Tropical Ecology **49**(2): 259-270, 2008 ISSN 0564-3295
© International Society for Tropical Ecology
www.tropecol.com

The use of a best-fit allometric model to estimate aboveground biomass accumulation and distribution in an age series of teak (*Tectona grandis* L.f.) plantations at Gambari Forest Reserve, Oyo State, Nigeria

E.I. MBAEKWE*[1] & J.A. MACKENZIE[2]

[1]*Department of Botany, Nnamdi Azikiwe University, Awka, Anambra State, Nigeria*
[2]*Department of Plant Protection and Environmental Biology, University of Ibadan, Oyo State, Nigeria*

Abstract: Biomass accumulation and distribution in four selected plots of an age series (5, 8, 11 and 14 years) of teak plantations were studied. Ten trees per plot (50 m x 50 m) were randomly selected and destructively sampled for the fresh and oven-dry weights of their tree components. The dry weights of the tree components were regressed with their trunk diameters at breast height. The log : log allometric model was used to estimate the biomass. The trends in the biomass accumulation and distribution, as well as those of the mean annual increase in biomass, percentage contribution of the leaf biomass to the overall tree biomass and the undergrowth and litter were discussed. Because of its rapid rate of biomass accumulation compared to species of natural and other timber plantations, the use of teak as an alternative source of timber is justified.

Resumen: Se estudió la acumulación y la distribución de la biomasa en cuatro parcelas seleccionadas de plantaciones de teca que conforman una serie de edad (5, 8, 11 y 14 años). Se seleccionaron al azar diez árboles por parcela (50 m × 50 m), de los cuales se tomaron muestras destructivas para determinar el peso fresco y seco de sus componentes. Se calcularon las regresiones de los pesos secos de los componentes arbóreos sobre sus diámetros del tronco a la altura del pecho. La biomasa fue estimada usando el modelo alométrico log:log. Se discuten las tendencias en la acumulación y la distribución de biomasa, así como aquellas correspondientes al incremento anual promedio en biomasa, la contribución porcentual de la biomasa foliar a la biomasa arbórea general, y la biomasa subterránea y el mantillo. Si se considera la rápida tasa de acumulación de biomasa en comparación con especies de plantaciones naturales y de otras maderas, el uso de la teca como una fuente alternativa de madera está justificado.

Resumo: A acumulação e distribuição de biomassa em quatro parcelas seleccionadas de uma serie etária (5, 8, 11, e 14 anos) de plantações de teca foram estudadas. Seleccionaram-se de forma casual dez árvores por parcela e, das árvores, foram retiradas de forma destrutiva amostras de cada componente para determinação dos pesos verdes e secos em estufa. Foi efectuada uma análise de regressão entre os pesos secos das componentes das árvores e os diâmetros das árvores à altura do peito. O modelo alométrico log: log foi utilizado para estimar a biomassa. As tendências da acumulação e distribuição da biomassa, bem como os dos acréscimos médios anuais da mesma, a contribuição percentual da biomassa foliar em relação à biomassa total, a subterrânea e a folhada foram discutidas. Por causa da sua rápida taxa de

---

* *Corresponding Author*; e-mail: drmbaekwe@yahoo.com

acumulação de biomassa quando comparada com as espécies naturais e outras plantações madeireiras, o uso da teca com o fonte alternativa de madeira é justificada.

Key words: Aboveground biomass, allometric model, biomass distribution, Gambari forest, net primary productivity, teak, teak plantations.

Introduction

Interest in the role of vegetation in the ecosystem includes dynamic aspects, such as the accumulation and distribution of organic matter, as well as the cycling of minerals and water, and the flow of energy. Biomass quantification is central to all such studies and it is generally defined as the dry weight of organic matter present in a given area of the ecosystem at a particular time. The need to study and monitor the net primary productivity (i.e., the rate of biomass accrual) of different world ecosystems necessitated the establishment, in 1964, of the International Biological Programme (IBP). According to Reichel (1970), one of the objectives of the IBP was to understand, through research and synthesis, the biological basis of productivity and human welfare.

The methods which have been used to estimate the biomass and net primary productivity of terrestrial ecosystems have been reviewed by various authors Buvaneswaran *et al.* 2006; Dreschsel *et al.* 1990; Egunjobi 1976; Hiratsuka *et al.* 2004; Kira & Shidei 1967; Liddel *et al.* 2007; Losi *et al.* 2003; Newbould 1967; Pitto *et al.* 2004; Segura & Kanninen 2005. Two main regression models have featured prominently in biomass studies:

(i) The linear model of the form:
$Y= a + b.X$
The variant of the linear model is given by:
$Y = a + b. 1/X$.

(ii) The exponential (or allometric model):
$Y = a.X^b$
The latter has the following variations:
$\text{Log}_e Y = a +b. \log X$
$\text{Log}_e Y=a+ b.X$
$Y = a + b. \log_e X$

where, a and b are regression constant and regression coefficient, respectively, X is the diameter at breast height (dbh), while Y is the biomass of the tree or its component.

Egunjobi (1976) examined the suitability of many other models and found the three variations of the allometric model and the variation of the linear model the most suitable for biomass estimates. Singh (1975) observed that the relationship between two parts or organs or between an organ and the rest of the body, which do not grow at the same rate, is given by the allometric equation. Although the biomass of some stands has been successfully estimated by the linear regression model: $Y = a + b. x$ (Egunjobi 1975; Whittaker & Woodwell 1968), the allometric model and its variants have been found to be more efficient and have been used by all the workers earlier mentioned.

Admittedly, some progress has been made and is still being made to understand the basic structure and functioning of our ecosystems in Africa, but a lot still has to be done; we certainly do not know enough, as yet, about the dynamic process in most of our natural and artificial ecosystems. It is against the above background that the present study is targeted at achieving the following aims and objectives:

- identify and employ the most suitable allometric model to estimate the biomass production of teak plantations in an age series;
- establish the pattern of dry matter accumulation and distribution among the various tree components in an age series;
- assess the biomass of the undergrowth and litter in order to determine the proportion of non-teak biomass in the teak plantations;
- compare the productivity of teak at the Gambari Forest Reserve with that of teak in other countries, as well as with other timber trees by reference to the literature;
- compare the productivity of teak, by reference to the literature, with that of the original natural forest species it is rapidly replacing, with a view to ascertaining whether or not the reforestation efforts with teak are justifiable.

Materials and methods

Four plots of different ages 5,8,11 and 14 years were selected from Ibusogboro village, Gambari Forest Reserve. The number of plots could not be increased because of the need to limit labour and cost.

Within each plot, a sample unit, 50 m x 50 m (0.25 ha) was delimited with pegs, making sure that it was located at least four meters away from the edge of the plot to avoid edge effect. In each sample unit, every teak tree was numbered with durable red paint and the dbh (1.30 m above ground level) was prominently marked around each trunk with the same paint. The dbh of all the trees within each sample unit was measured with a steel diameter tape.

In selecting the sample trees for destructive sampling, stratified random sampling was used. This involved grouping the tree diameters into eight convenient size classes with progressively larger diameter and recording the frequency of occurrence in each diameter class. According to Steel & Torrie (1960), stratified random sampling makes the decision on how many units will be taken from each stratum more efficient. Ten trees were selected in each plot for felling and other measurements, making sure that at least one was selected from each diameter class. The method of uniform sampling intensity was used to ensure that more trees were sampled from a diameter class with a greater number of trees.

Felling of trees started towards the end of July 2005. This period approximated the maximum vegetative growth, when the leaves had attained sufficient maturity and leaf fall had not yet actively started. At this time also, flower and fruit formation had reached an advanced stage in those trees that would flower. According to Taylor (1972), vegetative growth usually diminishes with the onset of the reproductive phase, and the advent of flowering thereby serves as an indication of the period of maximum productivity in most species.

Each tree was cut either at the ground level or about 50 cm above the ground level (for trees of larger diameter) with a power saw (Dolmar 144A). Where the tree was cut above the ground level, the following measurements were also made:

i. The height of the stump, and
ii. The diameter at the cutting height.

With these two measurements, and a knowledge of the specific gravity of teak, it was possible to estimate the dry weight of the stump and this was added to the estimate of the bole dry weight.

Other parameters measured include:

- total heights of the trees taken on the felled trees from the ground level to the tip of the crown;
- bole height;
- fresh weights of leaves, dead wood, living branches and boles. All the fresh weight measurements were done in the field using a 25 kg spring balance.

Subsamples of the above tree components were taken in the field for oven drying. For the bole, the sub-samples were taken at three different locations on the log: the base, the middle and the tip. Subsamples of the various tree components were put in plastic bags, labelled properly and taken to the laboratory where they were dried in a Gallenkamp oven (model OV-330) at 105^0C to a constant weight. The dried subsamples were weighed, using the 25 kg balance except for the leaves and floral parts, whose fresh and oven-dry weights were taken with a Mettler balance.

Twelve, 1 m x 1 m, quadrats were randomly located in each sample plot in order to sample the undergrowth and ground litter. All the undergrowth in each quadrat was clipped at the ground level, the species present in each quadrat were counted and identified and later transported to the laboratory in polythene bags. In the laboratory, they were sorted into stems and leaves (as there were no flowers and fruits) and dried on quadrat basis in an oven to a constant weight. The oven-dried samples were weighed with a Mettler balance. The ground litter was also sampled and sorted into leaf litter, dead wood and branches, as well as flowers, fruits and seeds. These were also weighed fresh in the field and sub-samples were taken to the laboratory and dried. The dry weights of the sub-samples were used to calculate the oven-dry weight of these components in each quadrat.

Computations and data analysis

The oven-dry weights of the tree components were calculated from the dry weights of the sub-samples and their corresponding fresh weights. From each of the sample trees, the various oven-dry weight values of the tree components were summed up to obtain the total dry weight. In any one plot the dry weights of each tree component was regressed with their corresponding diameter at breast height. This regression was done with the aid of a computer programme. The computer programme produced four regression equation models:

$\log_e Y = a + b \,\mathrm{Log}_e X$ … I
$\mathrm{Log}_e Y = a + b \log_e X$ … II
$Y = a + b.\ 1/X$ … III
$Y = a + b \log_e X$ … IV

The computer programme also generated the following statistics: the coefficient of determination (r^2) ; the standard error of the estimate; the F-ratio and the biomass correction factor. The biomass correction factor, e^s was suggested by Mountford & Bunce (1973) as a way of avoiding the bias resulting from the use of regressions with logarithmic transformations to estimate the biomass of various plant components. The biomass correction factor was applied to model 1, which was found to give the best fit by producing the highest level of significance of the regression and the least standard error of the estimate. Hence, the biomass estimate of all eight tree components in each of the four plots was computed using model 1 and the results compared in an age series.

The biomass estimates for the floral part and branches > 5 cm for the 5-years plot were not computed and no regression analysis was done on them. This is because the number of variables involved was too few; in the former only two trees bore flowers and fruits, while in the latter only one tree had branches > 5 cm.

Other computations included:

- mean annual increment in biomass, calculated by dividing the data for each plot by the age of plot;
- percentage distribution of biomass among the various tree components, based on the total biomass obtained by summing the component values;
- ratio of non-photosynthetic / photosynthetic biomass based on their mean values obtained by dividing the corresponding biomass by the total number of trees in the plot.

Possible sources of error

Some errors might have arisen from the measurements with the steel diameter tape. Other errors might arise from the measurements of fresh weights and oven-dry weights, using the spring balance. The small size of the weighing balance (25 kg) made weighing very cumbersome; a bigger balance would have made things easier, but was not available. There would have been some losses of plant materials in the form of dust during the cutting operation with both the power saw and the matchet, particularly with the former. Loss of floral parts, especially petals, sepals, pollen grains, fruit and seeds, was inevitable because they were tiny and light. Also, the falling tree sometimes dragged other trees along with it or at least their branches, leaves, flowers and fruits. This would have led to some recruitment and, consequently, over-estimate of all these components. These losses and recruitments might not have been effectively controlled, but a deliberate effort was made to reduce, as far as possible, the errors that could result from them.

Some errors might also have arisen during the sub-sampling and drying operations. Whereas great care was taken to ensure accurate weighing, errors resulting from malfunctioning equipment would be difficult to detect. Percentage error attributable to the regression models could not be determined because there was no direct method, such as the clear-felling method, with which to compare the result obtained from the model used. The authorities of the Ministry of Agriculture and Natural Resources (Forestry Division) could not have granted such permission; there was, in fact, great difficulty in obtaining permission to fell ten trees per plot.

Results

The biomass estimates ($\times 10^3$ kg ha^{-1}) in an age series based on model 1, with 95% confidence limits are given in Table 1.

There was an apparent trend in the biomass estimates of the leaves, dead wood, branches < 5 cm, total branch, and total tree; they generally increased to a maximum by the 8th year, dropped to a lower level by the 11th year before increasing again by the 14th year. In general, the increase in biomass of these tree components was much larger between the 5th year and the 8th year (in most cases more than double), while the increase from the 11th to the 14th year was considerably less. This implies that teak growth rate and biomass accumulation must be taking place more rapidly

Table 1. Biomass estimates of tree components, undergrowth and ground litter (x 10^3 kg ha^{-1}) in an age series based on Model 1, with 95% confidence limit on total tree biomass.

Age (years)	5	8	11	14
Leaves	5.01	5.74	4.50	4.80
Floral parts	-	0.44	0.62	0.30
Dead branches	0.26	4.59	2.56	3.06
Branches > 5 cm	-	7.38	9.47	9.12
Branches < 5 cm	7.37	15.31	12.73	13.96
Total branch	7.37	22.69	22.20	23.08
Bole	29.70	80.98	84.12	103.03
Total by summing above tree components	42.33	114.44	114.44	134.27
Total with 95% confidence limit Biomass under teak	42.33±2.40	114.44±2.22	114.00±2.22	134.27±2.02
Undergrowth (stem and)	2.60	2.45	0.38	0.27
Leaf litter	1.76	4.88	3.07	3.33
Dead branches	2.52	1.07	1.00	2.96
Fruits and/or seeds	0.01	1.04	0.37	0.46
Total biomass under teak ± standard error	6.89±0.22	9.44±0.09	4.82±0.40	7.02±0.08
Total above ground biomass	49.22	123.88	118.82	141.29

around the 8th year. The age of peak growth could not be known with certainly because of the three-year interval in the age series studied. The same level of consistency, as described above, could not be attributed to the biomass estimates of the floral parts and branches > 5 cm. On the other hand, the bole biomass increased steadily with age.

Over the nine-year period represented by the sample plots, the total teak biomass increased from about 42.0 x10^3 kg ha^{-1} to 134.0 x10^3 kg ha^{-1} , an increase of about 92.00 x10^3 kg ha^{-1} . Of this amount, the increase of 72.00 x10^3 kg ha^{-1} was recorded between the 5-and 8-year periods, pointing to the sigmoid nature in the growth of teak in these plots.

Biomass estimates of the undergrowth vegetation and the ground litter can also be seen in Table 1. The biomass of the undergrowth (stems and leaves) was highest in the youngest plot and declined steadily with the age of the plot. The leaf litter was low in the youngest plot and highest in the 8-year and 11-year plots, before declining in the oldest plot. The biomass of dead branches was highest in the youngest and oldest plots and lowest in the 8- and 11- year plots. The estimates of the biomass of fruits and /or seeds under teak showed some consistency; it was quite low in the 5-year plot and highest in the 8-year plot, declining again in the 11-year and 14-year plots.

The total biomass under teak showed that more organic matter accumulated in the 5 and 14 year plots, while the least was recorded in the 11-year plot. The trend resembles the biomass estimates for the leaves, total branches and total tree earlier analysed.

The trend in the biomass of the leaf litter resembled that of the leaf and branch biomass (Table 1); it built up to a maximum value in the 8-year plot and then declined. The biomass of the dead wood and fruit and / or seed litter was inconsistent as it did not follow any definite trend. The biomass under teak showed that much more was accumulated in the 8-year plot than in any other plot.

The mean annual change in biomass of the various tree components is tabulated in Table 2. Except for those of the floral parts which were highly inconsistent, in all other components , the annual change in organic matter approached that of a logistic curve; it started off gradually in the 5th year, attained a maximum value at about the 8th and declined gradually up to the 14th year. In all cases, the mean annual change in biomass was highest in the first 8 years. This suggests that the period of maximum biomass must be around this age.

The percentage contribution of the major tree components to the overall biomass (Table 3)

Table 2. Mean annual increase in biomass (x10^3 kg ha^{-1}) based on Model 1.

Age (years)	5	8	11	14
Leaves	1.00	0.72	0.41	0.34
Floral parts	-	0.06	0.06	0.02
Dead branches	0.05	0.57	0.23	0.22
Branches > 5 cm	-	0.92	0.86	0.65
Branches < 5 cm	1.47	1.91	1.16	1.00
Total branch	1.47	2.84	3.02	1.65
Bole	5.94	10.12	7.65	7.36
Total	8.47	14.31	10.36	9.59

Table 3. Percentage distribution of biomass in an age series among the various tree components, based on model 1.

Age (years)	5	8	11	14
Leaves	11.8	5.0	4.0	3.6
Floral parts	-	0.4	0.5	0.2
Dead branches	0.6	4.0	2.2	2.3
Living branches	17.4	19.8	19.5	17.2
Bole	70.2	70.8	73.8	76.7

increased in the order : leaves, living branches, bole. The percentage contribution of the leaf biomass decreased with the age of the plots, while that of the dead branches reached its peak at 8 years, before declining in the 11 and 14 years. Between the 5-and 8-year plots, leaf biomass contribution had fallen from about 12% to 5%, while the decline in the subsequent years was more gradual. The contribution of the floral parts reached its maximum by the 11th year. Remarkably, the contribution of the bole biomass increased steadily with the age of the plot.

In comparing the mean of the non-photosynthetic and photosynthetic biomass, it became clear from Table 4 that dry matter accumulation per unit of photosynthetic material was increasing with the age of the plot. For instance, the 14-year plot accumulated about three times more non-photosynthetic biomass than the 5-year plot, while the photosynthetic biomass reached its peak at age 8, before declining. Conversely, the percentage contribution of photosynthetic material to the total biomass was much less and decreased steadily with age.

Discussion

Because it is usually difficult to make measurements of a single tree over its complete lifespan, biomass studies in an age series provide a convenient way of obtaining information on the growth and development trends of trees or plantations. And so, in order to discuss the biomass production and distribution, the four plots will be assumed to represent the progressive development of a stand over years.

The inconsistency in the biomass trends of the floral parts as well as the obvious poor, size-weight relationship might have to do with the differing periods of flowering in teak. Longman & Jenik (1974) observed that the onset of the reproductive phase does not occur in most trees until they have attained a certain age. They also reported that half of the trees in some teak plantations near Ibadan started flowering 5 ½ years after planting. In the present study, of the ten trees sampled in the 5-year plot, two were in flower and this agrees fairly well with the observation of Longman & Jenik (1974). In contrast, the older plots had more trees with flowers. The onset of the reproductive phase is known to be related to genetic and some

Table 4. The ratio of the mean of non-photosynthetic/photosynthetic biomass and the percentage of non-photosynthetic and photosynthetic biomass of teak in an age series.

Age (years)	5	8	11	14
Total non-photosynthetic biomass (x 10^3 kg ha^{-1})	37.33	108.70	109.50	129.47
Mean	0.13	0.40	0.40	0.52
Total non-photosynthetic biomass (x 10^3 kg ha^{-1})	5.01	5.74	4.50	4.80
Mean	0.02	0.02	0.02	0.02
Ratio of non-photosynthetic/ photosynthetic biomass	7.4	18.9	24.3	27.0
Percentage of photosynthetic biomass	11.7	5.0	3.9	3.6

Note: The mean values were obtained by dividing biomass by the corresponding total number of trees in the plot. The total number of trees in each plot was 296, 272, 275, and 247 for the 5, 8, 11 and 14-year plots, respectively.

environmental factors as well as size and age of the trees. Fogg (1975) also reported that nutritional factors have some effect on reproduction. In general, for most crops under similar edaphic conditions, climatic factors may determine the degree of flowering and fruiting in any one year, as in some years flower and fruit formation might be high, while in others hardly any flowers and fruits would be formed. The degree of their production in Nigeria has always been linked with the intensity and duration of the harmattan (a dry, dusty wind that affects the whole of West Africa), more flowers and fruits being formed if the harmattan is more intense and more prolonged, but the physiological and ecological bases of this have not been studied. However, the variability in the flower and fruit formation in the plots under consideration cannot be attributed to variations in climate alone since they are less than two kilometres away from each other. From the data available, it appears that the formation of flowers and fruits does not become appreciable until much later in the life cycle, perhaps from the 8th year or older.

Of the environmental factors, light might be the most important, with relatively low light tending to reduce flowering. In the present study, it was observed that even small-suppressed trees which were exposed to full sunlight did flower, while those shaded by the dominant tree did not. Auxins, such as indole-acetic acid, and gibberellic acid, are also known to influence flowering and Kio (Personal communication) suggested that the influence of environmental factors on flowering may be exerted, in part, through their effects on the auxin economy of the plant.

Comparisons with other published data are difficult to make because most, such as Egunjobi (1976), Egunjobi & Bada (1979), Forrest & Ovington (1970), Kadeba & Aduayi (1982), Kira & Shidei (1967), Onyekwelu (2006), Ovington *et al.* (1967), Shanmughavel & Francis (2001), who have attempted to compare the efficiency of the biomass estimates of the tree components, have either omitted the flower or have worked on very young plots where flower and fruit formation had probably not started. However, Ovington (1957) reported that no appreciable cone-formation took place in *Pinus sylvestris* until about the 14th year, after which the weight of the cones per tree tended to increase considerably with the age of the tree.

The trend in the dry weight of dead wood conforms with the morphological observations made in the field. In the youngest plot most of the branches were still alive as little self-pruning had taken place. Consequently, the amount of dead wood was small. But in the 8-year plot a lot of self-pruning of the branches occurred, resulting in increased proportion of dead wood. In the 11-year old plot, much of the self-pruning had occurred in the earlier years and with it much of the dead wood was lost. This is confirmed by the fact that, at the time of sampling, the trees in this plot had more clean boles than those in the other years. The higher amount of dead wood recorded in the 14-year plot may be attributed to a probable stimulating effect which heavy self-pruning in the earlier years must have had on growth and development, leading to the formation of more branches and, therefore, additional pruning. Forrest & Ovington (1970) observed a similar trend for *Pinus radiata* plantation in Australia.

The trend in the dry weight of the leaves was similar to that of the dead wood and the explanation for this is probably similar to that of the dead wood given above.

The dry weight of living branches increased with age. In the younger plots the branches < 5 cm contributed the greatest portion of the branch biomass. For instance, in the 5-year plot only one tree recorded the dry weight of branches > 5 cm, but with the accumulation of organic matter with age, the situation changed and the contribution from branches > 5 cm increased considerably. This type of trend was also found by Egunjobi & Bada (1979) and Forrest & Ovington (1970) in their studies of *Pinus caribaea* and *Pinus radiata* plantations respectively.

The trend in the total biomass estimates (10^3 kg ha^{-1}) for teak based on model 1 confirms the observations of others notably Clark *et al.* (2004), Forrest & Ovington (1970), Kadeba & Aduayi (1982), that for a time, the growth capacity of a plant increases rapidly and, well before death, declines. This had also been observed by Fogg (1975) who concluded that this pattern is inherent in plant growth rather than the outcome of seasonal changes in environmental conditions. Odum (1971), looking at the trend in biomass changes from an ecosystem development point of view, put forward some explanations based on the trend in photosynthetic and respiratory rates with the progressive development of an ecosystem. According to Odum (1971), in early years, total organic matter production increases faster than respiratory rates so that a large net gain in organic matter productions results. However, with a progressive development of an ecosystem toward an equilibrium stage, the trend also continues to change; the increased gross primary production of organic matter results in increased respiratory activity, so that net organic matter production declines. The trend in the leaf biomass estimates can be explained in a similar manner as above. Barnes *et al*. (1998) also observed that the size and weight of the mature leaf often depend on the developmental age of the tree, as well as various other environmental factors.

The trend in the living branch biomass resembled that of the leaves. Forrest & Ovington (1970) reported a similar trend in *Pinus radiata* plantations. The problem of evaluating the dynamic relationship between branches lies in the fact that the trees prune their branches on a continual basis, even though the rate varies with the developmental age of the tree. Barnes *et al*. (1998) also explained the correlation, which exists between growth and development of the various parts of a plant in terms of supply and demand as well as the manner in which materials for growth are translocated. In general, according to them, the more actively a part is growing the more available material will be diverted to it and the more growth elsewhere will be restricted.

It is also obvious from the trend in the percentage distribution of the biomass among the various tree components (Table 3) that it is the correlation between supply and demand of organic matter with developmental age that affects such distribution. Initially, and necessitated by the need to produce a large amount of organic matter essential for growth and development, the percentage contribution of leaves in the 5-year plot, relative to that in the others, was quite high. In subsequent years, the proportion of leaves relative to the bole declined steadily. This does not necessarily imply that the leaf biomass was declining, or that it was becoming less efficient. On the contrary, the fact that the bole biomass was increasing steadily indicated that the leaves were still efficient, photosynthetically. With time, however, the dominance of the bole over the other tree components became very apparent.

By regressing the total tree biomass estimates, Y, against the corresponding plot ages, a regression equation was obtained on which predictions of the biomass status of any plot were made. This was done with the biomass estimates of the four plots and the following regression equation was obtained:

$$Y = 1.51 + 10.5X$$

where, Y = biomass (kg ha^{-1}) of the plot, and X = age of the plot in years. The regression coefficient (r) for the above regression equation was 0.88, which is quite high and indicates a near linear relationship. Table 5 summarizes the outcome of such a predictive model. The greatest weakness of the above method is that it assumes the growth pattern of teak is linear, but this has been shown not to be so by Bannister (1976) and Fogg (1975). It is because of this that the difference between the predicted and the observed for the 8-year plot is very large (Table 5). As pointed out earlier, around this period, teak growth was found to be exponential and any linear regression analysis will omit this. Another weakness of the predictive model is the low number of plots involved, that is, only four plots.

However, inspite of the weaknesses already pointed out, Forrest & Ovington (1970) were able to develop a similar relationship between the age of the plots in years and bole weight for *Pinus radiata* in Australia. Also Lugo (1974), developed a similar relationship based on biomass estimates of various tropical rain forests and their ages.

Table 5. Some predictions of biomass of teak (x10^3 kg ha^{-1}) based on the regression equation (Y = 1.51 + 10.5x) obtained by regressing total tree biomass, Y, against the age (x) the plot.

Year	Observed biomass	Predicted biomass
1	-	12.01
3	-	33.01
5	42.33	54.01
7	-	75.01
8	114.44	85.51
9	-	96.01
11	114.00	117.01
14	134.27	148.51
18	-	190.51
50	-	525.0

Teak biomass in comparison with natural forests and other timber plantations

The problem inherent in making any meaningful comparisons of biomass and productivity data include, but are not limited to: the different methods employed, variations in the tree components measured, the units of measurement, the ages of the plots, the number of trees per unit area and the sizes of the trees measured. In spite of these limitations, an attempt was made to compare the productivity data for teak with those of natural forests and other plantation species.

Biomass data for natural forests in Nigeria based on a method similar to the one used in the present study are hard to come by. Ola-Adams (1974) did, however, estimate the biomass of most of them from their volume and specific gravity data. Based on this, he obtained the biomass estimates of four major Nigerian forest types (Table 6).

Table 6. Estimated biomass of forest types.

Forest Type	Estimated Biomass ($\times 10^3$ kg ha^{-1})
High Forest	149.9 – 350.9
Disturbed Forest	87.9 – 128.3
Lowland Forest	74.1 – 165.2
Swamp Forest	87.2 – 193.3

From Table 5, it is apparent that, with the exception of that of the high forest, the biomass estimates for the 8,11, and 14-year plots of teak fall within these ranges. A problem to any meaningful comparison is that the ages of the forests were not given, but it is very probable that they were considerably older than those of the teak plantations studied.

Greenland & Kowal (1960) determined the biomass of a 50-year-old rainforest at Kade, Ghana, and estimated its biomass to be 360 x 10^3 kg ha$^{-1.}$ Also, *Bartholomew et al.* quoted by Greenland & Kowal (1960) estimated the biomass of an 18-year old secondary forest at Yangambi, Congo (now Zaire) at about 177 x 10^3 kg ha$^{-1.}$ If predictions are made for teak, based on the regression equation, $Y = 1.51 + 10.5\ X$, the following estimates, 190.5 x 10^3 kg ha^{-1} and 525.0 x 10^3 kg ha^{-1} are formulated for the 18-year old and 50-year old plots respectively. The teak biomass, therefore, compares favourably with the biomass data reported by Bartholomew *et al.* and Greenland & Kowal (1960) for those different ages, with the 50-year old teak plot being much more productive than a 50-year old natural forest.

Whitmore (1991) discussed the productivity data from estimates made in Thailand and in Ivory Coast. The mean annual biomass increase was estimated at 9 x10^3 kg ha^{-1} yr^{-1} for the Ivory Coast forest and 6.5 x10^3 kg ha^{-1} yr^{-1} for the Thailand forest. It must be pointed out that these estimates represent the net primary productivity of these forests since an account had been taken of losses due to tree mortality, death of branches and roots and herbivory. It is significant to point out that even without taking care of these losses, teak still achieved the productive capacity of these two rain forest regions in about its 5th year of growth (Table 2). Although the ages of these forests were not published, they are likely to be considerably older that the teak plantations studied.

Using the same method, Ola Adams (1974) also estimated the biomass of a number of plantations of timber species. His mean annual biomass estimates are given in Table 7.Egunjobi (1975) estimated the biomass of a 6-year-old *Pinus caribaea* L. plantation at Ibadan to be in the range of 76-78x10^3 kg ha^{-1} , using a method similar to the one adopted in this study. This gives a mean annual biomass accrual of between 12.67-13.00 x 10^3 kg ha^{-1} . When this is compared with Ola-Adam's figure of 24.24 x 10^3 kg ha^{-1} for the same plant (Table 7) the conclusion can be reached that the latter's method over-estimated the biomass for *Pinus caribaea*. Similarly, Ola-Adam's mean annual change for teak seems quite high. He pointed out (and his estimate showed it) that *Pinus caribaea* is much more productive than teak.

Table 7. Estimated mean annual biomass increment (Ola-Adams 1974).

Species	Mean annual biomass increment (kg ha^{-1})
Nauclea diderichii	8.326
Gmelina arborea	17.935
Triplochiton scleroxylon	7.873
Cedrela odorata	9.517
Tectona grandis	17.190
Azadirachta indica	21.670
Eucalyptus camadulensis	19.929
Pinus caribaea	24.238

However, the mean annual change in biomass computed for teak in the present study seems to be quite reasonable, especially if Egunjobi's data for *Pinus caribaea*, are accepted. The trend in Ola-Adam's data is, however, quite consistent with the fact that teak, which is an exotic timber tree is much more productive than the traditional sources of timber such as *Nauclea diderichii*, (De Wild. and Th. Dur.) Merrill *Triplochiton scleroxylon* K. Schum, and *Cedrela odorata* L. This makes teak a very suitable alternative to these more slow-growing species. Kio (1976), however, explained the comparative costs of the artificial and natural systems of regenerating high forest and arrived at the conclusion that it would not be in the long-term interest of tropical countries if all the high forest reserves are converted to plantations.

Conclusions

The log : log allometric model of the type, $\log_e Y = a + b \log_e x$, which was found to be the most suitable regression model, was used as the predictive model to estimate the biomass of various teak components in an age series. In general, the significance of the regression (based on the F-ratio) increased for the tree components in the order: leaves, branches, boles, total tree, suggesting that the efficiency of diameter as a predictor of biomass of these components also increases in the same direction. The predictive power of the allometric model for the dead wood and floral parts was generally not significant, indicating the poor predictive power of diameter for these components. No definite trend was discernible in the biomass trend of the floral parts, and this is probably related to the highly variable nature of flower formation observed in the study plots. It was also apparent from the study that flower formation did not become appreciable until much later in the teak life cycle, at about the 8th year. The fairly high leaf biomass in the first 8 years is thought to be linked with its role in actively providing the initial organic matter for growth and development.

Based on the age series studied, the biomass increased steadily with age, although the relative values differed significantly with time. The computed total tree biomass ($\times 10^3$ kg ha^{-1}) in an age series, with 95% confidence limit, were 42.33 ± 2.40, 114.44 ± 2.22, 114.00 ± 2.22, 134.27 ± 2.02 for the 5, 8, 11 and 14 year old plots respectively. There was also a continual accumulation of organic matter in the bole (though the rate declined with age) and this is a welcome trend in view of the importance of the bole in the timber industry. The highest proportion of dead wood was recorded in the 8-year plot in which self-pruning was observed to be actively taking place. Low values of dead wood for the other plots could be attributed to minimal self-pruning (as in the youngest plots) or to the fact that much self-pruning had already taken place (as in the oldest plots).

Initially, the percentage contribution of leaves to the overall biomass was quite high, but declined steadily with age, while that of the bole increased steadily with age, but, again, the relative values differed with age. The computed percentage contribution of organic matter by the various tree components emphasised the changing pattern of organic matter accumulation and distribution with developmental age, while the trend in the biomass of the undergrowth was related to the degree of the observed canopy closure.

In terms of biomass production, teak compares well with most natural forests. It is also much more productive than the equivalent age of natural plantations of some forest species. It is, therefore, recommended as a good alternative source of timber in Nigeria, although further studies are necessary in order to determine its maximum biomass production capacities in the sites where the other species are currently grown.

Acknowledgements

We gratefully appreciate the scholarship awarded to first author for postgraduate studies by the University of Ibadan and the generous funding of the project by the Department of Plant Protection and Environmental Biology of the same University.

References

Bannister, P. 1976. Physiological ecology and plant nutirtion. pp. 229-296. *In*: S.B. Chapman (ed.) *Method in Plant Ecology*. Blackwell Scientific Publication, Oxford.

Barnes, B.V, D.R. Zak & S.R. Denton. 1998. *Forest Ecology*. 4th edn. John Wiley and Sons, New York.

Buvaneswaran, C.M. George, D. Perez & M. Kanninen. 2006. Biomass of teak plantation in Tamil Nadu, India and Costa Rica compared. *Journal of Tropical Forest Science* **18**: 195-197.

Clark, K.L, H.L. Gholz & M.S. Castro. 2004. Carbon dynamics along a chronosequence of slash pine plantains in North Florida. *Ecological Applications* **14**: 1154-1171.

Dreschsel, P., S. Schmall & W. Zech. 1990. Relationship between growth, mineral nutrition and soils in young teak plantations in Benin and Liberia. *Water, Air and Soil Pollution* **54**: 651-656.

Egunjobi, J.K. 1975. Dry matter production by an immature stand of *Pinus caribaea* L. in Nigeria. *Oikos* **26**: 80-85.

Egunjobi, J.K. 1976. An evaluation of five methods for estimating biomass of an evenaged plantation of *Pinus caribaea* L. *Oecologia Plantarum* **11**: 199-206.

Egunjobi, J.K. & S.O. Bada. 1979. Biomass and nutrient distribution in stands of *Pinus caribaea* L. in the dry forest Zone of Nigeria. *Biotropica* **11**: 130-135.

Fogg, G.E. 1975. *The Growth of Plants*. Penguin Books, Middlesex.

Forrest, W.G. & J.D. Ovington. 1970. Organic matter changes in an age series of *Pinus radiata* plantations. *Journal of Applied Ecology* **7**: 177-186.

Greenland, D.J. & K.M.L. Kowal. 1960. Nutrient contents of the moist tropical forest of Ghana. *Plant and Soil* **12**: 154-174.

Hiratsuka, M., T. Toma, T.N. Mindawati, I. Henansyah & T. Morikawa. 2004. Biomass of man-made forest of timber tree species in the humid tropics of West Java, Indonesia. *Journal of Forest Research* **10**: 487-491.

Kadeba, O. & E. A. Aduayi. 1982. Biomass production in *Pinus caribaea* L. of different ages in the Savannah Zone of Nigeria. pp. 53-57. *In*: R.L. Ballard & S.P. Gessel (eds.) *I.U.F.R.B. Symposium on Forest Site and Continuous Productivity*. US Department of Agriculture. Portland.

Kio, P.R.O. 1976. What future for natural regeneration of tropical high forest? An appraisal with examples from Nigeria and Uganda. *Commonwealth Forestry Review* **55**: 309-318.

Kira, T. & T. Shidei. 1967. Primary production and turnover of organic matter in different forest ecosystems of the Western Pacific. *Japanese Journal of Ecology* **17**: 70-87.

Liddel, M.J., N. Nieullet, O.C. Campoe & M. Freiberg. 2007. Assessing the above-ground biomass of complex tropical rainforest using a canopy crane. *Austral Ecology* **32**: 43-58.

Longman, A.K. & J. Jenik. 1974. *Tropical Forest and its Environment*. Longman, London.

Losi, C.J., T.G. Siccama, R. Condit & J.E. Morales. 2003. Analysis of alternative methods of estimating carbon stock in young tropical plantations. *Forest Ecology and Management* **184**: 355-368.

Lugo, A. 1974. Tropical ecosystem structure and function. pp. 67-111. *In*: E.G. Franworth & F.B. Golley (eds.) *Fragile Ecosystems: Evaluation of Research and Application in the Neotropics*. Springer-Verlag, New York.

Mountford, M.D. & R.G.E. Bunce. 1973. Regression sampling with allometrically-related variables, with particular reference to production studies. *Forestry* **46**: 203-212.

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

Odum, E.P. 1971. *Fundamentals of Ecology*. 3rd edn. W.B. Saunders, Philadelphia.

Ola-Adams, B.A. 1974. Estimation of biomass and productivity of some natural forests and plantation in Nigeria. *Nigerian Journal of Forestry* **4**: 18-23.

Onyekwelu, J.C. 2006. Growth, biomass yield and biomass function for plantation grown *Nauclea diderichii* (De Wild. and Th. Dur.) Merrill in the humid tropical rainforest zone of South-Western Nigeria. *Bioresource Technology* **98**: 2679-2687.

Ovington, J.D. 1957. Dry matter production by *Pinus sylvestris* L. *Annals of Botany* **21**: 287-314.

Ovington, J.D., W.G. Forrest & J.E Armstrong. 1967. Tree biomass estimation. pp. 4-31. *In*: H.E. Young. *Symposium on Primary Productivity and Mineral Cycling in Natural Ecosystems*. University of Maine Press.

Pitto, D., F. Montaginini, M. Kanninen, L. Ugalda & E. Viquez. 2004. Forest plantations in Costa Rica and Nicaragua: performance of species and preference of farmers. *Journal of Sustainable Forestry* **18**: 59-77.

Reichel, D.E. 1970. *Analysis of Temperate Forest Ecosystems*. Springer Velag, Berlin.

Segura, O. & M. Kanninen. 2005. Allometric models for estimating volume and total aboveground biomass of seven dominant tree species in a tropical humid forest in Costa Rica. *Biotropica* **37**: 2-8.

Shanmughavel, P & K. Francis. 2001. Bioproductivity and nutrient cycling in bamboo and acacia forests. *Bioresource Technology* **80**: 45-48.

Singh, M. 1975. The theory of production methods. *Tropical Ecology* **16**: 14-27.

Steel, R.G.D. & J.H. Torrie. 1960. *Principles and Procedures of Statistics*. McGraw-Hill Book Co, New York.

Taylor, G. Jr. 1972. Phenodynamics of production in a mesic deciduous forest. pp. 133-124. *In*: H. Lieth & S.C. Stearns (eds.) *Proceeding of Symposium on Phenology and Seasonality Modelling*. University of Minnesota, Oak Ridge, Tennesee.

Whitmore, T.C. 1991. *An Introduction to Tropical Rain Forest*. Clarendon Press, Oxford.

Whittaker, R.H. & G.M. Woodwell. 1968. Dimensions and production relations of trees and shrubs in the Brookhaven forest. *Journal of Ecology* **56**: 1-25.