

## RADIATION USE EFFICIENCY AND ABOVE-GROUND BIOMASS PRODUCTION OF SELECTED FOREST TREE SPECIES

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### Abstract

*Radiation use efficiency (RUE), defined as biomass produced per unit of radiation intercepted, is considered a genotype-specific constant. If the amount of radiation intercepted is known, RUE can be used to predict the potential biomass production of a given tree species. A comparative growth analysis was done on some selected species, with the objective of determining their light interception characteristics, biomass production, and RUE. Similar-aged seedlings of six forest tree species: Acacia mangium, Eucalyptus grandis, Leucaena leucocephala, Swietenia macrophylla, Azadirachta indica, and Tectona grandis, were planted at the university farm, Peradeniya, from July 1995 to June 1996. Regular sampling was done to determine above-ground biomass and leaf area. Canopy radiation interception was estimated from simultaneous measurements of incident and transmitted radiation, by tube solarimeters. In all six species, above-ground biomass production was found to be linearly related to cumulative intercepted radiation. The slopes of the relationships, which indicate RUE, showed significant inter-species variation. The greatest RUE was observed in E. grandis ( $3.05 \text{ gMJ}^{-1}$ ) and the least in Azadirachta indica ( $0.296 \text{ gMJ}^{-1}$ ). The differences in RUE were primarily responsible for the differences between species in above-ground biomass production. Radiation interception by the canopies of the different species was characterized by the light extinction coefficient, which showed significant inter-species variation. These parameters offer a promising approach for modelling and prediction of biomass production by forest tree species.*

### Introduction

A high rate of above-ground biomass production is an important criterion in the selection of tree species for plantation forestry. Biomass production can be quantified on the basis of the primary physiological processes involved. One such approach is to quantify the capacity for interception of incident radiation by the tree canopy, and the tree's efficiency in using intercepted radiation to produce biomass by photosynthesis. A clear linear relationship exists between biomass accumulation and cumulative radiation interception in almost all annual agricultural crops (Monteith, 1977). The slope of this linear relationship, ie: the amount of biomass produced per unit of radiation intercepted, is defined as the radiation use efficiency

(RUE), which is a measure of the efficiency of the photosynthetic process. Several workers have shown that this mechanistic, process-based approach can be adopted also for the analysis of the growth of forest tree species (Jarvis & Leverenz, 1983; Linder, 1985; Landsberg, 1986; Cannell, 1989).

Reforestation has been an urgent need in Sri Lanka, especially during the last two decades, because of the increasing rate of deforestation (Bandarathillake, 1994). In view of the wide variability of the climatic conditions in different parts of the country, and the specific adaptability of different tree species to different environmental conditions, it is prudent to use a wide range of tree species in reforestation programmes. In the present study a selected group of tree species were screened at the seedling stage for radiation interception characteristics and RUE, with a view to demonstrating the possibility of using these criteria for species selection.

### Materials and methods

#### *Stand establishment and management*

A field experiment was conducted between June 1995 and July 1996, at the university farm at Peradeniya, in the mid-country wet zone, on an alluvial soil. Similar-aged seedlings of six tree species: acacia (*Acacia mangium*), eucalypt (*Eucalyptus grandis*), leucaena (*Leucaena leucocephala*), mahogany (*Swietenia macrophylla*), neem (*Azadirachta indica*), and teak (*Tectona grandis*), were planted in separate blocks. Spacing was 60 × 60 cm for acacia and 30 × 30 cm for the other species. Each block formed a uniform stand of 200 seedlings of one species. The blocks were laid out in an open field which received solar radiation directly, without any obstruction. The plants were grown completely rain-fed without any supplementary irrigation. No fertilizer was added, but diseases and pests were controlled by chemical applications.

#### *Measurements*

Growth, in terms of above-ground biomass accumulation, was measured by periodic destructive harvesting, at 175, 188, 202, 215, 248, 261, 282, 300, and 309 days after planting. Each harvest consisted of 5 plants, randomly selected but excluding outside rows. The total leaf area per plant was measured by an automatic leaf area meter. The leaf-area index was calculated as the leaf area per unit ground area. Leaf and stem dry weights were obtained by oven drying to a constant weight at 80°C.

Radiation interception measurements were made at weekly intervals on a pre-designated area in the middle of each block during the midday period between 1000 and 1400 hours. Two tube solarimeters (1 m long and 3 cm diameter) were used, of the type described by Szeicz et al. (1964). Each measurement consisted of two simultaneous solarimeter readings for a duration of 15 minutes. Total radiation incident on each tree canopy was measured by one solarimeter placed in open ground. The amount of radiation transmitted through each tree canopy was measured by the second solarimeter placed at ground level within the tree stand, in an exactly horizontal position, at an angle of 90° to the tree rows. The voltage outputs

generated by the two solarimeters were recorded and stored by an automatic data logger (CR10, Campbell Scientific Co. Ltd.).

**Theory and calculation of RUE**

The relation between cumulative standing biomass (W) and cumulative amount of radiation intercepted (R<sub>i</sub>) can be given as:

$$W = (\text{RUE}) R_i \dots\dots\dots(1)$$

R<sub>i</sub> for the periods between successive harvests was calculated by integrating the estimated daily radiation interception (R<sub>i</sub>)<sub>d</sub> by each of the different tree canopies.

$$R_i = \int_{t_1}^{t_2} (R_i)_d dt \dots\dots\dots(2)$$

where, t<sub>1</sub> and t<sub>2</sub> are the times of two successive destructive harvests.

(R<sub>i</sub>)<sub>d</sub> can be computed as the product of daily incident radiation (I<sub>d</sub>) and the fraction of incident radiation intercepted by the tree canopy (f<sub>i</sub>):

$$(R_i)_d = I \cdot f_i \dots\dots\dots(3)$$

f<sub>i</sub> was determined by the simultaneous measurements of the two solarimeters as:

$$f_i = (I - T)/I = 1 - (T/I) \dots\dots\dots(4)$$

where I and T are the incident and transmitted radiation respectively, as measured simultaneously by the two solarimeters.

The fraction of incident radiation transmitted beneath a canopy (T/I) is determined by the leaf area index (L) and leaf orientation of the respective canopies, according to the relationship described by Monsi & Saeki (1953):

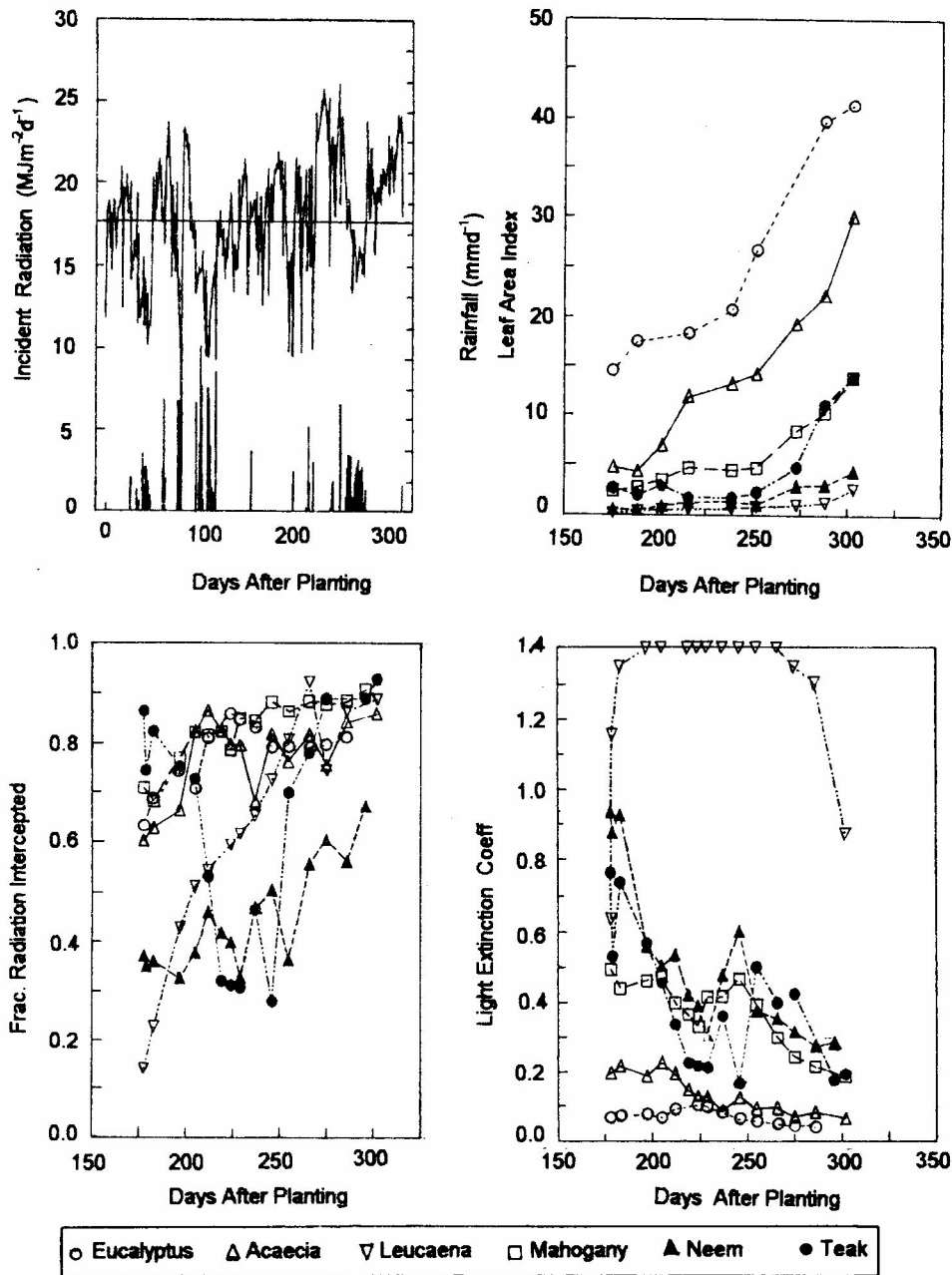
$$(T/I) = e^{-kL} \dots\dots\dots(5)$$

and  $f_i = 1 - e^{-kL} \dots\dots\dots(6)$

where, k is a measure of the leaf orientation of the canopy, known as the canopy light extinction coefficient. Equation 5 was used to compute periodic k values for the different tree canopies from periodically measured values of T, I, and L. Calculation of periodic k values enabled computations to be made of f<sub>i</sub> for the days on which radiation interception was not measured (ie: for days between two successive solarimeter measurements), by equation 6.

The estimated values of f<sub>i</sub> for the different tree canopies were then used in equation 3 to compute (R<sub>i</sub>)<sub>d</sub>. The daily totals of incident radiation (I) required in equation 3 were computed from the values of daily sunshine duration (S) measured by a sunshine recorder. Conversion of S to I was by the following empirical equation, developed by Samuel (1991):

$$I = I_0 [a + b (S/Z)] \dots\dots\dots(7)$$



Figures 1, 2, 3 & 4. Variation of incident radiation, rainfall, leaf area index, fraction of incident radiation intercepted and canopy light extinction coefficient during the experimental period. for eucalypt, acacia, leucaena, mahogany, neem and teak. Horizontal line in Fig. 1 is the long-term average of daily incident radiation.

where  $I$  is the daily global radiation ( $\text{MJm}^{-2}\text{d}^{-1}$ ) incident on tree canopies;  $I_0$  is the daily global radiation ( $\text{MJm}^{-2}\text{d}^{-1}$ ) at the top of the atmosphere;  $S$  is the measured sunshine duration (hours) and  $Z$  is the day length (hours). The parameters  $a$  and  $b$  depend on the location; the respective values for Peradeniya (latitude  $7.27^\circ\text{N}$ ) are 0.27 and 0.42 (Samuel, 1991). Daily values of  $I_0$  and  $Z$  for the period of the experiment were computed by a set of meteorological equations (Rosenberg et al., 1983; Monteith and Unsworth, 1990).

Calculation, by equation 3, of the daily radiation intercepted ( $R_i$ )<sub>d</sub> enabled the radiation intercepted during the periods between successive harvests ( $R_i$ ) to be computed, by equation 2.

Finally, RUE was estimated for each tree species by fitting a linear regression between the respective values of standing biomass ( $W$ ) and periodic  $R_i$  (equation 1).

## **Results**

### ***Meteorological conditions***

Daily incident solar radiation showed considerable fluctuations around the long-term average value of  $17.6 \text{ MJm}^{-2}\text{d}^{-1}$  (shown by the horizontal line in Fig. 1). The average incident radiation during the experimental period was  $17.86 \text{ MJm}^{-2}\text{d}^{-1}$ . The rainfall record (Fig. 1) showed that there were several periods of drought during the experimental period.

### ***Canopy growth***

Canopy growth as measured by the leaf-area index (LAI) showed significant differences between the species tested (Fig. 2). Eucalypt and acacia had extremely high rates of LAI growth and developed very high LAI values. In contrast, neem and leucaena had very low rates of leaf area increase which resulted in very low LAI values, even 10 months after planting. Mahogany and teak underwent periods of very slow LAI growth during the drought period, until 250 days after planting (DAP). However, during the subsequent period, these two species showed rates of LAI growth which were comparable to those of eucalypt and acacia. Consequently, they (mahogany and teak) had intermediate levels of LAI at the end of the experimental period.

### ***Radiation interception characteristics***

The radiation interception capacity of the different tree canopies can be described in terms of the fraction of incident radiation intercepted,  $f_i$  (Fig. 3) and the canopy light extinction coefficient  $k$  (Fig. 4). There were clear differences between the tree species in both the above characteristics. Eucalypt and acacia had higher values of  $f_i$  throughout the experimental period. These two species also had significantly lower  $k$  values, indicating a canopy structure with relatively more erect leaves. The lower  $k$  values also signified that there were more "gaps" in the canopy resulting from smaller and more erect leaf elements. Mahogany also maintained a high  $f_i$  throughout the experimental period, but with a considerably smaller canopy than eucalypt or acacia. This meant that the canopy had more horizontally-oriented

leaves and fewer gaps, as was confirmed by the  $k$  values, which were higher than those of eucalypt and acacia. Teak also had a high level of  $f_i$  at the beginning of the experimental period. However, there was a considerable decrease in its light interception between 205 and 246 DAP. The decrease coincided with the very dry months of February and March, when a slight reduction in LAI was observed in teak (Fig. 2) due to leaf shedding. After a rapid increase of the LAI, the  $f_i$  values of teak increased again (Fig. 3). The  $k$  values of teak during the initial period (178-205 DAP) were significantly higher than those of eucalypt, acacia, and mahogany. These high values were clearly related to the more horizontally oriented and considerably larger leaves of teak, which allowed very little in the way of gaps in the canopy. The increase of gaps following leaf shedding is shown by the decrease of  $k$  during the period 205-246 DAP (Fig. 4). At the beginning, leucaena had a very small  $f_i$ . Despite its very slow canopy growth, the  $f_i$  of leucaena showed a rapid increase throughout the experimental period. This increase was possible because of the almost perfectly horizontal orientation of leucaena leaves, confirmed by very high  $k$  values. Neem also showed a continuous, but relatively slow increase of  $f_i$  throughout the experimental period. The  $k$  value of neem showed a continuous decrease from a very high to a low level during the course of the experiment. This pattern of  $k$  values indicated a canopy architecture with more horizontal leaves at the beginning, and a shift towards a more vertically oriented canopy as the LAI increased. This trend of decreasing  $k$  with increasing LAI was common to the canopies of all tree species tested here.

### ***Biomass production***

The comparative patterns of biomass production (Fig. 5) of the different species were similar to those of LAI. Eucalypt and acacia had the highest rates of biomass growth. However, growth rates were extremely low during the drought period between 197 to 256 DAP, i.e. February and March 1996 (Fig. 1). All other species had biomass growth rates significantly lower than those of eucalypt and acacia. Teak, mahogany, and leucaena, however, showed significant increases in growth rates during the period subsequent to 256 DAP. This period coincided with substantial rainfall following drought (Fig. 1).

### ***Radiation use efficiency (RUE)***

The mean RUE of the different tree species, estimated for the 303 day period of the experiment, is shown as the slope of the relation between biomass accumulation and cumulative intercepted radiation (Fig. 6). The tree species tested differed significantly in their mean RUE (Table 1). Eucalypt and acacia had the greatest values, whereas neem had the least. Leucaena, teak, and mahogany had intermediate values. While the mean RUE over the total duration of the experiment was useful for comparing the overall biomass production efficiency, there were noticeable within-species variations in some species (Fig. 6). Despite having high mean RUE, eucalypt and acacia showed significant reductions in RUE during the severe drought period. On the other hand, leucaena and teak showed a significant increase in RUE after the severe drought was relieved by rains during April (Fig. 1). Neem and mahogany did not show significant within-species variation.

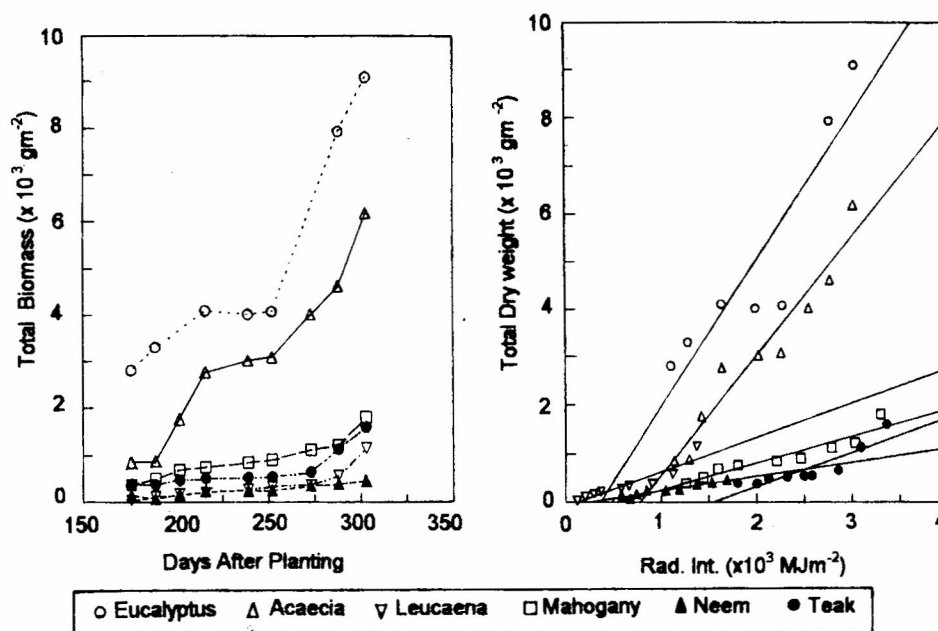


Figure 5: (Left) Accumulation of biomass during the experimental period.

Figure 6: (Right) Relationship between biomass production and radiation interception.

Table 1 : Radiation interception, biomass production and radiation use efficiency (RUE) of selected tree species over a period of 303 days

Species	Total intercepted radiation (MJ/m <sup>2</sup> )	Overall % of incident radiation intercepted	RUE ± Standard Error (g/MJ)	Final biomass (g/m <sup>2</sup> )	Adj. R <sup>2</sup>
eucalypt	3057	54.0	3.05 ± 0.59	9090	0.93
acacia	3024	53.4	2.48 ± 0.25	6179	0.81
leucaena	1377	24.3	0.71 ± 0.11	1148	0.88
mahogany	3303	58.3	0.55 ± 0.07	1809	0.76
teak	3366	59.4	0.70 ± 0.14	1595	0.90
neem	1690	29.8	0.30 ± 0.03	454	0.83

### Discussion

The results of the present study showed that significant differences exist between different tree species in the efficiency of radiation use in biomass production, as quantified by RUE.

This variation in RUE indicates differences in the efficiency of the physiological processes responsible for biomass production, which include photosynthesis, respiration, and the conversion of photosynthates to biomass. Extensive work with annual crop species has shown that RUE has a constant value for a given species when the plants are growing under non-limiting conditions (Monteith, 1977). The RUE of a tree species is also likely to be constant when it is growing under the environmental conditions which are optimum for its growth (Landsberg, 1986). Therefore, RUE can be used as a predictor of the biomass production potential of different species when they are being screened for plantation forestry. It was evident from the present study that the RUE of a given tree species decreases under non-optimum growing conditions such as drought or shortage of nutrients. Adequate quantification of the variation of RUE under non-optimum conditions could extend the use of RUE to predict the actual biomass production of different tree species under a wider range of conditions.

### References

- Bandarathillake, H.M. (1994). *Administration Report of the Conservator of Forests, Sri Lanka for the year 1994*. Forest Department.
- Cannell, M.G.R. (1989). *Light interception, light use efficiency and assimilate partitioning in poplar and willow stands*. In J.S. Pereira and J.J. Landsberg (Eds.). *Biomass production by fast-growing tree species pp. 1-12*. Dordrecht, Netherlands. Kluwer Academic Publishers.
- Jarvis, P.G. and Leverenz, J.W. (1983). *Productivity of temperate, deciduous and evergreen forests*. In O.L. Lange, P.S. Nobel, C.B. Osmond and H. Zeigler (Eds.) *Encyclopedia of plant physiology*, Vol. 12D. *Physiological plant ecology. IV Ecosystem processes: mineral cycling, productivity and man's influence pp. 233-280*. Berlin, Springer-Verlag.
- Landsberg, J.J. (1986). *Physiological ecology of forest production*. London, Academic Press.
- Linder, S. (1985). *Potential and actual production of Australian forest stands*. In J.J. Landsberg and W. Parsons (Eds.) *Research for forest management pp. 11-35*. Melbourne, CSIRO.
- Monsi, M. and Sacki, T. (1953). The light factor in plant communities and its significance for dry-matter production. *Japanese Journal of Botany* **14**, 22-52.
- Monteith, J.L. (1977). Climate and the efficiency of crop production in Britain. *Philosophical Transactions of the Royal Society (London)*, Series B **281**, 277-294.
- Monteith, J.L. and Unsworth, M.H. (1990). *Principles of environmental physics*. 2nd Edition. London, Edward Arnold.
- Rosenberg, N.J., Blad, B.L. and Verma, S.B. (1983). *Microclimate: the biological environment*. New York, John Wiley & Sons.
- Samuel, T.D.M.A. (1991). Estimation of global radiation in Sri Lanka. *Solar Energy* **47**, 333-337.
- Szeicz, G., Monteith, J.L. and dos Santos, J. (1964). A tube solarimeter to measure solar radiation among plants. *Journal of Applied Ecology* **1**, 169-174.