Matrix models using stand parameters such as stem density, in-growth, rates of growth and mortality were used to predict the stand structures of the most complex tropical rainforest ecosystem in Southern Nigeria. The model represented all tree species covering matrix for 6 years. The forest decline due to dominant eigenvalue (\lambda) of the matrix R was 0.977, which is the intrinsic rate of natural increase with less than zero. A sensitivity analysis revealed that large recruitment rate of 87% was required to restore stability to the forest while only 16% improvement in growth rate would ensure sustenance and hence stabilized the forest.

INTRODUCTION

The natural tropical rainforest is vulnerable to interruption in the form of natural and artificial hazards. Such disturbances often produce residual forests which may appear different from the primary forests in terms of the stand structure, number and distribution of species and trees sizes. However, the forest may be able to readjust through a process of reconstruction with variation in the stand structures from place to place within the same location over a long period of time. It is therefore essential to search for explanation of the present stand structure in the past in order to understand the system in terms of history rather than their goals (Harper, 1977). In the context of forest stand demography, it warrants searching for the past influences which have contributed to the present stand structure. Invariably, the whole processes centered on prediction and the matrix models have been described as one of the most feasible options (Usher, 1966). This is apparent when it comes to the issue of forecasting future composition of trees in the natural ecosystem. Therefore, modeling the natural tropical rainforest required first, the reconstruction of the past stands structures and then prediction of the future states. The first processes had been frustrated by shortcomings especially through lack of funds which normally jeopardized accurate records keeping of the past influences. However, the availability of the tree demographic data on ingrowths, increment and mortality provided the basic inputs that necessitated this study. Besides, the theoretical framework of matrices had revealed the predictive potential of matrix models as a veritable tool for the study of most complex ecosystem like the tropical rainforest (Usher, 1969). This paper, therefore, adopts matrix model approach to investigate the forest stand dynamics and to predict its future state within a specified period of time.

Data Collection

The inventory data collection from the permanent sample plots 1.44ha, established in Cross River North Forest Reserve (5° 65’ N, and 8° 65’ E) in the high forest zone of South Eastern Nigeria in 1955. The climate of the area has been used in classification of the vegetation in Nigeria (Keay, 1959). Annual rainfall is high with marked high temperature throughout the year. The major geological formation within the area is the basement complex rocks. The weathering of these rocks gives rise to the major soil types within the area. The soils of the area are mainly red clayey soil with sandy properties around the catchment areas. The vegetation is vaguely broken into distinguishable layer. The upper layer is characterized by emergent species like Antiaris Africana, Pterocarpus osun, Lophira alata being a Moraceae/Papilionoideae/Ochnaceae association. The upper storey species were represented by Brachystegia eurycoma, Piptadeniastrum afromanum, and Hylocodendon excelsa being an Annonaceae/Euphorbiaceae association. The middle storey species include Treculia obvoidea, Standitia stiplata, Allamblackia floribunda, and Funtumia elastica representing Moraceae/ Sapotaceae/Myristicaceae association.

The forest structure was gradually driving towards climax vegetation with species composition and families’ relative positions changing both in space and time. The plot was divided into 16 squares subplots of 30m x 30m or 0.09ha each. The area was established for the purpose of obtaining data on girth increment, stem density and mortality of trees in the stands. Assessment was carried out on all trees in each subplot with 5cm and above in diameter at breast height (dbh). The first assessment was in 1956. Subsequent assessments were done in 1962, 1973 and 1998.

Growth Matrix Model

Using the matrix models modified by Usher (1966 and 1969), the Cross River North Forest Reserve was studied to unveil the existing mechanisms of dynamics of the tree population of the study site. The first step in the stand structure projection involves the construction matrix by pooling together data on all tree species in the study area. The pooled tree species were presented by a square matrix R(6 x 6) whose rows and
columns represents the six diameter classes of 4.8–10cm; 10–20cm; 20–30cm; 30–40cm; 40–50cm and over 50cm, thus:

\[
R = \begin{pmatrix}
a_{11} & f_{12} & \cdots & f_{16} \\
a_{21} & a_{22} & \cdots & a_{26} \\
\vdots & \vdots & \ddots & \vdots \\
a_{61} & a_{62} & \cdots & a_{66}
\end{pmatrix}
\]

Where \( f_{ij} \) is the average recruitment per individual tree in size class \( j \) (\( j = 2, 3, 6 \))
Aij is the contribution over a unit time interval of trees in size
Class i (\( i, j = 1, 2, \ldots, 6 \)).

All the pooled tree species were assigned to their respective diameter size classes. The mean periodic annual increment (MPAI) equivalent to the tree with average diameter in the size class was added to the initial diameter of each tree at the end of each subsequent measurement period. All trees whose new diameter exceeded the old diameter classes were recorded and promoted to the next higher class. The proportion of trees which were not promoted, form the complement and remained in the same class during the growth period. Thus, the proportions of trees moving up and those remaining were automatically determined.

**Table 1:** Life table for the pooled species (1956 - 1998)

<table>
<thead>
<tr>
<th>Diameter class</th>
<th>Status</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Live trees (1956)</td>
<td>885</td>
<td>387</td>
<td>116</td>
<td>82</td>
<td>38</td>
<td>52</td>
</tr>
<tr>
<td></td>
<td>Live trees (1962)</td>
<td>792</td>
<td>358</td>
<td>114</td>
<td>79</td>
<td>42</td>
<td>53</td>
</tr>
<tr>
<td></td>
<td>Proportion moving</td>
<td>0.07</td>
<td>0.06</td>
<td>0.15</td>
<td>0.19</td>
<td>0.20</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>Proportion remaining</td>
<td>0.93</td>
<td>0.94</td>
<td>0.85</td>
<td>0.81</td>
<td>0.80</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td>Survival Rate*</td>
<td>0.66</td>
<td>0.87</td>
<td>0.96</td>
<td>0.94</td>
<td>0.89</td>
<td>0.89</td>
</tr>
</tbody>
</table>

**In Growth**

299

*Survival rate was determined relative to initial tree population of 1956.

The elements of matrix R were computed thus:

\[(a_{ij}) = 1 - (P_{j})_{j}\]

are the diagonal elements of matrix R. \( P_{j} \)
refers to the probability of trees moving from class \( j \) to
class \( j + 1 \) at the end of the growth period. \( S_{j} \)
represents the survival rate of trees in class \( j \), (1 - \( j \)) is
the probability of trees remaining in class \( j \) at the end of
the growth period. \( (a_{i} + 1, j) = P_{j} \). \( S_{j} \) is the sub-diagonal
elements of matrix R. \( F_{ij} \) are the elements of the first
row for R (\( j = 2, 3, \ldots, 6 \)). These elements represent
the average contribution per individual tree in each of the
classes to the recruitment of the stand during the growth
period. \( A_{ij} = 0 \) (\( i = 3, 4, \ldots, 6 \) and \( j = 1, 2, \ldots, 6 \)).
Other elements of matrix R were zero apart from the diagonal
and sub-diagonal elements and the elements of the first
row of the matrix R. This is in line with the basic matrix
model assumptions that no tree would move backwards,
that is neither shrinkage nor any tree would be deemed
to have moved up more than one class during the
growth period. Moreover, any tree in the population
could make one and only one of these move, that is
move to a higher diameter class \( i + 1 \) or remain in class \( i 
and die in class i.

The elements of matrix R are obtained based on
computation from data as shown in table 1, thus: \( a_{11} = \)
\((1 - P_{1}) S_{1} = 0.93 \times 0.66 = 0.613. \) Also, \( a_{21} = P_{2} S_{1} = 0.07 \)
x 0.66 = 0.0462 and \( a_{22} = (1 - P_{2}) S_{2} = 0.94 \times 0.87 = 0.8178.\)

\[
R = \begin{pmatrix}
0.61 & 0.00 & 0.46 & 0.66 & 1.69 & 2.45 \\
0.05 & 0.82 & 0 & 0 & 0 & 0 \\
0 & 0.05 & 0.82 & 0 & 0 & 0 \\
0 & 0 & 0.14 & 0.76 & 0 & 0 \\
0 & 0 & 0 & 0.18 & 0.71 & 0 \\
0 & 0 & 0 & 0 & 0.18 & 0.88
\end{pmatrix}
\]
The estimation of fij was cumbersome. There was no exact measurement of the contribution of different size classes to the recruitment of trees to the smallest diameter class. In growth function adopted was developed by Buon-giorno and Michie (1980) and was given as:

\[ l_i = \beta_0 + \beta_1 \sum_{i=1}^{6} (y_{it} - h_{it}) + \beta_2 \sum_{i=1}^{6} (y_{it} - h_{it}) \]

where \( \beta_1 \) is the basal area of the average tree diameter in size class i; \( y_{it} \) is the number of dead (harvested) trees of class i; \( h_{it} \) is the number of live trees of size class i (i=1, 2…6); \( \beta_0 \), \( \beta_1 \) and \( \beta_2 \) are coefficients of multiple regression and \( f_{ij} = \beta_0 \beta_1 + \beta_2 (i,j = 2,3,…6) \). The fitted equation based on linear regression approach from 1560 trees alive in 1956 was given as:

\[ l_i = \beta_0 + \beta_1 \sum_{i=1}^{6} (y_{it} - h_{it}) + \beta_2 \sum_{i=1}^{6} (y_{it} - h_{it}) \]

R-square was 0.18 which was an extremely poor fit. The result indicates that modeling of in growth as uniform contribution by the mature trees in the diameter classes 3,4,…6 but weighted proportionally to the number of trees present in each diameter class, had little or no effect on the performance of the model. Invariably, 75 samplings were contributed to each diameter class 3, 4, 5 and 6 from the total 299 new recruits recorded throughout the growth period. The average recruitment per contribution of individual tree in class j (j = 3, 4,…6) was \( f_{ij} = (0, 0.45, 0.66, 1.69, 2.45) \).

The stand structure could now be predicted over some period using the notation: \( Y_{m,i} = R^m Y_i \) where \( Y_i \) is the initial stand structure at the end of the growth period. In this case, \( m \) is the matrix time step which was equal to 6 years.

**RESULTS**

The projected stand structures for the forest were as shown in Figure 1 below. Matrix R predicted a total tree population size of 1319 (916 trees ha\(^{-1}\)) for 1998 as against the observed tree population size of 1311 (910 trees ha\(^{-1}\)) for the same year.

![Figure 1: Projected Population Structure (1998-2052)](image)

The relative distributions of tree in diameter classes for the matrix R are shown in Figure 2 below. The predicted and the observed stand structure distributions for 1998 were similar. There was no significant value of \( x^2 \) - test – (p ≤0.05) and when the equilibrium stand structures were compared with the initial stand structures, there was a marked difference between the two.
The life table data for this study concerned with numerical stability of the tree population. This work involved predictions of successive population structure or calculation of the infinite rate of increase \( R \) of populations using stage projection matrix \( R \). In this case, the population size would remain unchanged and this is difference from the species composition stability which was considered and determined by finding the dominant eigenvalue \( \lambda \) in association with the population projection matrix. Therefore, a value of \( \lambda = 1 \) indicates a stable population; \( \lambda < 1 \) signifies a declining population and \( \lambda > 1 \) would mean an increase in population size. The dominant eigenvalue \( \lambda \) for the population projection matrix \( R \) was 0.977 which signifies a declining population. This was actually the case because the population decreased from 1560 stems in 1956 to 1311 stems in 1998 – a decline of 16% as illustrated in Figure 1. The effect of change of recruitment and growth on the stability of the tree population was simulated. Simulation involved changing the rate of recruitment into forest stand and keeping the other stand parameters constant. This was followed by changing the growth rate of the tree species while other elements were held constants. By comparing the dominant eigenvalue of the new matrix with the initial matrix it was possible to gauge the amplitude effects of these changes (Table 2 and 3). The result revealed that a regeneration improvement of about 187% over the observed recruitment would be required to stabilize the forest given the present growth and survival rates. This indicates that about 559 new recruits would be required to stabilize the forest.

### Table 1: Effect of Change of Recruitment on the rate of increase of population

<table>
<thead>
<tr>
<th>Number of In-growth</th>
<th>Percentage of Observed In-growth</th>
<th>Dominant Eigen-value (( \lambda ))</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>0.88</td>
</tr>
<tr>
<td>299*</td>
<td>100</td>
<td>0.977</td>
</tr>
<tr>
<td>388</td>
<td>129.8</td>
<td>0.987</td>
</tr>
<tr>
<td>478</td>
<td>159.9</td>
<td>0.995</td>
</tr>
<tr>
<td>559</td>
<td>186.9</td>
<td>1.001</td>
</tr>
<tr>
<td>643</td>
<td>215.1</td>
<td>1.007</td>
</tr>
<tr>
<td>748</td>
<td>250.2</td>
<td>1.014</td>
</tr>
</tbody>
</table>

* The observed in-growth during period of growth.
Table 2: Effect of Change of growth rate on the population rate of increase

<table>
<thead>
<tr>
<th>Growth Rate</th>
<th>Increase (%)</th>
<th>Dominant Eigen-value ( )</th>
</tr>
</thead>
<tbody>
<tr>
<td>(0.05 – 0.18)b</td>
<td>Observed</td>
<td>0.977</td>
</tr>
<tr>
<td>(0.055 – 0.198)</td>
<td>10</td>
<td>0.992</td>
</tr>
<tr>
<td>(0.058 – 0.207)</td>
<td>16</td>
<td>1.00</td>
</tr>
<tr>
<td>(0.006 – 0.0216)</td>
<td>20</td>
<td>1.006</td>
</tr>
<tr>
<td>(0.065 – 0.234)</td>
<td>30</td>
<td>1.02</td>
</tr>
<tr>
<td>(0.07 – 0.252)</td>
<td>40</td>
<td>1.036</td>
</tr>
</tbody>
</table>

b The observed growth rate during the growth period.

The improvement of 10 to 16% in growth rate would ensure sustenance and stability of the forest, given the present level of recruitment and survival rates.

DISCUSSION

The tree diameter at breast height (dbh) was used as surrogates for the age since tree ages were unknown owing to the absence of annual growth rings. This is based on the assumption that there is a relationship between the tree size and their age. The principle is that large trees in the canopy were likely to be old. It is reported that a wide range of herbaceous and woody plants exhibit different mortalities among their young individuals based on their size or biomass rather than age (Surakhan, 1984). He also showed that determination of plant size from height was extremely good predictor of reproductive performance of *Astrocaryum mexicanum*. It was observed that the probability that a rosette would flower was highly correlated with its size but independent of its age (Gross, 1981). For example, rosette of *Verbascum thapsus* less than 9cm in diameter did not flower at all, but the likelihood of flowering increased steadily with size thereafter. All rosettes with a diameter greater than 41cm flowered in the subsequent years. The implication is that the use of tree diameter as an age surrogate is rational.

Information on the stand growth is required particularly by forest resources managers to make rational decisions when confronted with conflicting issues. Forest managers are interested in understanding future changes in forest structures to determine if their objectives would be achieved economically in terms of availability of forest growing stocks and the expected revenues. It is obvious that under the prevailing circumstances, the possibility of increasing the size of the existing forest estate seems very remote. Therefore, this model has demonstrated the simplest means of providing basic information on the evolution of stand structures within a specified time scales. It would avert the possibility of non-payment for trees harvested since government revenue targets would be based on expected yields. Forest management in Nigeria is characterized by lack of information on the continuous demographic data on forest stand parameters and harvesting schedules. The matrix model offers a simple but a more efficient approach given the present level of our forest management.

REFERENCES


