bryant (1968), discrepancies between known age and ring counts were found to be few, although the accuracy is impeded by the presence of bands of parenchyma and false rings resulting from defoliation by natural agents. Groome *et al.* *(1957)* added 10 years to cover establishment and growth to breast height. *Lilly (1977)* gave *Pterocarpus angolensis* a 2-rating on a dendrochronological potential scale ranging from -10 for the least suitable for dendrochronological usage to +13 for the most suitable species. This made it a weak "possible species" with many disadvantageous characteristics for dendrochronological usage.

Groome *et al.* (1957) suggested treatment with iodine and photography with appropriate filters to improve the visibility of growth rings of *Pterocarpus*. However, no references could be found on the application of these recommendations. Apart from ring counts, other methods used for age determination of trees include C^{14} dating, X-ray photography and densitometric measurements using gamma ray absorption (Woods and Lawdon, 1974).

The basic premise of radiocarbon dating is that the C^{14} level in the environment has remained constant over time. This is, however, not the case and over the past centuries considerable fluctuations have occurred, which often makes it difficult to derive a precise age from a C^{14} measurement, even though the analyses are very accurate. Thus a radiocarbon age for plant material in the southern hemisphere that lies between 100 and 240 years may correspond to as many as four different historical dates between AD 1670 and AD 1974 (Vogel, 1972; Vogel *et al.*, 1986, in press). In addition to this affect, environmental C^{14} in the atmosphere was increased significantly above natural levels after 1955 as a result of the nuclear weapon tests between 1954 and 1962 (Vogel, 1971). The subsequent gradual decrease in the artificial C^{14} content of the atmosphere makes it possible to actually date plants that have grown since 1964 to an accuracy of approximately one year by means of C^{14}. This contrasts with the limiting uncertainty of about 20 years for normal radiocarbon dating. Mozeto *et al.* (1988) used this artificial fallout to determine growth rates in the outer portions of tropical trees in the Amazon region. These data was then extrapolated to provide an estimate of minimum tree age.

Owing to the variations in the C^{14} level, radiocarbon dating of trees may involve considerable effort. The first step would be to date the inner annual growth rings of the trunk. If the age lies between 130 and 230 years, two or three further samples along the radius would indicate which of the possible historical dates apply to the core. Lacking this, other considerations may be used to arrive at the "most probable" age for the specimen.

During the formation of heartwood organic substances that are up to 20 year younger than the annual rings are deposited in the cells. This organic matter can significantly increase the C^{14} level of the sample and make it appear younger. The degree of this contamination depends on the species and is as yet not well known. To avoid this complication all organics that are soluble in acid and alkali are removed prior to analysis. In cases where this treatment is not adequate, pure cellulose can be prepared from the sample. This carbon definitely dates to a single year.

As gamma rays traverse matter they are absorbed exponentially according to the following equation (Malan and Marais, 1991):

$$I/I_0 = e^{-\mu t}$$

where:

I = intensity of radiation after passing through the sample (counting rate)
I_0 = intensity of radiation through air (reading through zero sample thickness) (counting rate)
μ = linear attenuation coefficient (cm^{-1})
t = thickness of sample (cm)

The value μ is dependent on the following:

$$\mu = \mu' D$$

where:

μ' = mass attenuation coefficient (cm^2/g)
D = density (g/cm^3)

I and I_0 for a wood sample of a given thickness is determined by the densitometer. These values are used to calculate μ whereas μ' is a material value. With both μ and μ' known the density of the wood can be calculated.

METHODS

Sampling

A few mature indigenous forest trees of known age were sampled in the Concordia arboretum just north of Knysna in the southern Cape. These were used to verify the accuracy of the C^{14} dating of trees. Subsequently, in 1990, *Pterocarpus angolensis* trees were sampled at three sites in KaNgwane: one next to the Mzinti Nature Reserve on the sandy Lebombo Flats north of Swaziland, one on the eastern side of Mananga Mountain in the Lebombo Mountain range, close to the village called Thambokhulu not far from the Mozambique border, and one in the Mthethemusha Nature Reserve in the granite mountains south-west of the Kruger National Park (Figure 1). Later a few samples were received from *Pterocarpus angolensis* stumps left after clearing a strip for a power line close to Boschfontein on the Lebombo Flats.

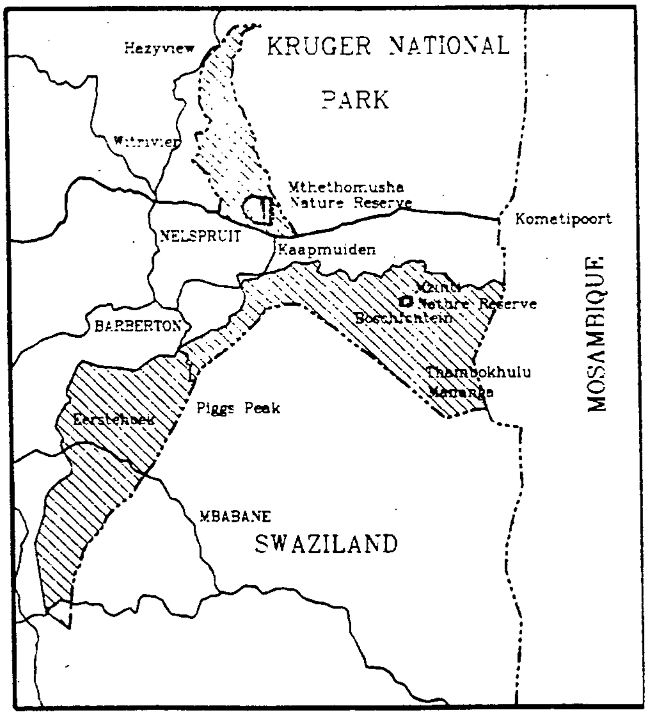


FIGURE 1. Location of study sites. The shaded area represents KaNgwane. Pterocarpus angolensis *trees were sampled for dating in the Mthethomusha Nature Reserve, next to the Mzinti Nature Reserve and on the eastern side of Mananga Mountain, close to Thambokhulu.*

Samples were collected as close as possible to ground level. In order to obtain a large enough sample for C^{14} dating the lower 30 cm of a bole was removed and divided into three discs for easier handling. The core of these discs (i.e. about the inner 10 rings) were removed and used for dating. This implies that the determined age of the tree will be the average date for the inner few rings. A further 10 cm disc was removed from the bole to be used for age determination by means of X-ray photographs and gamma ray densitometric measures.

Dating

The C^{14} dating was done in the Quaternary Dating Research Unit of the Division of Earth, Marine and Atmospheric Science and Technology of the CSIR in Pretoria. Before the discs were broken up to remove the core for dating, we counted the visible rings.

Cylinders with diameters of about 20 mm were cut from the core of the discs to give 25 g of wood for the C^{14} analyses. All the samples were rigorously treated with diluted acid and alkali to remove soluble organics before combustion to carbon dioxide. The gas was measured in a large volume high-precision proportional counter for several days and the results were corrected for variations in the initial isotope ratio of the carbon.

To test the consistency of visual growth ring counting, rings on some smaller samples were counted by two different people, both with no experience of ring counting on this species.

Various X-ray exposures were needed to make the growth rings in the sapwood and heartwood visible. Furthermore, the thicknesses of the discs used for these photographs varied somewhat. Therefore, a series of X-ray photographs were taken from each sample and printed on one sheet to enable direct comparison among the different exposures. The photographs (= negatives) were placed on a light table to count the growth rings.

Densitometric determinations were carried out at air-dry moisture content using a system developed recently by the Division of Forest Science and Technology (Malan, 1991). Three collimator sizes were used. Two provided rectangular beams (10 × 0.25 mm and 10 × 1 mm) with the smallest dimensions in the radial direction, and the third one provided a 1 mm diameter circular beam. Count rates were recorded from pith to bark for 10 seconds per measuring point. These points were 0.2 mm apart for the 10 × 0.25 mm rectangular beam collimator and 1 mm apart for the two other collimators.

For the densitometric scanning strips of 20 × 20 mm were cut along two radii from some of the discs and air-dried. To avoid any burning of the wood sample and to provide smooth surfaces and strips of uniform thickness in the traverse direction of the rays, carbide tipped saw blades were used to cut these samples.

Radial variation in density was plotted and the peaks (i.e. the denser areas) counted as estimates of the number of annual rings. For those samples where readings were taken at 0.2 mm intervals, the X-axes were exaggerated and a series of graphs prepared to enable the more accurate counting of the peaks.

RESULTS

The C^{14} dating of the indigenous forest trees from the southern Cape were very close to their real ages (*Table 1*). This proved the reliability of this dating technique, at least within a time frame of about 100 years.

TABLE 1. C^{14} ages of indigenous forest trees from the Concordia arboretum, southern Cape. All three trees were planted between 1897 and 1900, i.e. they were 90 to 93 years old.

Species	**Calibrated C^{14} age (year)**
Curtisia dentata	80-100
Podocarpus falcatus	80-100
Ocotea bullata	90

The results from the different age determinations on *Pterocarpus angolensis* are listed in *Table 2*. The first sample, No. 17(Mt), had a C^{14} content of 49 % above normal. On the conventional C^{14} age scale this corresponded to a "negative" age of -3 203 ± 16 years. However, when this derived age was corrected for the increased atmospheric C^{14} levels resulting from nuclear weapon tests, the resultant age was 22±4 years in 1990. This is a good agreement with the visual ring count of 25 years. Sample 18(Mt) showed a slightly elevated C^{14} content, 2.2 % above normal, or -164±24 years old, suggesting a calibrated germination date of around 1956. The same result could also be obtained if the tree was actually older but the corewood contained a small amount of post-1954 carbon. To check this possibility, pure cellulose was prepared from a further 40 g of corewood and analysed. This material gave an age of 160±18 years BP (Before Present, i.e. before 1950), which calibrates to AD 1930, 1818 or 1710. Since the deposition of younger organics in the wood cells is unlikely to take place for more than 40 or 50 years after the rings are formed, it can safely be concluded that the tree started growing in AD 1930±5 or 60 years ago. The derived age again compares well with the ring count of 57.

Two other samples, No. 19(Mt) and 16(Mz), also showed slightly elevated C^{14} levels or "negative" ages, indicating that they started growing before 1957. For the same reason as that given above the ring counts can thus in all probability be accepted as approximately correct.

The rest of the samples all gave "positive" C^{14} ages of between 71 and 152 years. The oldest, No. 3(Ma), calibrated to AD 1710, 1820 to 1880 or 1926. The visual ring count for this specimen of 116 suggests that the tree started growing in 1874 so that the 19th century date seems the most acceptable, viz. 140±30 years old. The youngest C^{14} age obtainable in the prenuclear bomb era is about 100 years. This age corresponds to AD 1900. The remaining samples that were dated in this way had an average C^{14} age of 101±15 years, which indicates that the results are compatible with the hypothesis that these trees started growing in about AD 1900. The visual ring counts for these 10 specimens is 113 years – slightly more than the age of 90 years inferred from C^{14}.

Although unlikely, the possibility remains that organic compounds produced during the past 30 years did find their way to the core of boles of the older (i.e. ≥ 90 years) trees, causing C^{14} dates that appear too young. To test this, pure cellulose was prepared and analysed from the core of sample No. 7(Mz), which yielded the highest visual ring count. The result was 143±19 years BP, 34±25 years older than the standard analysis of 109±17 years BP. Although the difference is

TABLE 2. Results from different age determinations on Pterocarpus angolensis *samples collected in KaNgwane. The suffices to the sample numbers indicate the sites where the samples were collected: Mz = Mzinti, Ma = Mananga Mountain, Mt = Mthethomusha Nature Reserve and Pl = power line at Boschfontein. The conventional radiocarbon ages are given in years BP (Before Present, i.e. before 1950). The core of sample 10(Mz) was very acentric and rings were counted along the shortest and longest radii. For sample 15(Mz) two different strips were used for densitometric measurements using the 1* mm *circular beam*

Sample number	**DBH (mm)**	**Conventional C^{14} age (years BP)**	**Calibrated C^{14} age (years)**	**Visual ring count**	**X-ray ring count**	**Gamma ray densitometric measurements**		
						Rectangular beam, 0,2 mm intervals	**Rectangular beam, 1 mm intervals**	**Circular beam, 1 mm intervals**
17 (Mt)	127	-3 203 ± 16	18	25	16			
18 (Mt)	266	160 ± 18 (-164 ± 24)	60 ± 5 (>33)	57				
19 (Mt)	213	-48 ± 24	>34	57				
3 (Ma)	434	152 ± 21	140 ± 30	116				
4a (Ma)	314	128 ± 21	90	103	57			
4b (Ma)	360	84 ± 18	90	133	72			41
5 (Ma)	240	94 ± 22	90	140	65			
6 (Ma)	270	103 ± 21	90	82	68			31
16 (Mz)	274	-180 ± 24	>33	64	38			
7 (Mz)	450	109 ± 17	90	166	107			
8 (Mz)	432	75 ± 15	90	141	62			
10 (Mz)	367	106 ± 21	90	45 & 81	54 & 68			
11 (Mz)	377	113 ± 21	90	75	95			
13 (Mz)	317	100 ± 19	90	88	62			
15 (Mz)	410	99 ± 22	90	118	83			47 & 41
1 (Pl)						52	21	
2 (Pl)						101	33	29
3 (Pl)						99	42	40
4 (Pl)						111	40	
5 (Pl)						98	39	

not statistically significant, it may indicate some translocation of organics in the stems of this tree species. If so, the actual tree ages would be somewhat older than 90 years. Further investigations would be required to establish the magnitude of the contamination that can take place.

Although the correlation between DBH and the C^{14} dates was highly significant (*Table 3*), the discrepancies were too large to use DBH as an indication of age (*Table 2*). The C-ray ring counts correlated slightly better with the C^{14} results than the visual ring counts. The correlation between the visual and C-ray ring counts was just below the 5 % level of significance.

TABLE 3 Spearmann correlation coefficients for DBH and various aging techniques for Pterocarpus angolensis

Variable 1	**Variable 2**	**Correlation coefficient**	**Probability > |r|. $H_0: \rho = 0$**
DBH	C14 date	0.717	0.003
C^{14} date	Visual ring count	0.591	0.043
C^{14} date	X-ray ring count	0.652	0.022
Visual ring count	X-ray ring count	0.571	0.053

The visual ring counts of smaller *Pterocarpus angolensis* samples by inexperienced people provided very divergent results (*Table 4*). This indicates that degree of subjectivity present when determining the age of this species in this way.

The densitometric density variation, as determined at intervals of 1 mm, is given in *Figure 2*. For those samples where readings were taken at intervals of 0.2 mm, the X-axes were exaggerated and a series of graphs plotted, covering successive parts of the discs' radii analysed (*Figure 3*). Only relative densities are of importance here, the density values on the Y-scale of the graphs have been omitted.

TABLE 4. Growth ring counts of Pterocarpus angolensis *samples done by two different people. The number of figures reflect the number of radii of a samplee counted by a particular person*

Sample number	Number of growth rings as counted by	
	Person 1	Person 2
1	15	33
2	15	31
3	14, 13, 14, 12	25, 21, 22
4	14, 15, 12, 14	18, 25
5	11, 14, 14, 13	34
6	5, 5, 5	14
7	6, 7, 6	15, 14
8	9, 9, 9	15
9	3, 4, 5	10
10	4, 5, 4, 3	10
11	7, 8, 7	21, 19

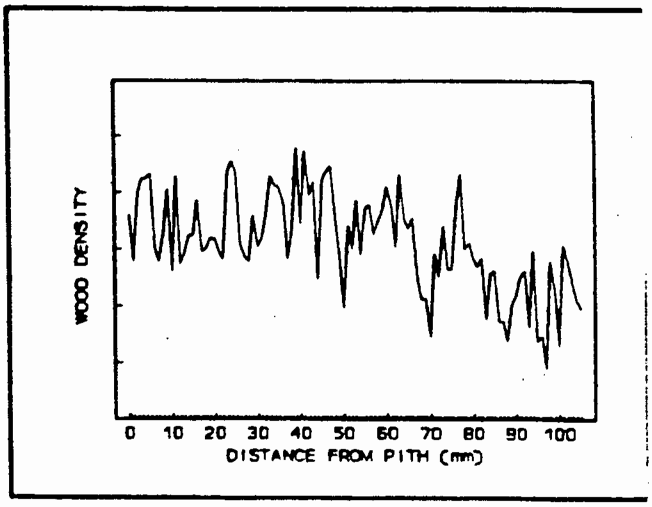


FIGURE 2. Results from gamma ray densitometric measurements on Pterocarpus angolensis *sample No. 2(P1), using the collimator with a round hole and measuring at 1* mm *intervals. All peaks were taken as representing growth rings*

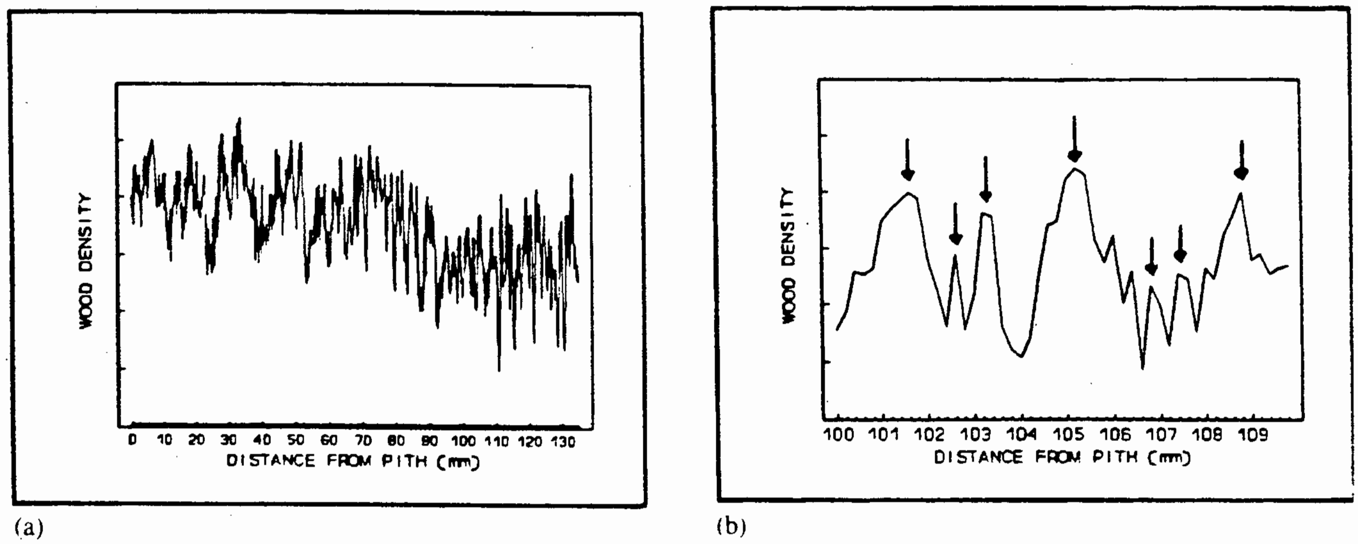


FIGURE 3. Gamma ray densitometric measurements on Pterocarpus angolensis *sample No. 5(P1). The collimator providing a rectangular 10 × 0,25* mm *beam was used and measurements taken at 0,2* mm *intervals (a). To enable the counting of peaks in the graph the same data were plotted as a series of graphs on a drawn-out X-axis. Only a small portion of the total data is represented in (b). Seven growth rings were counted on this portion of the graph (those taken to represent a year's growth are marked with an arrow)*

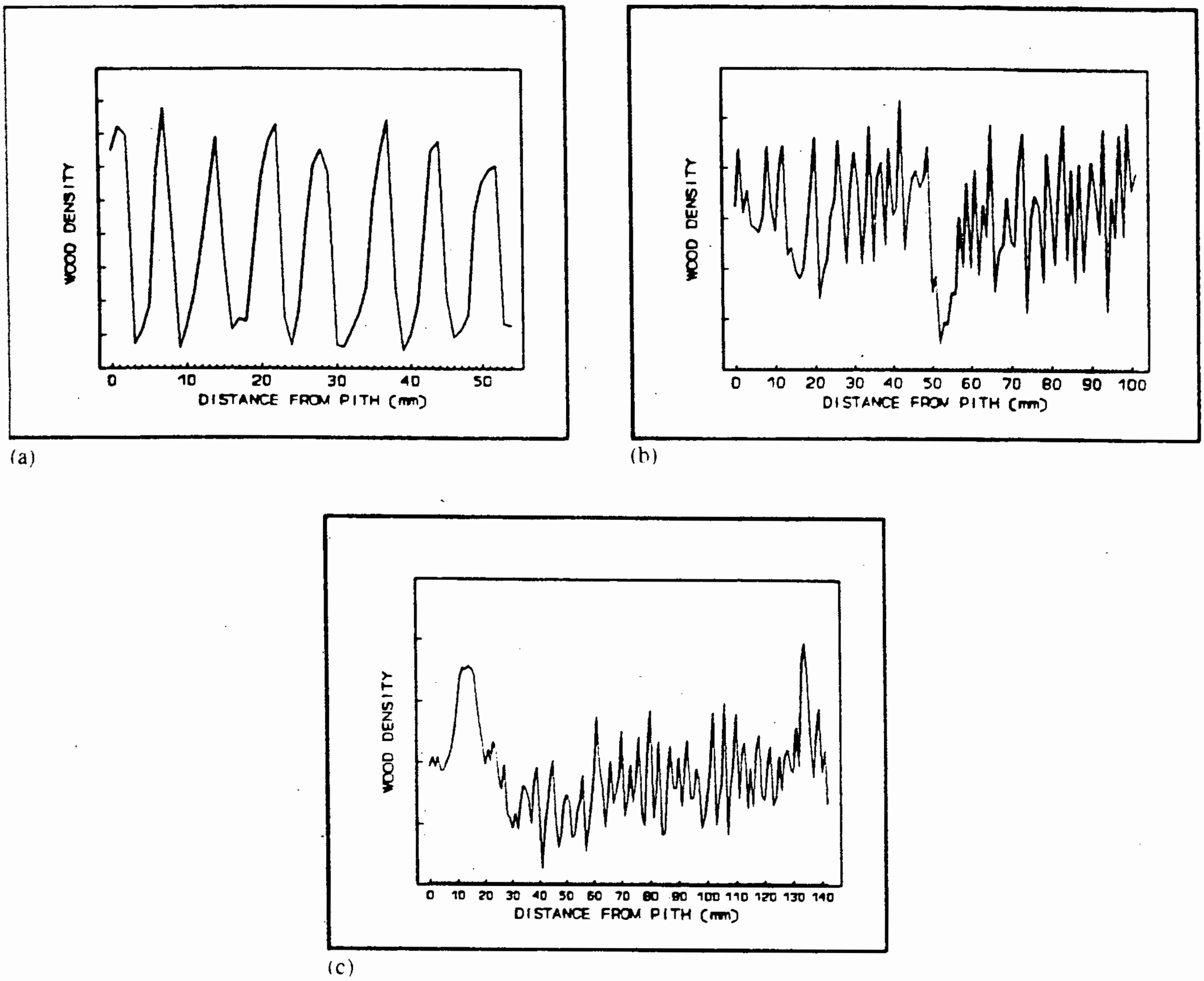
For comparison, samples from three other species with distinct annual rings were scanned by the densitometer from pith to bark taking measurements at intervals of 1 mm (*Figure 4*). In these cases visual ring counts agreed precisely with the peaks in density values indicated by radiation densitometry. This confirms the reliability of radiation densitometry provided rings are demarcated by latewood zones of higher density.

If the C^{14} dates are accepted as correct, densitometric measurements, using the existing system, did not provide an accurate estimate of age (*Table 2*). Although a 10 × 0,25 mm rectangular beam enabled the scanning of samples at very small intervals, the curvature of the rings and the misalignment of the aperture with the growth rings, as well as the fact that the grain of the wood often did not run parallel with the radiation path, caused poor resolution which made it very difficult to detect ring boundaries if present. The use of the 1 mm circular beam solved the problem of ring curvature but the larger beam size gave poor resolution for the very narrow rings, (*Table 2*). It also did not solve the problem of grain deviation from the radiation path despite the fact that the samples were later reduced in thickness to 10 mm.

CONCLUSIONS

At present C^{14} dating seems to be the most reliable method of estimating the age of *Pterocarpus angolensis* trees in the time-range of a few hundred years, provided that the measurements have a high enough accuracy (with an uncertainty of ≤ 25 years). Adequate care must be taken with the chemical pretreatment of the material.

Visual ring counting and ring counting from X-ray photographs are subjective as a result of the indistinctness of these rings. It is often difficult to decide whether or not an apparent



(a) (b) (c)

FIGURE 4. Gamma ray densitometric measurements on samples of Pinus *(a),* Robinia *(b) and* Populus *(c). The collimator providing a rectangular 10 × 1* mm *beam was used and measurements were taken at 1* mm *intervals.*

ring is real and should be counted. Experience is necessary to provide reasonable age estimates of this species using these methods and precision cannot be claimed. Groome *et al.* (1957) described the species as ring-porous, i.e. not very distinct but sufficiently so to be counted over a wide radius. According to them the growth rings are marked on the end surface by a band of terminal light-coloured parenchyma and by a zone in the early wood with a few distinctly larger and widely spaced vessels. The latewood zone has fibres with thicker walls and fewer vessels.

In the samples investigated the parenchyma and larger vessels were often not arranged in visible bands. Where some stratification could be detected, the rings seem to disappear and re-appear on the transverse surface. This caused very divergent results when counting rings on different radii of the same disc cut out of a bole.

The major disadvantages of the C^{14} dating technique are the high costs (about R800 per sample) and the time needed for the analyses (about four months). It does, however, provide a reliable technique for dating tropical trees, which in turn provides the basis for harvest control in forest areas where more detailed growth data are not available. With tree ages known, mean growth rates can be calculated and harvest levels determined to ensure sustained timber production.

Various researchers have proved that gamma ray densitometry is a reliable and relatively cheap method for tree ring analyses for species with distinct growth rings (Kanowski, 1985; Moschler and Dougal, 1988). Since *Pterocarpus angolensis* is semi-ring-porous with reasonably well defined terminal parenchyma it should be possible to detect the density differences caused by the presence of these anatomical features. It would, however, be necessary to reduce beam size to at least 2.0 mm × 0.1 mm. In this way, the effects of ring curvature and ring misalignment will be reduced too. Thinner samples will have to be used (preferably less than 5 mm thick) to reduce the effect of grain deviation from the radiation path. This will, in turn, require a radiation source that emits softer rays, such as Fe^{55}, to obtain the required absorption by the thin samples and to estimate density accurately. Such alterations to the existing system are being planned at present.

The similar ages of the trees sampled on the Lebombo Flats and on the Mananga Mountain is difficult to explain. In the Mzinti area this could be related to the presence of old fields. Unfortunately aerial photographic records do not go back very far. The area around the village Thambokhulu is cultivated today, but the *Pterocarpus* trees occur only on the rocky mountain slope, which is unsuitable for cultivation. Therefore, a more likely explanation would be the occurrence of fires before seedfall and above average rainfall soon afterwards (Van Daalen, 1991). Grazing could also play a pronounced role in eliminating regeneration.

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SECTION 3

EVALUATION AND CONCLUSIONS

EVALUATION AND CONCLUSIONS

MODELLING FOREST SUCCESSION

Most regression models on forest growth explain growth directly in terms of other observations such as DBH, basal area, soil type and rainfall. Despite the fact that these regression equations suggest possible theoretical models, in itself they normally have little theoretical foundation. Often they are only the first step in formulating a theory (Bragg and Henry, 1985).

Forest growth models are really developed to compute outcomes for situations not actually represented in the data base. For this purpose, regression models have limited application. With these models extrapolation beyond the limits of the available data can easily lead to erroneous conclusions. Models which are constrained by tested and reasonable theories should be more reliable in extreme behaviour than models based on regressions alone.

The OUTENIQUA model reflects the reductionistic approach to succession. It yielded satisfactory simulations of measured short term (i.e. 15 year) forest growth and seemed to reflect the longer term forest dynamics reasonably well. Although it could best be described as an ecological model which attempts to describe and predict long-term successional behaviour in the southern Cape forests, it is capable of producing sustained yield calculations. It is written in such a way that it can be modified relatively easy to reflect another succession theory and results of the modified model could then be compared with the present simulations.

The time scale for which a model is developed is of paramount importance. When one is interested in evolutionary time scales, one's modelling approach will differ substantially from the case where one is interested in succession denoted by the recovery of the forest after natural tree falls or managed logging operations designed on a sustained yield basis where individual trees are marked and the forest canopy is not unduly disrupted. The OUTENIQUA model was developed with the latter approach in mind.

Scale of mechanism is equally important for model development. For example, biomass increase of a disturbed forest that is growing back can be considered at the photosynthesis level within a leaf, or at the larger mechanism scale of stomata controlling the energy balance of the leaf, or at the scale of leaf geometry, where the shape and orientation of the leaf can have a pronounced effect on the ability of the plant to take in CO_2 for photosynthesis while giving up little H_2O. At a still larger mechanism scale vertical light extinction as a result of the orientation and layering of leaf layers of the tree can be considered, and finally, the tree effect of shape on the horizontal light extinction can be contemplated. Any of these mechanisms can be important over some time scale. All of these mechanisms cannot be included in a single growth model. For instance, it is impractical to consider the growth of a large tree by simulating the energy balance of each individual leaf on that tree, for the number of interactions among the leaves increase as a function of the square of the number of leaves (Shugart, 1984). The OUTENIQUA model simulates tree birth (by considering sprouting, seed production, seed dispersal, seed phenology, seed longevity and germination), diameter and height growth of trees (as a function of tree size, leaf area and crowding from other trees), competition (as a function of shade tolerance, available light, and density and species composition of tree groups) and mortality of individual trees. The small mechanism scale photosynthesis and energy balance of individual leaves are, therefore, absorbed into the model parameters such as tree size, leaf area and available light. In this model seedling recruitment plays an important role because it determines which species will increase or decrease over several tree generations. In a model of a commercial plantation, seedling recruitment will probably not even be considered. Plantations are initiated with a given number of seedlings planted on some fixed spacing. Therefore, the level of detail in different models cannot be taken as a criterion for using the one and not the other for a particular situation.

For the purposes of this study the OUTENIQUA model served, and succeeded, as a research tool in that it was directed towards summarising existing information on the southern Cape forest dynamics and identifying inadequacies. Research topics (of which some were addressed in this thesis) could be identified and a context provided for the studies on forest dynamics and biology in the southern Cape forests. During the model development much data was inferred from general experience, such as what we think the maximum age a trees of a specific species would be, what we think the maximum height would be, do we think the tree will sprout when felled etc. To compile the data used for the model, I had to sit for days with my colleagues to discuss their experience on every variable for every species used - very similar to the process necessary to develop an Expert System on a specific topic. This in itself was a very valuable and enriching exercise and probably highlighted gaps in our knowledge more than anything else. Often we think that we know something until somebody starts asking us specific questions about it.

When evaluating any growth or succession model it must be remembered that it can only represent a limited part of the processes and dynamics of a forest. "Even where the model works, it is intended only to be sufficient as a caricature of reality, rather than necessary as a mechanistic explanation" (Horn, 1981). It can never replace the scientifically trained, experienced and commonsense forest ecologist or forest manager and it can never be more than a tool developed by people with imperfect understanding of the total forest processes and dynamics.

FOREST GROWTH AND SUCCESSION

The forest growth observed on the study area is slow when compared to for example that of *Pinus radiata* D. Don. plantations (with a mean annual increment of about 15 m^3/ha) in the same area. However, the gross rate of 2 m^3/ha per annum appears to be comparable to those of tropical and subtropical forests elsewhere in the world. If this apparent global uniformity of growth rates could be confirmed it could be a unique opportunity for the refinement and standardisation of forest succession models such as OUTENIQUA. Then these models could be applied on a much wider scale with much less laborious and time-consuming calibration than at present.

Many aspects of the observed growth and mortality rates could be explained in terms of the developmental phases of the forest as described by Bormann and Likens's (1979) model of biomass accumulation. It was concluded that growth rates are declining and mortality rates are increasing, indicating competition for space and other resources. Some species, such as *Curtisia dentata* (Burm. f.) C.A. Sm., *Gonioma kamassi* E. Mey., *Pterocelastrus tricuspidatus* (Lam.)

Sond., *Podocarpus latifolius* (Thunb.) R. Br. ex Mirb. and *Cassine papillosa* (Hochst.) Kuntze are favoured by this situation and are increasing their numbers relative to other species, whereas recruitment rates of *Olinia ventosa* (L.) Cufod., *Ocotea bullata* (Burch.) E. Mey., *Olea capensis* (L.) subsp. *macrocarpa* (C.H. Wr.) Verdoorn and *Apodytes dimidiata* E. Mey. ex Arn. are less than their mortality rates.

Two questions need to be asked at this stage: First, is the southern Cape forest succession predictable, and secondly, is it directional? Gómez-Pompa and Vásquez-Yanes (1981) state that it is impossible to predict what the regeneration process (and consequently succession) for rain forest in Mexico will be in the next hundred years. Franklin and Hemstrom (1981) found the same unpredictability in the species composition in the early successional stages of coniferous forests of coastal northwestern America. In both cases the only predictable succession was on the physiognomic scale. Cottam (1981) mentioned that the only succession that appeared to be predictable at the species level is in the arctic, an extreme climatic area. Because of their failure to define floristic vegetation changes Gómez-Pompa and Vásquez-Yanes (1981) emphasised growth rates, seed size, seed dormancy, tree geometry and shade-(in)tolerance. In the tropical Mexican forests they were studying there were so many species capable of filling a particular niche that they had to place the accent on physiognomy and tree physiology.

To a large extent this is true of the southern Cape forests too, at least the medium-moist forest type studied. As such most sites are suitable for most species. Certain trends have been observed during the study period, but it is impossible to predict the long-term species composition of a particular stand. This phenomena is reflected in the OUTENIQUA model in that species are selected at random to recruit on a given site. After selection of a species it is subjected to various establishment criteria before incorporating it in the simulated forest development. With our present understanding of the forest ecosystem we cannot define or describe all the "random" aspects of forest development and have to maintain stochasticity to smaller or larger degrees in forest models. The beauty of the modelling approach followed in this study is that these "undefinable" aspects are arranged in separate subroutines in the model, allowing forest scientists to research these aspects in a structured way and to incorporate every newly discovered part of the total jigsaw puzzle into the model without redoing the whole simulation. The latter would be necessary for a regression model.

The second question, that of (uni)directional succession, normally implies that succession leads to a climax. I am aware of the fact that the term "climax" is very fuzzy, and in some circles it is considered close to a swear word. For our purposes I will define it as the stable community which will be perpetuated indefinitely, provided the environmental conditions remain constant and human interference (such as agriculture and man-made fires) could be eliminated. Apart from the interminable time span needed to determine whether or not a particular plant community is the climax, it will be very difficult, if not impossible with our present understanding, to determine the floristic climax for a particular site in the southern Cape, be it forest or any other vegetation type. The general view seems to be that succession proceeds from shade-intolerant to shade-tolerant species, and from small, herbaceous species to trees, if the climate will support trees (Cottam, 1981). Yet there are postulated exceptions to this conviction. Assuming that forest is the vegetative climax (and this would be open to debate) for the southern Cape under the present climatic regime, from the above it should be clear that we would not be able to predict this climax beyond the physiognomic scale.

This now leaves the manager with a dilemma. What must his long-term conservation goal be? Must he manage the forests in such a way that the *status quo* is maintained? Can he maintain the *status quo*? Or must he aim at allowing the forest to develop? And if so, develop to what? And how must he manage the fynbos areas under his control? Is the fynbos the vegetative climax, or is it simply maintained as such by fire? To be practical, I think the climax concept should not be part of the forest management goal for the southern Cape, except perhaps for small areas where the forest appears to be disturbed, such as some of the fynbos "islands" (Midgley and Bond, 1990; Van Daalen, 1981). Rather follow a conservative management approach and aim to maintain the present physiognomic *status quo*, but closely monitor the long-term changes in species composition (on sufficient permanent sample plots) and adjust harvesting practices as soon as any detrimental trends (in terms of recruitment, growth and mortality) are observed. Guard against a too pragmatic approach where the rate of changes of management styles do not allow proper evaluation and follow-up of management activities, as has been the case to some degree in the southern Cape.

COMPETITION AMONG TREES

Results from the competition study (chapter 3) indicated that both inter- and intraspecific competition do play significant roles in the forest dynamics. However, it does not apply unconditionally to all species interactions. *Pterocelastrus tricuspidatus* and *Apodytes dimidiata* did not compete with each other. *Curtisia dentata* inhibited the growth of *Podocarpus falcatus* (Thunb.) R. Br. ex Mirb. and *Pterocelastrus tricuspidatus* only to a limited extent. Furthermore, the most abundant tree species, *Olea capensis* subsp. *macrocarpa*, exhibited weaker than expected competition with other trees. Both *Curtisia dentata* and *Apodytes dimidiata* (a weak interspecific competitor) showed strong intraspecific competition, whereas *Ocotea bullata*'s growth rate was increased by the presence of other individuals of the same species.

In the OUTENIQUA model the primary assumption is that trees compete primarily for light. This is in accordance with the general view that succession proceeds from shade-intolerant to shade-tolerant species (mentioned above). With this I do not imply that light is the only driving force in competition for the southern Cape forests. To the contrary. However, at present light is the easiest means of defining competition for simulation purposes. Other competition factors are treated as stochastic features, such as the chance of a particular species being available as seedlings or sprouts immediately after a disturbance. It must be realised that most species can grow on a much wider range than they actually occur. However, each species is found where it can compete successfully with the other species present. If a dominant *Olea capensis* subsp. *macrocarpa* tree, with its heavy crown dies, the chances are greater that another species will take its place than a tree of the same species. This will depend on the availability of a particular species to occupy the gap. The first tree that can utilise the increased light levels will have the competitive advantage over the other trees.

Small gaps are of vital importance in the evolution of these forests. As in the case of most tropical and subtropical mixed evergreen forests, catastrophes capable of creating large gaps (such as fires) are so rare that it would have little or no evolutionary significance. Furthermore, despite very low light levels, regeneration of many species can persist on the undisturbed forest floor for many years. Most of the light reaching the forest floor is in the form of sunflecks. In undisturbed Australian rain forests light levels are often as low as 1 % or less of that in the open. The light intensity at the centre of small flecks is often surprisingly low and sometimes sunflecks do not appear to provide sufficient energy for the growth of any plants except specialised understorey species (Stocker, 1985). Under these circumstances most regeneration will eventually die off in the absence of disturbances. However, normally there are enough seedlings and saplings that can "hang on" long enough to utilise the increased light levels following the death of one or more trees. This strategy appears to be, apart from obvious competitive advantages it provides, a response to the greater relative significance of seed predation compared to herbivory (Stocker, 1985). Thus, for both growth in small gaps and survival on the forest floor beneath an undisturbed canopy, a degree of shade-tolerance is required of most of the tree species which could be expected to occur in the typical forest assemblages. Most of the trees in the southern Cape are shade-tolerant. This also implies that they can grow in close proximity to other trees, despite the fact that the growth rate of various species is retarded by competition. This fact is emphasised by the observation that the distances between competing and non-competing trees were similar. Although this is most probably an artifact of the stocking density of the forest, it could in part explain why trees of equal size in natural forests can have vastly different ages.

The results from the study on competition indicated that the two *Podocarpus* species have the ability to increase their numbers. These species were very popular for furniture, building and railway sleepers and were heavily over-utilised in the past. Their survival can probably be attributed to their competitive abilities. Today *Podocarpus latifolius* is one of the more abundant tree species in these forests. The study confirmed results from other studies (e.g. the growth study reported in chapter 2) that the forests are in a late successional stage (judged physiognomically), and it indicated that the present management approach of harvesting trees that would probably die before the next harvesting cycle is a sound one.

TREE GROWTH INDICATORS

Having a forest growth model, knowing the average growth rates of trees in a particular forest stand, having determined the successional stage of the forest, being aware of the importance of avoiding large gaps in the forest canopy and knowing which trees and tree species compete, does not help the forest manager much in selecting specific trees for harvesting. He needs some practical criteria for selecting the harvest. For this reason the next logical step in this study was to determine tree growth indicators.

Crown position proved to be a useful growth indicator for the canopy tree species in the forest (see chapter 4). Crown form correlated positively with most of the canopy species tested, as well as with a number of subcanopy species. These results could, however, not be applied unconditionally. *Ocotea bullata*'s growth, for example, was affected by its crown form, but not by its crown position. Although the tree grows well in the shade of others, it still needed adequate foliage to photosynthesize sufficiently. On the other hand, *Olinia ventosa*, one of the most pioneer-like trees in the forest, is much more dependent on growing in full sunlight than on the form of its crown.

Cambial electrical resistance readings, measured with an instrument called a Shigometer (after its inventor, Dr Alex Shigo), proved to be of little use for management purposes. Standard deviations of the measurements were too high to use any relationships between cambial electrical resistance and tree vigour for predictive purposes. Much more thorough experimentation and plant physiological studies will be needed to make this instrument practically useful. As early as 1976 Newbanks (*ex* Tattar and Blanchard, 1977) tried out a similar instrument for determining tree vigour. He calculated the correlation between electrical resistance readings and visual crown classification (as an indication of tree vigour) of sugar maple in the United States of America, but found little or no relationship. This could have been expected in the light of the limited reliability of visual assessments of tree crowns as indicators of tree vitality. However, linking electrical resistance readings in the outer wood and cambium layers of trees with the presence of diseases such as fungal infections, cold temperature injury, discolouration and decay, root rot, vascular wilt disease, air pollution injury, cankers and proliferation disease, proved to be more successful and seems to be the only usable application of relative electrical resistance readings in wood tissue (Newbanks and Tattar, 1982; Tattar and Blanchard, 1977).

DATING OF TREES

One of the most complicating factors in (sub)tropical hardwood forest management is the difficulty of determining a tree's age. Should this have been possible it would have been a relative simple exercise to calculate growth curves for the main timber species on different sites and harvest them at the point in their life cycles where growth rates start declining. Lilly (1977) classified a large number of South African indigenous trees according to their dendrochronological potential. According to him the ages of several southern Cape forest tree species could possibly be determined with some kind of reliability. The savanna hardwood, *Pterocarpus angolensis*, is classified as a tree species with a better potential for dendrochronological work than most of the forest hardwoods. Therefore, when the opportunity arose to obtain a large enough sample of *Pterocarpus* stumps for this purpose I grabbed it with both hands. It would be easier to develop aging techniques on *Pterocarpus* and then apply them to the forest trees than to work on tree species with very little or no visible growth rings only.

All the ring counting techniques (chapter 5) proved to be subjective and considerable experience was necessary to obtain reasonable results. C^{14} dating is expensive and it takes a few months to complete, but is the most objective and reliable method for dating hardwoods where growth rings are absent or indistinct. Due to the cost of this technique (about R800 per sample) it is not a method to apply indiscriminately. However, if the real cost of long-term growth measurements in forests would be taken into account, R800 per sample becomes less prohibitive. Add to this the relative short period needed for determining the mean growth rates (as compared to long-term measurements) and C^{14} dating becomes a viable management technique, especially for extensive forest management over large areas, as is the case in many of the tropical countries. Deforestation and mismanagement in some of these countries is so widespread that there is no time left for long-term measurements on permanent sample plots.

CONCLUDING REMARKS

The modelling and follow-up approach followed in this study, i.e. the development of a deterministic distance-independent individual tree model, followed by the verification of assumptions made during the modelling process, provides a framework for a systematic and management orientated study of mixed forests. The present world-wide economic situation is the cause of dwindling research funding, and the luxury of research for the sake of research cannot be afforded any more. Researchers are forced to spell out the practical benefits of their (intended) research more and more clearly. To do this and to convince the financing bodies that their money will be well spent research motivations must be presented in a logical way with clear indications where the specific research project(s) fit into the whole. The approach followed here tried to do just that.

At this stage I must ask myself: Did I succeed in my goal of "providing the manager with a framework for determining and selecting the tree to be harvested"? The answer is not a simple yes or no:

* A framework has been provided, but it is still incomplete and open for improvement. For example, the succession model was developed in FORTRAN V. Today (within four years since the development) more efficient fourth generation computer languages and modelling packages are freely available. Few, if any, managers would still have FORTRAN compilers on their computers, and most will probably not be interested in purchasing a compiler and acquainting themselves with it. Therefore, I would not recommend to incorporate the new information into the existing FORTRAN V programme. Rather use the tested structure and information and rewrite it using the more up to date tools. To my mind this should be the next research priority. It might even be possible to switch to a stochastic distance-independent modelling approach, based on data collected during recurrent measurements on permanent sample plots. Given sufficient data become available for a specific forest, eventually a distance-dependent modelling approach can be followed. At the same time the principles, and the basic model, of the distance-independent individual tree modelling approach could be

applied to lesser known forests that are managed more extensively. As experience and information are gained models can be improved following the exact same principles followed here.

- Just as the modelling approach served the researcher to collate and contextualise a vast amount of (often apparently diverging) information it can serve the manager in exactly the same way. Here is a model, he does not have to develop it, but if he acquaints himself with the basic structure of and the information used in it, it will highlight the "grey" areas in his understanding of forest ecology. He is the one who must have sufficient understanding to react in a sound way in situations not investigated by research yet.

What direction should be followed by research from here onward? We now do have a modelling approach that works (although it should be rewritten using more modern software), the central growth function adequately reflects forest growth and there seem to be no major errors in the assumptions used for constructing the model. We have a fair idea of the growth rates of trees (in the forest types used for timber production), and have some indications that these are very similar to growth rates in (sub)tropical forest regions elsewhere. It is clear that the forests are in a late successional stage, that competition among trees is an important factor and that many later successional species have superior competitive abilities under the present circumstances. Together with the senility indices that are used by forest planners and managers in the southern Cape already (Seydack *et al.*, 1992), crown position and crown form can be useful tree growth indicators. In this way suppressed and senile trees can be selected for harvesting effectively, preempting mortality to a large extent. Finally, C^{14} dating (and possible radiation densitometry) of trees provides a viable method of dating trees and determining their growth rates.

There are obvious omissions in this study, such as the study of the germination and establishment of forest seedlings, their development into saplings, the animal/plant interactions and the plant physiological processes involved. These needs were not overlooked, but could not be addressed in this study. Some are/were already addressed in other studies. Examples are Lübbe and Geldenhuys's (1991) and Koen's (1991) studies on forest regeneration, studies on the decline and regeneration of *Ocotea bullata* (Lübbe 1990; Lübbe and Geldenhuys 1990; Lübbe 1991; Lübbe and Mostert 1991), Koen and Crowe's (1987) and Koen's (1988) studies on animal-plant interactions (his 1991 study also deals with this subject), Midgley and Bond's (1990) study on the occurrence of and reasons for fynbos "islands" in the forest and Kotze and Geldenhuys's (1992) study on the root systems of some forest trees. To my mind studies of the germination and establishment of tree seedlings and their development into saplings should receive priority. Apart from the fact that the model simulations yielded satisfactory results, there is no information to test or improve the model assumptions in this respect. Management's present attitude towards this phase of tree development is to consider it as a huge resource of potential trees from which adequate numbers will survive to maintain the tree composition of the forest - a type of "black box" with young trees that should be left alone. That this assumption might work in a natural forest that is left alone is not denied, but what is the effect of management practices on this phase of forest development and what can be done to improve or accelerate the survival and growth of seedlings and saplings without violating conservation principles? Nobody knows. Most of these "unknowns" are treated in a stochastic way in the OUTENIQUA model, and these are the subjects that should be researched. For research purposes the model is a vehicle that reflects our current knowledge of the forest dynamics. It enables us to identify the strengths and weaknesses in our understanding, and in this way future research efforts can be guided into directions where information is needed most.

Forestry research in South Africa is predominantly applied (this was in fact the case in this study too), and research topics are more and more prescribed by managers in top positions deciding what research should or should not be funded. The danger of this situation is that basic research (as might be required to answer simulation model questions) will be increasingly pushed into the background in favour of applied research. For instance, if management is satisfied with considering the regeneration phase of forest development as "black box" which need not be researched, it will be difficult to obtain funding for any projects on forest regeneration. This will require special skills on the researcher's side, and training in compiling well motivated project proposals might have to become an important aspect of his training in future. Too many important research projects are never executed simply because the original proposal and planning did not meet up to the required standards.

Lastly, the value of permanent sample plots cannot be emphasised enough. Once they are established, remeasurements can be done with relative low cost and manpower input. Data from these plots form the backbone of any forest growth study. The present study would not have been possible without at least some of the long-term growth data which I had available. Fortunately, a network of permanent sample plots do exist throughout the indigenous forest of South Africa (Geldenhuys and Van Daalen, 1992). It is of vital importance that these plots are properly maintained and data computerised and systematically indexed. Techniques for remeasurements of these plots and analyses of data obtained should be flexible enough to adjust to altered needs and new methods. But at the same time care must be taken that adjustments are not done so frequently that extrapolation of results become impossible.

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for

Abstract, Section 1 and Section 3

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