

# 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 The model is used as a research tool to summarize published and unpublished knowledge on the southern Cape forests and to highlight aspects where knowledge is insufficient.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 addi-

tion 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 be 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

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

1. The wet mountain forests are typically Afro-montane forests (White 1978). Canopy height ranges from 12 to 30 m. *Cunonia capensis* and *Ocoteabullata* 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 north-eastern 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 latifolius*, *P. falcatus*, *Pterocelastrus tricuspidatus*, *Apodytes dimidiata*, *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), multi-storied 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 Wian-garee 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

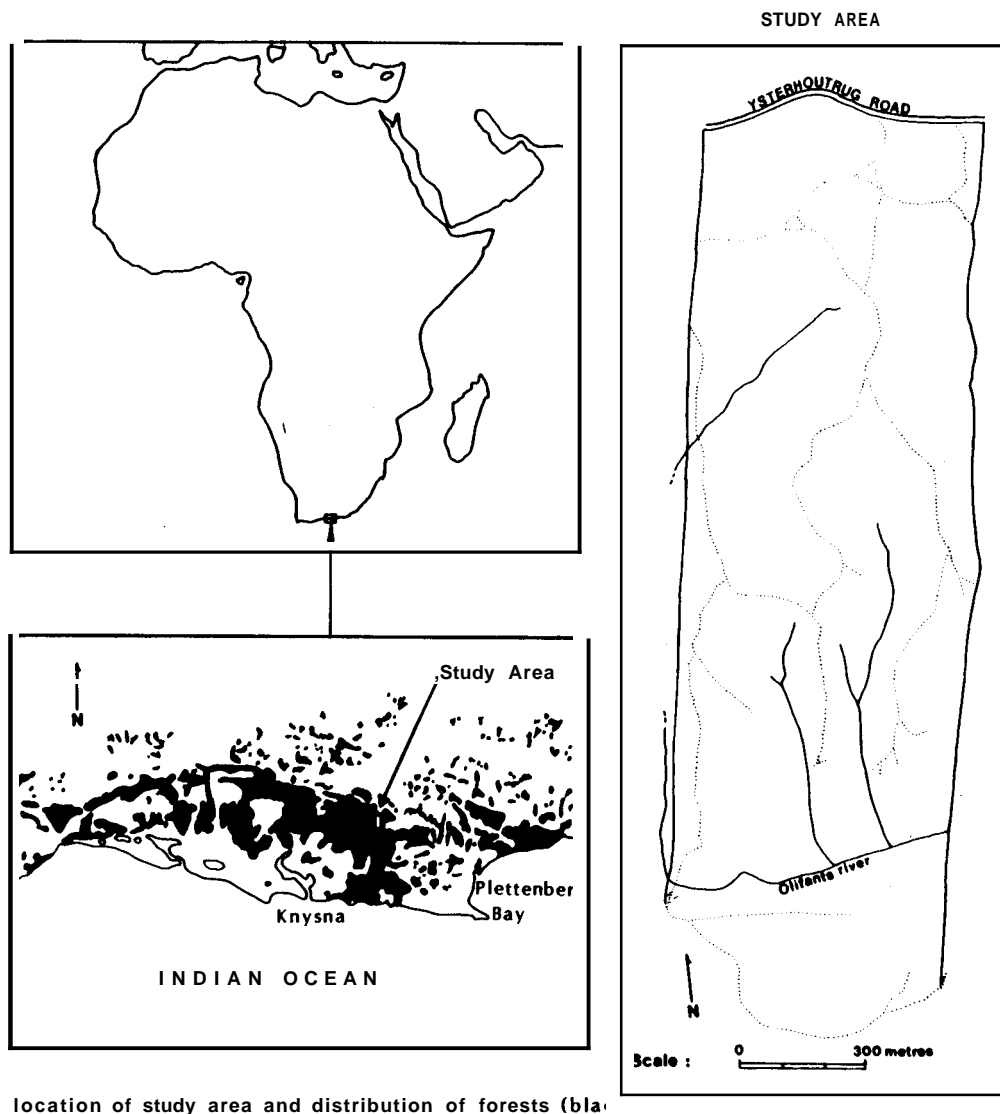
of the narrow belt of indigenous forests in the southern Cape. These mountains cause the orographic rain and mist that enable the forests to grow and survive. The model is implemented as FORTRAN V code that has been modified where appropriate to run on a 16bit Data General minicomputer with 64K byte 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 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).



location of study area and distribution of forests (bla.

**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 validation.

to implement a modified version of the KIAM-BRAM 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 Moun-

tains 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).

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
<i>Podocarpus falcatus</i> (Thunb.) R.Br. ex Mirb.	29.09	.048	1463	4500	2 7 2	2	4	3	2	1	3	T F T F T F						
<i>Podocarpus latifolius</i> (Thunb.) R.Br. ex Mirb.	44.84	.149	437	3500	7 0 1	1	2	3	2	1	2	T F T F T F						
<i>Ocotoa bullata</i> (Burch.) E.Mey.	67.26	.336	289	3500	106 2	2	2	1	1	1	1	T F T F F F						
<i>Platylophus trifoliatus</i> (L.f.) D.Don	71.57	.447	252	3000	104 2	2	2	1	1	1	1	F T F F F T						
<i>Luchmostylis hirtu</i> (L.f.) Muell. Arg.	105.02	1.167	295	2500	7 4 3	2	3	1	2	2	3	F T F F T F						
<i>Ilex mitis</i> (L.) Radlk.	56.05	.234	403	3500	7 6 2	2	2	2	2	1	3	T F T T F F						
<i>Maytenus peduncularis</i> (Sond.) Loes.	71.57	.447	401	3000	6 5 2	1	2	2	1	1	1	T F T F F F						
<i>Pterocelstrus tricuspoides</i> (Lam.) Sond.	81.80	.584	243	3000	108 2	2	3	3	2	1	3	T F T F F F						
<i>Cussine eucliformis</i> (Eckl. & Zeyh.) Kurtze	94.52	.945	244	2500	8 9 1	2	3	3	2	1	2	T F T F F F						
<i>Cussine peraquua</i> L.	94.52	.945	349	2500	6 3 2	2	3	3	2	1	2	T F T T F F						
<i>Cussine papillosa</i> (Hechst.) Kuntze	72.71	.559	264	2500	8 4 1	1	4	3	2	1	1	T F T T F F						
<i>Apodytes dimidiata</i> E. Mey. ex Arn	84.07	.525	395	3500	7 1 2	2	3	2	1	2	3	T F T T F F						
<i>Rhamnus prinoides</i> L'Herit	136.30	3.407	139	1500	9 4 3	1	2	3	3	1	2	T F T T T F						
<i>Ochna arborea</i> Burch ex DC	60.58	.673	619	1500	2 2 1	2	3	3	2	2	1	T F T F F F						
<i>Kiggelaria africana</i> L.	95.43	.795	297	3000	8 8 3	2	3	2	2	3	1	T F T T T F						
<i>Curtisia dentata</i> (Burm.f.) C.A. Sm	96.09	.686	250	3500	121 2	2	4	3	2	1	3	T F T T F F						
<i>Rapanea melanophloes</i> (L.) Mez	96.09	.686	299	3500	101 3	2	3	3	1	1	3	T F T T F F						
<i>Diospyros dichrophyllu</i> (Sand.) De Wint.	93.15	1.164	201	2000	8 8 3	2	4	2	2	2	2	T F T T T F						
<i>Diospyros whyteana</i> (Hiern) F. White	82.80	.920	223	2000	8 0 1	2	4	2	2	1	3	T F T T T F						
<i>Chionunthus foveolatus</i> (E. Mey.) Stearn	105.02	1.167	296	2500	7 3 2	2	4	3	2	1	2	T F T T F F						
<b><i>Oleu capensis</i> subsp.</b> <b><i>L. macrocarpa</i></b> (C.N. Wr.) Verd	56.05	.234	186	3500	165 1	2	4	3	3	1	3	T F T T						
<b><i>Oleu capensis</i> subsp.</b> <b><i>L. capensis</i></b>	72.71	.559	340	2500	6 5 3	1	4	2	1	1	1	T F T T F F						
<i>Nuxia floribunda</i> Benth.	71.57	.447	161	3000	163 1	2	1	2	1	2	3	F T F F F F						
<i>Coniolum kamassi</i> E. Mey.	82.80	.920	271	2000	6 5 2	1	2	2	1	1	1	F T F F F F						
<i>Halleria lucida</i> L.	85.93	.781	465	2500	4 7 3	2	2	2	2	2	2	T F T T F F						
<i>Burchellia bubalina</i> (L.F.) Sims	109.04	2.181	425	1500	3 1 2	1	2	3	2	1	1	T F T T F F						
<i>Canthium mundianum</i> Cham & Schlecht.	93.15	1.164	207	2000	8 5 3	2	3	3	2	3	2	T F T T F F						
<i>Canthium obovatum</i> Klotzsch	84.07	.525	335	3500	9 1 2	2	3	3	2	1	2	T F T T F F						

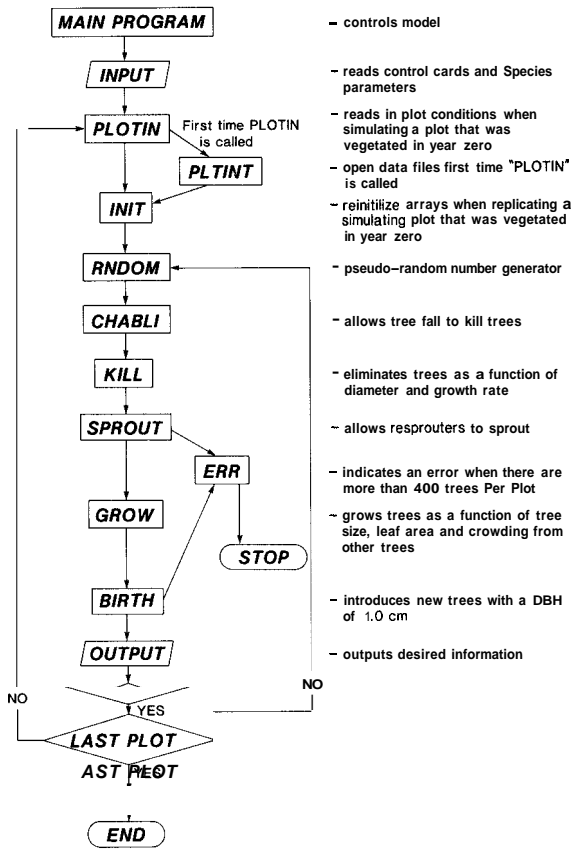


Fig. 2. Flow diagram for calls to subroutines in the OUTENIQUA model.

**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

'underbos' 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:

$$P_s = 1 - \exp(-4.605/\text{AGEMX}),$$

where  $P_s$  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:

$$\frac{dD}{dt} = \frac{G \cdot D(1 - D \cdot H / D_{\max} H_{\max}) \cdot S(\text{BAR}) \cdot r(\text{AL})}{(274 + 3b_2D - 4b_3D^2)}$$

where:

$D$  = diameter of tree ( $D_{\max}$  = maximum possible diameter)

$H$  = height of tree ( $H_{\max}$  = maximum possible height)

$S(\text{BAR})$  = stand basal area affecting nutrient competition

$r(\text{AL})$  = 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  $1.0 \text{ m}^2/\text{m}^2$ .

After 'filtering' (*sensu* Harper 1977) the species regeneration requirements against the site conditions and computing the outcome of the probabilistic factors 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  $1.0 \text{ m}^2/\text{m}^2$ ). This process is repeated between 1 and 32 times per year (according to a selected uniform random number). Ail 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 over-mature, 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 OUTENIQUA 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 consistency 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

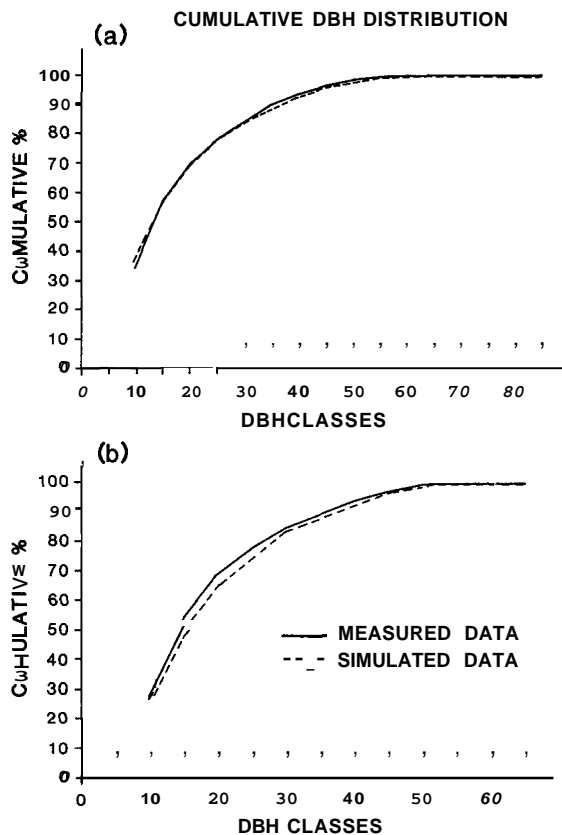


Fig. 3. Comparison of cumulative percentages of diameter distributions between actual observations in 1983 and model simulations initialized with 1972 inventory data and projected to 1983. a. Comparison based on the data from 63.04 ha inventory plots located north of the Olifants River. These data were 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.

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.

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

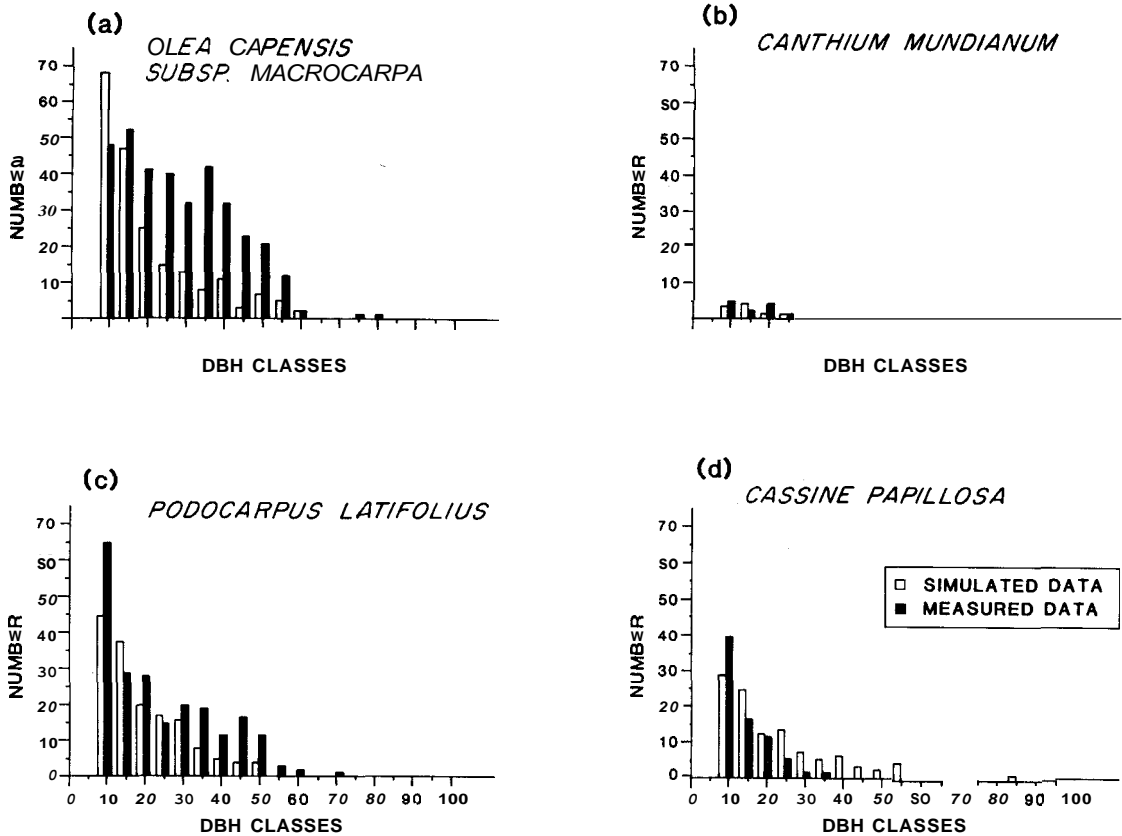


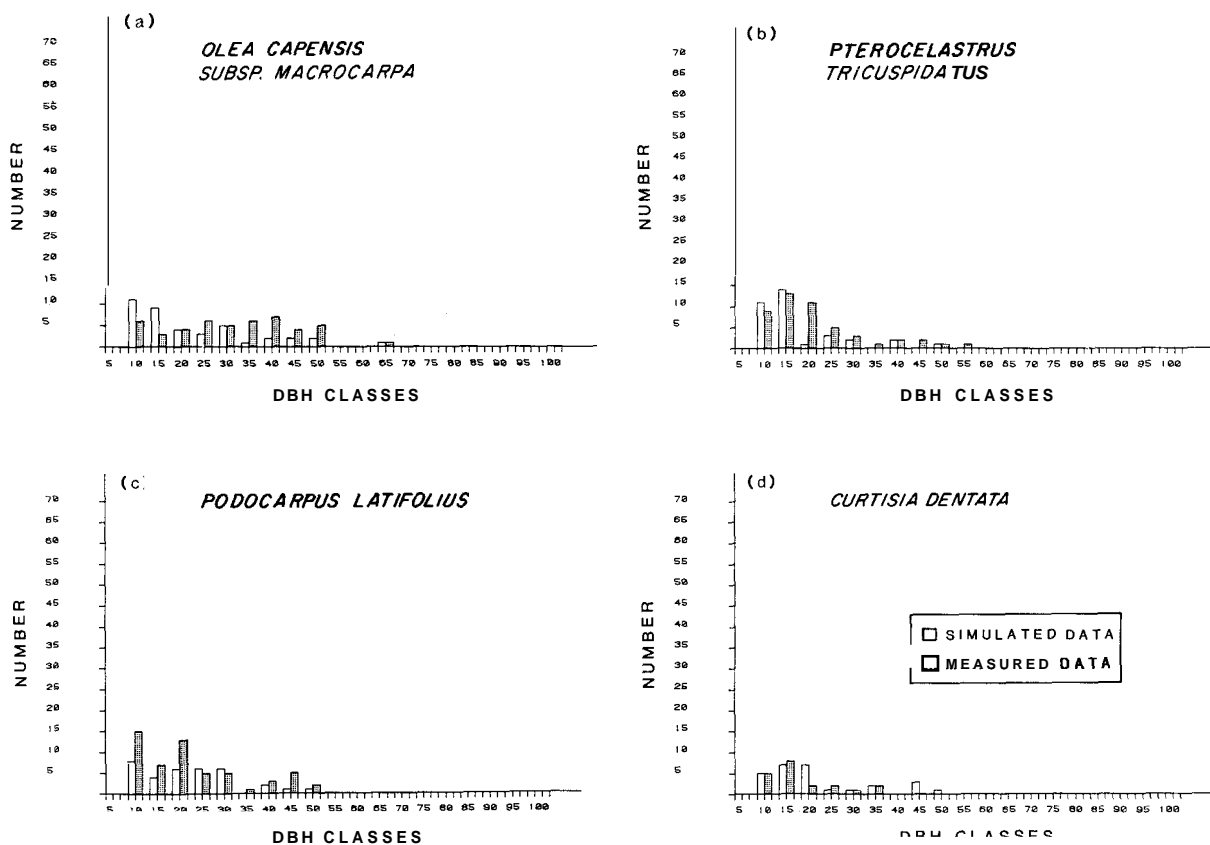
Fig. 4. Comparisons between numbers of stems in 5 cm diameter intervals measured on 63 0.04 ha inventory plots (in 1983) from the part of the study area north of the Olifants River and the results obtained by initializing the model with data from 1972 and projecting the stand dynamics forward for 11 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 cumulative DBH curve (Fig. 3b) is apparent, the simulation appears satis-



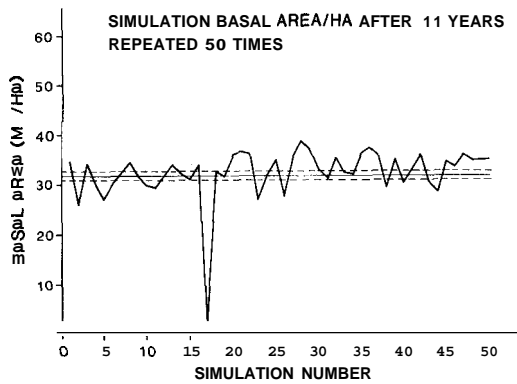
**Fig. 5.** Comparisons between numbers of stems in 5 cm diameter intervals measured on 63 0.04 ha inventory plots (in 1983) from the part of the study area south of the Olifants River and the results obtained by initializing the model with data from 1972 and projecting the stand dynamics forward for 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  $\text{m}^2/\text{ha}$ ) at the end of each simulation is plotted in Fig. 6. Mean simulated basal was  $32.3 \text{ m}^2/\text{ha}$  (compared to  $33 \text{ m}^2/\text{ha}$  measured) with a 95% confidence interval of  $\pm 1.5 \text{ m}^2/\text{ha}$ . The simulation varied between 26 and 36  $\text{m}^2/\text{ha}$ , except where a Chablis occurred. In the gap resulting from this Chablis, the basal area dropped to  $3 \text{ m}^2/\text{ha}$ . 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.

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