

Ecosystem Level Carbon and Net Primary Productivity of an Old-Growth and a Regenerating Humid Tropical Forest of North-Eastern India

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Abstract

Ecosystem level carbon and net primary productivity (NPP) estimates for old-growth and regenerating tropical forests of India are lacking. The study was conducted to estimate ecosystem level carbon contents and NPP, based on above and below ground biomass of trees, shrubs and herbs in an old growth and a regenerating humid tropical forest of Nongkhyllem Wildlife Sanctuary, Meghalaya in north-eastern India. Soil carbon contents were also estimated in both the forest types to estimate ecosystem level carbon. The tree above ground biomass values in old-growth and regenerating forests were 313.8 and 152.4 Mg ha⁻¹ and the below ground values were 50.8 and 30.3 Mg ha⁻¹, respectively. The corresponding total above ground biomass values including trees, litter, herb and shrub components were 323.7 and 159.3 Mg ha⁻¹, respectively. Of the total ecosystem biomass values of 374.5 Mg ha⁻¹ in the old-growth forest, 86% was in the above ground and 14% was in the below ground compartment. The corresponding proportions in the regenerating forest with total biomass of 189.6 Mg ha⁻¹ were 84% and 16%, respectively. The total ecosystem carbon contents in old-growth and regenerating forests were 265.5 and 147.8 Mg C ha⁻¹, of which soil organic carbon was 83.2 and 55.6 Mg C ha⁻¹, respectively that contributed 31.3% and 37.6% to the total ecosystem carbon in the respective forests. However, ecosystem NPP in the regenerating forest (18.4 Mg ha⁻¹ yr⁻¹) was greater than the old growth forest (13.6 Mg ha⁻¹ yr⁻¹).

Key words: Above ground biomass, Below ground biomass, Old growth forest, Regenerating forest, Net primary productivity, North-eastern India.

1. Introduction

Carbon cycle is one of the most important biogeochemical cycles of the earth, and its study in different ecosystems has increasingly become important as the concentration of CO₂ in the atmosphere continues to rise. One of the major challenges of forest management for effective carbon sequestration is the quantification of carbon stock in different forests (Montero *et al.*, 2005). Terrestrial carbon sequestration in above ground woody biomass has received much attention recently, as it is a promising carbon sink to mitigate global warming. Carbon stored in vegetation can be modified through silvicultural practices such as crop rotation length and thinning regime. Although many types of carbon sequestration have been identified, this study focuses on terrestrial sequestration of carbon in forest ecosystem where the above ground woody biomass is the main carbon pool.

Tropical forests are critical to the global carbon cycle because about half of the world's biomass carbon and 14% of the world's soil carbon is located in these forests (IPCC, 2000). The tropical forests spread over 13.76 million sq km area worldwide and accounts for 60% of the

global forests (FAO, 1988, 2005). These forests significantly influences carbon cycle due to high rate of net primary production (NPP) besides large pool and flux sizes (Brown and Lugo, 1982). Very few tropical forests are at their maximum potential level of biomass density because of prevailing or past cultural disturbances. The tropical forests have higher NPP and larger carbon sequestration capacity than any other forests and hence would have the potential to increase the global carbon pool beyond the present value (Brown *et al.*, 1989; Iverson *et al.*, 1993; Soni, 2003). Recent advances in estimation methods of carbon stock and flux rates have led to improved carbon estimation in the tropical forests (Malhi *et al.*, 1998, 1999; Gurney *et al.*, 2002). Carbon sequestration of tropical forests can be assessed by estimating either the carbon pool or annual carbon sequestration rate (Iverson *et al.*, 1993). The main carbon pools of a forest ecosystem are the biomass of live and dead trees, understorey plants, litter and woody debris, and soil organic matter (Pignard *et al.*, 2004). Other pools such as soluble soil carbon or higher-order producers, consumers and decomposers represent a very negligible portion of the total ecosystem carbon (Baishya and Barik, 2011).

The role of tropical old-growth forests in storing carbon remains particularly unclear (Houghton, 1991; Melillo *et al.*, 1993). Global estimation of terrestrial carbon sinks often ignores tropical old-growth forests as they are assumed to be in a state of dynamic equilibrium (Salati and Vose, 1984). Recent studies have indicated that a major portion of the above ground biomass (AGB) in old-growth tropical forests is present in large trees (Brown and Lugo, 1992; Brown *et al.*, 1995). In contrast, several researchers have argued that old-growth forests have less potential for carbon sequestration as the constituent older trees cease to grow (Terakunpisut *et al.*, 2007). As such trees generally have marginal carbon sequestration capability beyond maturity (Lal and Singh, 2000). Tropical forests world-wide have also changed into other land uses (Silver *et al.*, 2000) impacting various carbon pools. Due to large variation in complexity of forest structure and function, and also the on-going land use/ management practices at different experimental sites, it is difficult to compare and generalize tropical forest C data (Schulze *et al.*, 2000; Harmon, 2001; Clark, 2002). Therefore, there is no consistent conclusion on the role of tropical old-growth forests in carbon sequestration, i.e. whether these forests are sources or sinks of C.

Secondary and regenerating forests along the tropics are extensive and account for more than 40% of the tropical forest land. The extent of secondary forests is continuously increasing throughout the tropical region due to rapid land-use changes (Brown and Lugo, 1990; Hughes *et al.*, 1999). Quantification of carbon accumulation by secondary forests which have experienced intensive deforestation in the past would help in carbon budgeting of tropical forests with improved accuracy.

Net primary productivity and tree mortality are two key processes of forest carbon budget, both of which change over time as stands develop. Net primary production is largely a function of growing conditions and age or stage of forest development. Through photosynthesis, the organic matter is accumulated in standing live trees, in short-lived tissues such as leaves, fruits, flowers, and in the below-ground components such as coarse and fine roots. It is important to note that only increase in photosynthetic carbon fixation does not necessarily lead to carbon sequestration. The carbon must be fixed into long-lived pools. Otherwise, it would simply alter the flux sizes in the carbon cycle and will not increase carbon sequestration.

Above ground biomass is usually estimated from forest inventory data using biomass equations and expansion factors at different spatial scales (Isaev *et al.*, 1995; Schroeder *et al.*, 1997; Fang and Wang, 2001; Barrio-Anta *et al.*, 2006). Below ground biomass (BGB) is indirectly estimated from the

above ground biomass (Cairns *et al.*, 1997). Information for other biomass components such as litter, dead organic matter or soil carbon is less available, because these elements are difficult to measure and in many cases are more spatially variable than other components (Isaev *et al.*, 1995; Schlesinger and Andrews, 2000).

Allometric equations are used as a non-destructive alternative to harvest method in which tree AGB is estimated on the basis of easily measured attributes of trees such as tree height, diameter at breast height (dbh) and wood density as independent variables. The allometric relationship between AGB and dbh has been proved to be the best fit for tree biomass estimation in several forests (Brown *et al.*, 1989; Brown, 1997; Baishya and Barik, 2011). Biomass estimation method is widely used because of its simplicity and ease in deriving biomass values using regression models. Although development of best fit models is difficult and tedious initially, tree dimension value as the only input data required for subsequent estimations has made the regression-based biomass estimation method extremely popular (Baishya and Barik, 2011). The biomass present in other compartments of the ecosystem such as shrub, herb, litter, woody debris, root biomass is added to the tree AGB and BGB values to obtain the total forest ecosystem carbon pool. The total biomass data obtained from such models is then converted into carbon content for estimating carbon pools in different compartments by multiplying with a conversion factor derived from the study (Table 1).

The north-eastern region of India with 99,260 km² of tropical forests (Roy and Joshi, 2002) spreading up to an elevation of 900 m a.s.l. in the Eastern Himalayas and sub-Himalayan areas with mosaic of old growth primary and regenerating secondary forests offers appropriate situation for examining the carbon sequestration potential of old-growth forests vis-a-vis regenerating forests. These forests include undisturbed evergreen, and semi evergreen forests, secondary forests developed by shifting cultivation and forest degradation, and plantation forests raised by various agencies. With the exception of a few pockets of undisturbed forests, most tropical forests of the region are affected by one or the other form of cultural disturbances (Baishya *et al.*, 2009). The objective of the present study is to quantify and compare the ecosystem level biomass/carbon stock and net primary productivity (NPP) between tropical old-growth and regenerating broad-leaved forests of north-eastern India.

2. Study Site

The present study was conducted in two tropical forest ecosystems viz., old-growth broad-leaved forest and regenerating broad-leaved forest. While the old-growth forest represents the primary tropical forests of north-eastern India, the regenerating forest

represents the secondary forests recovering from a disturbance event. The two forest types are part of the humid tropical forest of Nongkhylllem wildlife sanctuary in Meghalaya, north-eastern India. The experimental plots lie between 25°55.578'–25°56.062' N latitude and 91°46.212'–91°46.561' E longitude. The wildlife sanctuary covers an area of 29 km² on a steep hill slope (20° to >65°) with an elevation ranging from 208 to 295 m and is 30 km from Nongpoh, the headquarters town of Ri-Bhoi district. The old-growth forest is currently undisturbed and is characterized by dense canopy and constitutes about 21% of the total sanctuary area.

2.1. Climate

The area is characterised by distinct warm-wet (May–October) and cold-dry (December–February) periods. The rainy season starts from May and extends up to October. About 90% of the total annual rainfall occurs during this period. The meteorological data were collected from the meteorological station of District Horticulture office, Government of Meghalaya located at Nongpoh. The mean total annual rainfall was 1355 mm during the years 2006–2009. The mean maximum temperature of 35°C was recorded in August and mean minimum temperature of 14°C was recorded in January.

3. Methods

The estimation of biomass/carbon pool and NPP in the tropical forest ecosystems was undertaken through the measurement/estimation of the following components: soil organic carbon (SOC), microbial biomass carbon (MBC), herb and shrub biomass, litter pool, above ground biomass (AGB) and below ground biomass (BGB). The estimation of carbon flux includes litter fall and net primary productivity (NPP). The methods for each of the above components are described below.

3.1. Field sampling

In each forest ecosystem, a forest of 20 ha area was demarcated. Six permanent plots each of size 250 m x 20 m (0.5 ha) were demarcated randomly within each forest type. In each plot, all trees with ≥ 5 cm DBH were tagged, measured and identified. The girth of each individual tree was measured and species were identified with the help of regional flora (Kanjilal *et al.*, 1934–40; Joseph, 1982; Haridasan and Rao, 1985–87). The ASSAM herbarium at Botanical Survey of India, Shillong was consulted for confirmation. Frequency, density, basal area and IVI were calculated following Misra (1968). Diversity indices i.e. Shannon's diversity index, Simpson's dominance index, and α diversity were also determined. For depicting tree population structure in the old-growth forest, all trees were grouped into 11 diameter classes i.e. >5–10, >10–20, >20–30, >30–40, >40–50, >50–60, >60–70, >70–80, >80–90, >90–100 and >100 cm. For the regenerating broad-leaved forest where the tree diameter ranges

were low, trees were grouped into first four diameter classes only i.e. >5–10, >10–20, >20–30 and >30–40 cm.

3.2. Soil sampling

Soil samples were collected from each forest type at seasonal interval over a period of three years i.e. from 2006–2009. The four seasons were: May–September (summer/rainy), October–November (autumn), December–February (winter) and March–April (spring). Soils were collected from random locations from each forest type using a steel auger (11.46 cm diameter) from the surface (0–10 cm) and subsurface (10–20 cm) layers. The soil samples collected were mixed thoroughly to obtain one composite sample for each forest type. Fresh soil was used for analysis of soil moisture content and microbial biomass C. The remaining soil was air-dried and sieved through 2 mm sieve and stored for analysis of soil organic carbon.

3.3. Soil analysis

3.3.1. Soil Organic Carbon (SOC)

SOC was determined by colorimetric method following Anderson and Ingram (1993). Soil organic matter (SOM) was obtained by multiplying the SOC content by 1.724 assuming that the SOM contains 58% carbon (Allen *et al.*, 1974). The carbon stock density of soil organic carbon was calculated following Pearson *et al.* (2007).

3.3.2. Microbial Biomass Carbon (MBC)

MBC was determined by chloroform fumigation extraction method (Vance *et al.*, 1987). The organic C in the extracts of fumigated and non-fumigated soil samples were determined by digesting 4 ml filtered extract with 0.0667 M K₂Cr₂O₇ (1 ml) and 5 ml of H₂SO₄ (98% acid) for 30 minutes. The digested samples were titrated with acidified ferrous ammonium sulphate solution using 0.3 ml (3–4 drops) of indicator (o-phenanthroline monohydrate and ferrous sulphate hexahydrate).

3.4. Plant biomass estimation

3.4.1. Evaluation of allometric models

Ten general tropical allometric models were tested for fitness of the models for determination of tree biomass for both the forest types (Table 1). The models developed by Chambers *et al.* (2001) for AGB and Cairns *et al.* (1997) for BGB estimation emerged as the best-fit models. The allometric model fitted for broad-leaved tree above ground component (AGB) was $(Y1) = \exp [-0.37 + 0.333 \cdot \ln(D) + 0.933 \cdot \ln(D)^2 - 0.122 \cdot \ln(D)^3]$ and that for below ground component (BGB) was $(Y2) = \exp [-1.0587 + 0.8836 \cdot \ln(AGB)]$.

3.4.2. Estimation of carbon content in plant biomass

The oven-dried plant components were used for determination of carbon content. 1 g of oven dried material of different plant components were taken in silica crucible and allowed to heat at 550°C for 6 hours in a muffle furnace. The carbon content was expressed as the carbon percentage (Table 2).

Table 1: Allometric models used for estimation of biomass for the broad-leaved tree species in the tropical old-growth and regeneration broadleaved forests

| Model No | Regression equation | R ² | Reference |
|----------|---|----------------|-------------------------------------|
| AGB1 | $Y = 42.69 - 12.800(D) + 1.242(D^2)$ | 0.87 | FAO. 3.2.3 (1997) |
| AGB2 | $Y = \exp \{-2.134 + 2.530 \ln(D)\}$ | 0.80 | FAO. 3.2.4 (1997) |
| AGB3 | $Y = 21.297 - 6.953(D) + 0.740(D^2)$ | 0.87 | FAO. 3.2.5 (1997) |
| AGB4 | $Y = \exp[-3.114 + 0.972 \ln(D^2H)]$ | 0.87 | Brown <i>et al.</i> (1989) (>5 cm) |
| AGB5 | $Y = \exp[-2.409 + 0.952 \ln(pD^2H)]$ | 0.88 | Brown <i>et al.</i> (1989) (>10 cm) |
| AGB6 | $Y = \exp(-2.00 + 2.42) \ln(D)$ | 0.82 | Chave <i>et al.</i> (2001) |
| AGB7 | $Y = \exp[-0.37 + 0.33 \ln(D) + 0.933 \ln(D)^2 - 0.122 \ln(D)^3]$ | 0.93 | Chambers <i>et al.</i> (2001) |
| AGB8 | $Y = 1.276 + 0.034(D^2H)$ | 0.86 | Brown and Iverson 1992 |
| AGB9 | $Y = 38.4908 - 11.7883(D) + 1.1926 D^2$ | 0.88 | Brown <i>et al.</i> (1989) |
| AGB10 | $Y = 13.2579 - 4.8945(D) + 0.6713(D^2)$ | 0.86 | Brown <i>et al.</i> (1989) |
| BGB1 | $Y = \exp[-1.0587 + 0.8836 \ln(AGB)]$ | 0.83 | Cairns <i>et al.</i> (1997) |

Table 2: Carbon content (%) in different tree components of the two tropical forest types of North-Eastern India

| Forest types | Above ground(%) | | | | | Below ground(%) | | Litter(%) | | | |
|--------------|-----------------|------|-----------------|------|------|-----------------|----------------|-----------|------|-----------------|-------|
| | Leaf | Twig | Branch/ culm | Cone | Stem | Fine root | Coarse root | Leaf | Twig | Branch/ culm | Misc. |
| Old-growth | | | 49 | | | | 47 | 48 | 47 | 48 | 47 |
| Regenerating | | | 48 | | | | 47 | 47 | 47 | 48 | 47 |

3.4.3. Estimation of herb and shrub biomass

The biomass of herbs and shrubs were estimated through harvest method following Misra (1968). Herbs were sampled from 10 plots of 1m x 1m size and shrubs from 10 plots of 5m x 5m size at seasonal interval for biomass and productivity estimation.

3.4.4. Estimation of total biomass and carbon of the forest

The total forest biomass was estimated by adding the biomass of the following components: (i) herbs and shrubs (ii) litter, (iii) tree above ground biomass and (iv) tree below ground biomass. The mean biomass value obtained from the 6 permanent plots from each forest type was presented.

3.5. Estimation of carbon flux

3.5.1. Litterfall

Litterfall was estimated at seasonal interval over a period of three years from summer, 2006 to spring, 2009 (n=60). Prior to the commencement of sampling, 1m x 1 m x 0.15 m litter traps were randomly placed in each permanent plot during spring season of 2006. The litter traps were made of bamboo culms to check litter loss through runoff water during rainy season. Five litter traps were placed in each forest type. The litter present in each litter trap were collected and brought to the laboratory. The samples were washed under a fine jet of water to remove adhered soil particles. The collected litter components were segregated into five fractions viz., leaf, twig, branch, bark and reproductive parts, and were oven dried at 80°C until constant weight. Litter biomass and annual

litter production values were based on the data recorded from summer 2006 to spring 2009.

3.5.2. Estimation of NPP

The NPP of the forest was determined from the NPP estimates for each component i.e. tree, herb, shrub and litter in the six permanent sample plots. The NPP was estimated for all the components for three consecutive years i.e. 2006-2009, and the mean values were presented. Only the positive increments in each of the component were taken into account. The tree NPP was estimated by subtracting tree biomass value estimated in July, 2006 from that of June, 2007 and biomass value in July, 2007 from that of June, 2008, and biomass value in July, 2008 from that of June, 2009, respectively and the mean biomass values were presented. The above ground NPP was determined by summing the tree NPP and annual litter production measured during the same time interval (Kira and Shidei, 1967). The annual root production was measured by sampling roots using a soil sugar during four seasons each year. The roots were washed and segregated into fine and coarse roots and the biomass was determined for each component after oven drying the samples at 80°C till constant weight was achieved. The annual root production was measured by summing up the positive increments in live root biomass and concurrent positive increment in the dead root biomass during the successive samplings (Persson, 1978). The NPP for shrubs and herbs was estimated using the biomass data for the same time interval as standing tree biomass component.

4. Results

4.1. Tree species composition and community characteristics

4.1.1. Density diameter distribution

The total tree density in the old-growth broad-leaved forest was 1090 individuals ha⁻¹, while that in the regenerating broad-leaved forest was 1728. The diameter class >5-10 cm had 372 individuals ha⁻¹ in the old-growth forest while the diameter class >10-20 cm had 950 individuals ha⁻¹ in the regenerating forest. These diameter classes contributed 34.1% and 55% to the total tree density in the respective forest type. The higher diameter classes i.e. >60 cm and >30-40 cm in old-growth and regenerating

forests, respectively had 74 and 26 individuals ha⁻¹ contributing to 6.8% and 1.5% to the total tree density, respectively.

Schima wallichii was the dominant species (IVI 25.88) in the old-growth forest. The total basal area of trees in this forest was 65.18 m² ha⁻¹. *Schima wallichii* had the highest basal area of 12.52 m² ha⁻¹. *Polyalthia jenkinsii* had the highest density in the forest with 64 individuals ha⁻¹. The total density of the forest was 1090 individual ha⁻¹. Based on A/F ratio, 92.6% of total tree species exhibited clumped distribution and 7.4% exhibited random distribution pattern (Table 3).

Table 3: Tree species composition, basal area, IVI and A/F ratio in the tropical old-growth broad-leaved forest and regenerating broad-leaved forest of north-eastern India

| Sl. No. | Species | Old-growth forest | | | Regenerating forest | | |
|---------|---|---------------------------------|-------|------|---------------------------------|-------|------|
| | | Basal Area (m ² /ha) | IVI | A/F | Basal Area (m ² /ha) | IVI | A/F |
| 1 | <i>Acacia concinna</i> (Willd.) DC. | 0.03 | 1.57 | 0.22 | - | - | - |
| 2 | <i>Actinodaphne obovata</i> (Nees) Blume | 0.10 | 2.13 | 0.16 | 2.86 | 54.45 | 0.04 |
| 3 | <i>Albizia odoratissima</i> (L.f.) Benth. | 0.28 | 1.33 | 0.25 | - | - | - |
| 4 | <i>Albizia procera</i> (Roxb.) Benth. | 0.19 | 1.19 | 0.25 | - | - | - |
| 5 | <i>Alseodaphne khasyana</i> (Meissn.) Kosterm. | 1.70 | 3.95 | 0.17 | - | - | - |
| 6 | <i>Alstonia scholaris</i> R.Br. | 0.77 | 2.98 | 0.13 | - | - | - |
| 7 | <i>Amoora wallichii</i> King | 0.87 | 2.87 | 0.22 | - | - | - |
| 8 | <i>Aphanamixis wallichii</i> (King) Haridasan & R.R.Rao | 3.38 | 7.01 | 0.88 | - | - | - |
| 9 | <i>Artocarpus chaplasha</i> Roxb. | 0.59 | 1.54 | 1.00 | 2.64 | 52.36 | 0.13 |
| 10 | <i>Artocarpus heterophylla</i> Lam. | 0.19 | 8.14 | 25.5 | - | - | - |
| 11 | <i>Bauhinia purpurea</i> Wall. | 0.10 | 0.61 | 0.50 | - | - | - |
| 12 | <i>Bauhinia purpurea</i> Wall. | 0.02 | 1.29 | 0.38 | - | - | - |
| 13 | <i>Beilschmiedia assamica</i> Meisn. | 0.46 | 5.84 | 0.09 | - | - | - |
| 14 | <i>Bischofia javanica</i> Blume | 0.03 | 5.34 | 0.16 | - | - | - |
| 15 | <i>Butea parviflora</i> Roxb. | 0.02 | 0.48 | 0.50 | - | - | - |
| 16 | <i>Caesalpinia crista</i> L. | 0.05 | 0.97 | 0.25 | - | - | - |
| 17 | <i>Callicarpa arborea</i> Roxb. | 0.03 | 0.49 | 0.50 | 0.03 | 11.71 | 0.10 |
| 18 | <i>Calophyllum polyanthum</i> Wall. | 1.96 | 3.90 | 0.25 | - | - | - |
| 19 | <i>Casearia glomerata</i> Roxb. | 2.25 | 6.33 | 0.10 | 0.01 | 1.44 | 0.75 |
| 20 | <i>Cassia fistula</i> L. | 0.07 | 12.59 | 0.08 | - | - | - |
| 21 | <i>Castanopsis indica</i> A.DC. | 3.45 | 8.16 | 0.10 | - | - | - |
| 22 | <i>Castanopsis tribuloides</i> A.DC. | 0.01 | 1.37 | 0.17 | - | - | - |
| 23 | <i>Celastrus championi</i> Benth. | 0.05 | 1.16 | 0.38 | - | - | - |
| 24 | <i>Celastrus paniculatus</i> Willd. | 0.02 | 0.92 | 0.25 | 0.00 | 1.75 | 0.33 |
| 25 | <i>Chonemorpha fragrans</i> Alston | 0.02 | 0.48 | 0.50 | - | - | - |
| 26 | <i>Cinnamomum bejolghota</i> Sweet | 0.01 | 0.65 | 1.00 | - | - | - |
| 27 | <i>Cinnamomum pauciflorum</i> Nees | 0.70 | 1.53 | 0.50 | - | - | - |
| 28 | <i>Cinnamomum tamala</i> T. Nees and Eberm. | 0.25 | 11.26 | 0.04 | - | - | - |
| 29 | <i>Combretum punctatum</i> A. Rich. | 0.12 | 1.63 | 0.63 | - | - | - |
| 30 | <i>Combretum roxburghii</i> G. Don | 0.02 | 1.11 | 0.38 | - | - | - |

| | | | | | | | |
|----|--|------|-------|------|------|-------|------|
| 31 | <i>Cyathostemma argenteum</i> (Blume) J. Sincl. | 0.02 | 1.29 | 0.50 | - | - | - |
| 32 | <i>Dillenia indica</i> L. | 0.50 | 1.66 | 0.25 | 0.03 | 5.92 | 0.07 |
| 33 | <i>Dillenia pentagyna</i> Roxb. | 0.96 | 5.87 | 0.07 | 0.01 | 2.88 | 0.18 |
| 34 | <i>Diospyros variegata</i> Kurz | 1.97 | 22.24 | 0.03 | 0.01 | 1.22 | 0.50 |
| 35 | <i>Drimycarpus racemosus</i> Hook. f. | 0.00 | 0.45 | 0.50 | 0.01 | 1.79 | 0.33 |
| 36 | <i>Duabanga grandiflora</i> Walp. | 0.92 | 2.75 | 0.17 | 0.01 | 0.64 | 1.00 |
| 37 | <i>Dysoxylum binectariferum</i> Hiern. | 0.08 | 1.47 | 0.17 | 0.01 | 1.11 | 0.38 |
| 38 | <i>Dysoxylum gobara</i> (Buch.-Ham.) Merrill | 1.18 | 9.34 | 0.04 | - | - | - |
| 39 | <i>Elaeocarpus aristatus</i> Roxb. | 0.19 | 2.72 | 0.12 | 0.11 | 3.4 | 0.61 |
| 40 | <i>Elaeocarpus tectorius</i> Poir | 1.41 | 13.31 | 0.03 | - | - | - |
| 41 | <i>Entada phaseoloides</i> Merrill | 0.02 | 0.92 | 0.25 | - | - | - |
| 42 | <i>Eugenia kurzii</i> Duthie | 0.17 | 1.16 | 0.25 | - | - | - |
| 43 | <i>Eugenia tetragona</i> Wight | 0.03 | 1.58 | 0.22 | - | - | - |
| 44 | <i>Eurya acuminata</i> DC. | 0.01 | 0.46 | 0.50 | - | - | - |
| 45 | <i>Ficus altissima</i> Blume | 0.36 | 1.00 | 0.50 | 0.01 | 0.65 | 1.00 |
| 46 | <i>Ficus concinna</i> Miq. | 0.33 | 0.95 | 0.50 | 0.01 | 0.66 | 1.00 |
| 47 | <i>Ficus fulva</i> Spreng. | 0.26 | 5.71 | 0.24 | - | - | - |
| 48 | <i>Ficus hirta</i> Vahl | 0.01 | 0.46 | 0.50 | 0.29 | 6.59 | 0.19 |
| 49 | <i>Ficus maclelandi</i> Alli | 0.01 | 0.65 | 1.00 | - | - | - |
| 50 | <i>Ficus virens</i> Ait. | 0.66 | 1.90 | 0.25 | 0.06 | 3.57 | 0.22 |
| 51 | <i>Fissistigma polyanthum</i> (Hook. f. & Thomson) Merr. | 0.03 | 2.28 | 0.10 | - | - | - |
| 52 | <i>Garcinia cowa</i> Choisy | 0.16 | 2.32 | 0.39 | - | - | - |
| 53 | <i>Garcinia paniculata</i> Roxb. | 0.01 | 0.46 | 0.50 | - | - | - |
| 54 | <i>Glochidion hirsutum</i> Voigt | 0.02 | 0.48 | 0.50 | - | - | - |
| 55 | <i>Gmelina arborea</i> Roxb. | 1.23 | 2.97 | 0.38 | - | - | - |
| 56 | <i>Goniotalamus simonsii</i> Hook.f. & Thomson | 0.09 | 3.87 | 0.89 | - | - | - |
| 57 | <i>Grewia disperma</i> Rottl. ex Spreng | 0.03 | 0.94 | 0.25 | - | - | - |
| 58 | <i>Hibiscus macrophyllus</i> Roxb. | 0.63 | 2.05 | 0.38 | 0.02 | 2.55 | 0.25 |
| 59 | <i>Knema linifolia</i> (Roxb.) Warb. | 0.12 | 2.87 | 0.08 | - | - | - |
| 60 | <i>Kydia calycina</i> Roxb. | 0.01 | 0.65 | 1.00 | 0.01 | 1.23 | 0.50 |
| 61 | <i>Lagerstroemia parviflora</i> Roxb. | 0.42 | 1.54 | 0.25 | - | - | - |
| 62 | <i>Lasianthus lucidus</i> Blume | 0.01 | 0.46 | 0.50 | - | - | - |
| 63 | <i>Leea alata</i> Edgew. | 0.89 | 16.5 | 0.03 | 0.32 | 8.01 | 0.13 |
| 64 | <i>Lithocarpus elegans</i> (Blume) Hatus | 0.02 | 0.48 | 0.50 | - | - | - |
| 65 | <i>Litsea khasyana</i> Meissn. | 0.96 | 5.34 | 0.11 | - | - | - |
| 66 | <i>Litsea laeta</i> Benth. & Hook. f. | 0.14 | 1.55 | 0.17 | 0.03 | 1.53 | 0.63 |
| 67 | <i>Litsea monopetala</i> (Roxb.) Pers. | 0.13 | 3.53 | 0.08 | - | - | - |
| 68 | <i>Litsea salicifolia</i> Hook. f. | 0.01 | 0.46 | 0.50 | - | - | - |
| 69 | <i>Macaranga denticulata</i> Muell. Arg. | 0.59 | 3.15 | 0.10 | - | - | - |
| 70 | <i>Macropanax undulatum</i> Seem. | 0.04 | 0.51 | 0.50 | - | - | - |
| 71 | <i>Magnolia pterocarpa</i> Roxb. | 0.02 | 0.48 | 0.50 | - | - | - |
| 72 | <i>Mesua ferrea</i> L. | 3.90 | 16.51 | 0.04 | 0.32 | 11.86 | 0.08 |
| 73 | <i>Michelia oblonga</i> Wall. | 0.81 | 1.68 | 0.50 | - | - | - |
| 74 | <i>Miliusa roxburghiana</i> Hook. f. & Thomson | 0.31 | 1.11 | 1.00 | - | - | - |
| 75 | <i>Millettia caudata</i> Baker | 0.02 | 1.11 | 0.38 | - | - | - |

| | | | | | | | |
|--------------|---|--------------|---------------|--------------|-------------|---------------|--------------|
| 76 | <i>Millettia cinerea</i> Benth. | 0.05 | 1.15 | 0.38 | - | - | - |
| 77 | <i>Millettia pachycarpa</i> Benth. | 0.01 | 0.92 | 0.25 | - | - | - |
| 78 | <i>Ostodes paniculata</i> Blume | 0.02 | 0.93 | 0.25 | - | - | - |
| 79 | <i>Phlogacanthus thyrsoiflorus</i> Nees | 0.01 | 0.46 | 0.50 | - | - | - |
| 80 | <i>Polyalthia jenkinsii</i> Benth. & Hook. f. | 2.80 | 22.68 | 0.03 | 0.25 | 25.29 | 0.04 |
| 81 | <i>Polyalthia simiarum</i> Benth. & Hook.f. ex Hook. f. | 0.39 | 1.94 | 0.17 | - | - | - |
| 82 | <i>Pterospermum acerifolium</i> Benth. | 0.01 | 0.65 | 1.00 | - | - | - |
| 83 | <i>Pycnarrhena planiflora</i> Hook. f. & Thomson | 0.05 | 1.34 | 0.50 | - | - | - |
| 84 | <i>Sapindus rarak</i> DC. | 0.01 | 0.46 | 0.50 | - | - | - |
| 85 | <i>Sarcosperma griffithii</i> Hook. f. | 1.07 | 6.15 | 0.10 | - | - | - |
| 86 | <i>Schefflera hypoleuca</i> Harms | 0.03 | 0.49 | 0.50 | 0.13 | 16.2 | 0.07 |
| 87 | <i>Schima wallichii</i> Choisy | 12.52 | 25.88 | 0.07 | 1.35 | 15.33 | 0.33 |
| 88 | <i>Shorea robusta</i> A.DC. | 1.79 | 4.53 | 0.13 | 0.28 | 8.35 | 0.09 |
| 89 | <i>Spondias axillaris</i> Roxb. | 1.47 | 3.16 | 0.25 | - | - | - |
| 90 | <i>Spondias pinnata</i> Kurz | 0.70 | 1.53 | 0.50 | - | - | - |
| 91 | <i>Sterculia villosa</i> Roxb. | 0.52 | 1.24 | 0.50 | - | - | - |
| 92 | <i>Syzygium diospyrifolium</i> (Wall. ex Duthie) S.N. Mitra | 0.01 | 0.46 | 0.50 | 0.27 | 9.81 | 0.41 |
| 93 | <i>Terminalia chebula</i> Retz. | 0.32 | 1.13 | 1.00 | - | - | - |
| 94 | <i>Terminalia citrina</i> Roxb. ex Flem. | 0.24 | 1.27 | 0.25 | - | - | - |
| 95 | <i>Terminalia myriocarpa</i> Heurck & Muell. Arg. | 3.79 | 8.96 | 0.07 | - | - | - |
| 96 | <i>Tetrastigma leucostaphylum</i> (Dennst.) Alston | 0.14 | 3.98 | 0.07 | 0.07 | 4.73 | 0.14 |
| 97 | <i>Toona ciliata</i> M. Roem. | 0.71 | 2.16 | 0.38 | - | - | - |
| 98 | <i>Uvaria lurida</i> Dalz. & Gibs. | 0.06 | 0.90 | 1.50 | - | - | - |
| 99 | <i>Vitex peduncularis</i> Wall. | 1.85 | 4.19 | 0.17 | - | - | - |
| 100 | <i>Wendlandia ligustrina</i> Wall. | 0.01 | 0.46 | 0.50 | - | - | - |
| Total | | 65.18 | 300.00 | 33.93 | 9.98 | 300.00 | 36.90 |

In the regenerating forest, *Actinodaphne obovata* (IVI 54.45) and *Artocarpus chaplasha* (IVI 52.36) were the dominant species. The total tree basal area of this forest was 9.98 m² ha⁻¹. *Actinodaphne obovata* had the highest basal area of 2.86 m² ha⁻¹. *Artocarpus chaplasha* had the highest density in the forest with 302 individuals ha⁻¹. The total density of the forest was 1728 individuals ha⁻¹. Based on A/F ratio, 91.2% of total tree species exhibited clumped distribution and 8.8% exhibited random distribution pattern (Table 3).

The Shannon's diversity, Simpson's dominance and α diversity indices were higher in the old-growth forest (3.8, 1.0 and 24.3, respectively) than the regenerating forest (2.9, 0.9 and 6). However, the Species evenness index was similar in both the forest types (0.5).

4.2. SOC pool

The soil organic carbon pool down to a depth of 0.2 m varied significantly ($p < 0.01$) among the four

seasons in both the forest types. It was highest during summer and lowest during winter season. SOC declined with depth ($p < 0.01$). The mean seasonal value of total SOC pool was higher in the old-growth forest (83.2 Mg C ha⁻¹) than the regenerating forest (55.6 Mg C ha⁻¹). Three-way ANOVA revealed significant variation due to forest type, season and depth ($p < 0.01$).

4.3. Microbial biomass carbon pool

The microbial biomass carbon (MBC) in both the surface and sub-surface soil layers peaked during summer season (655.4 and 389.6 $\mu\text{g g}^{-1}$, respectively) in the old-growth forest and it was minimum during the winter season (166.6 and 110.2 $\mu\text{g g}^{-1}$) in the regenerating forest. The mean seasonal MBC values in the surface and sub-surface layers were significantly higher (ANOVA $p < 0.01$) in the old-growth broad-leaved forest (338.2 and 207.0 $\mu\text{g g}^{-1}$, respectively) than the regenerating forest (278.4 and 169.4 $\mu\text{g g}^{-1}$, respectively). Three-way ANOVA

showed significant variation due to forest type, season and depth ($p < 0.01$). The percentage contribution of MBC to SOC was highest during summer season in both the forest types while it was lowest during winter season. The percentage contribution was greater in the surface soil layer than the sub-surface soil layer.

4.4. Litter pool

The total litter fall in the old-growth and regenerating forests were $9.8 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ and $6.9 \text{ Mg ha}^{-1} \text{ yr}^{-1}$, respectively. The leaves, twigs, branches and miscellaneous parts accounted for 68.9, 14.1, 11.2 and 5.8%, and 76.8, 19.3, 2.1 and 1.8% to the total litter fall in the old-growth and regenerating forests, respectively. The litter fall was maximum during winter and spring seasons and minimum during summer season in both the forest types. Two-way ANOVA revealed significant variation in litter fall among the forest types (ANOVA $F = 4.95$; $p < 0.01$) and seasons (ANOVA $F = 5.59$; $p < 0.01$).

4.5. Above ground and below ground biomass pool

The diameter class $>60 \text{ cm}$ and $>10\text{-}20 \text{ cm}$ contributed 42.5% and 53.5% to the total tree

above ground biomass in the old-growth forest and regenerating forest, respectively. The tree above ground biomass values for the two forest types were 313.8 Mg ha^{-1} and 152.4 Mg ha^{-1} , respectively and the corresponding C values were $153.8 \text{ Mg C ha}^{-1}$ and $74.6 \text{ Mg C ha}^{-1}$ (Table 4).

Tree below ground biomass in the old-growth forest and regenerating forest were highest in the $>40\text{-}50 \text{ cm}$ and $>10\text{-}20 \text{ cm}$ diameter classes, respectively. The total below ground biomass and carbon were 50.8 Mg ha^{-1} and $23.9 \text{ Mg C ha}^{-1}$ in the old-growth forest, and 30.3 Mg ha^{-1} and $14.2 \text{ Mg C ha}^{-1}$ in the regenerating forest (Table 5).

4.6. Herb and shrub biomass and carbon

The herb and shrub biomass were 12.4 and 37.1 kg ha^{-1} in the old-growth forest, and 8.2 and 32.1 kg ha^{-1} in the regenerating forest, respectively. The corresponding figures for biomass carbon were 5.8 and $17.8 \text{ kg C ha}^{-1}$ in the old-growth forest, and 3.9 and $15.4 \text{ kg C ha}^{-1}$ in the regenerating forest. The herbs and shrubs contributed 0.004 and 0.012% to the total biomass in the old-growth, and 0.005 and 0.021% in the regenerating forest.

Table 4: Above ground biomass and biomass carbon in different diameter classes of the old-growth forest and regenerating forest of north-eastern India

| DBH class (cm) | Old growth forest | | | Regenerating forest | | |
|----------------|------------------------|--------------------------|------|------------------------|--------------------------|------|
| | (Mg ha ⁻¹) | (Mg C ha ⁻¹) | % | (Mg ha ⁻¹) | (Mg C ha ⁻¹) | % |
| >5-10 | 11.5 | 5.7 | 3.7 | 16.2 | 7.9 | 10.6 |
| >10-20 | 28.2 | 13.8 | 9 | 81.5 | 39.9 | 53.5 |
| >20-30 | 20.7 | 10.1 | 6.6 | 43.6 | 21.4 | 28.6 |
| >30-40 | 38.2 | 18.7 | 12.2 | 11.1 | 5.4 | 7.3 |
| >40-50 | 47.7 | 23.4 | 15.2 | - | - | - |
| >50-60 | 34.1 | 16.7 | 10.9 | - | - | - |
| >60-70 | 47.9 | 23.5 | 15.3 | - | - | - |
| >70-80 | 34.9 | 17.1 | 11.1 | - | - | - |
| >80-90 | 24.4 | 11.9 | 7.8 | - | - | - |
| >90-100 | 16.8 | 8.2 | 5.4 | - | - | - |
| > 100 | 9.5 | 4.7 | 3 | - | - | - |
| Total | 313.8 | 153.8 | 100 | 152.4 | 74.7 | 100 |

Table 5: Below ground biomass and carbon in different diameter classes of old-growth forest and regenerating forest of north-eastern India

| DBH class (cm) | Old growth forest | | | Regenerating forest | | |
|----------------|------------------------|--------------------------|------|------------------------|--------------------------|------|
| | (Mg ha ⁻¹) | (Mg C ha ⁻¹) | % | (Mg ha ⁻¹) | (Mg C ha ⁻¹) | % |
| >5-10 | 2.7 | 1.3 | 5.3 | 3.8 | 1.8 | 12.5 |
| >10-20 | 5.8 | 2.7 | 11.4 | 16.6 | 7.8 | 54.7 |
| >20-30 | 3.8 | 1.8 | 7.5 | 8 | 3.8 | 26.5 |
| >30-40 | 6.5 | 3 | 12.7 | 1.9 | 0.9 | 6.2 |
| >40-50 | 7.7 | 3.6 | 15.1 | - | - | - |
| >50-60 | 5.3 | 2.5 | 10.4 | - | - | - |
| >60-70 | 7.1 | 3.3 | 14 | - | - | - |
| >70-80 | 5 | 2.4 | 9.9 | - | - | - |
| >80-90 | 3.4 | 1.6 | 6.7 | - | - | - |
| >90-100 | 2.3 | 1.1 | 4.5 | - | - | - |
| > 100 | 1.3 | 0.6 | 2.5 | - | - | - |
| Total | 50.8 | 23.9 | 100 | 30.3 | 14.2 | 100 |

Table 6: Total ecosystem, above and below ground biomass, carbon content and net primary production of old-growth and regenerating forests of north-eastern India

| Components | Biomass and carbon | | | | NPP | |
|---------------------------|------------------------|--------------|--------------------------|--------------|---|--------------|
| | Old-growth | Regenerating | Old growth | Regenerating | Old growth | Regenerating |
| | (Mg ha ⁻¹) | | (Mg C ha ⁻¹) | | (Mg ha ⁻¹ yr ⁻¹) | |
| Tree above ground | 313.8 | 152.4 | 153.8 | 74.7 | 8.3 | 12.5 |
| Herbs | 0.01 | 0.01 | 0.01 | 0.005 | 0.002 | 0.002 |
| Shrubs | 0.04 | 0.03 | 0.02 | 0.02 | 0.004 | 0.004 |
| Detrital biomass | | | | | | |
| Leaves | 6.8 | 5.3 | 3.2 | 2.5 | 2.5 | 2.9 |
| Twigs | 1.4 | 1.3 | 0.7 | 0.6 | 0.2 | 0.4 |
| Branches | 1.1 | 0.1 | 0.5 | 0.1 | 0.8 | 0.2 |
| Misc. | 0.6 | 0.1 | 0.3 | 0.1 | 0.5 | 0 |
| Total detrital | 9.8 | 6.9 | 4.6 | 3.3 | 4 | 3.6 |
| Total above ground | 323.7 | 159.3 | 158.4 | 77.9 | 12.3 | 16.1 |
| Tree below ground | 50.8 | 30.3 | 23.9 | 14.2 | 1.4 | 2.3 |
| Total forest | 374.5 | 189.6 | 182.3 | 92.2 | | |
| Total soil organic carbon | | | 83.2 | 55.6 | | |
| Total ecosystem | 374.5 | 189.6 | 265.5 | 147.8 | 13.6 | 18.4 |
| BNPP/NPP | | | | | 0.1 | 0.1 |
| ANPP/NPP | | | | | 0.9 | 0.9 |

4.7. Ecosystem level biomass and NPP

Total ecosystem biomass of the old-growth forest was 374.5 Mg ha⁻¹, of which 86.4% was in the above ground compartment and 13.6% in the below ground compartment. Trees contributed 83.8%, herbs 0.003%, shrubs 0.01%, and litter 2.6% to the total forest biomass. The total AGB of the forest including trees, litter, herb and shrub components was 323.69 Mg ha⁻¹. The total ecosystem NPP of the forest was 12.3 Mg ha⁻¹ yr⁻¹. The leaf litter, twig, branch and miscellaneous parts contributed to 63.1, 6.3, 19.1 and 11.5% to the total litter production. The total ecosystem carbon content of the forest was 265.5 Mg C ha⁻¹. The soil organic carbon was 83.2 Mg C ha⁻¹ contributing 31.3% to the total ecosystem carbon. The above ground NPP of the forest was 90.1%, while below ground was 9.9% to the total ecosystem NPP (Table 6).

In the regenerating forest, total ecosystem biomass was 189.6 Mg ha⁻¹, of which 84% was in the above ground compartment and 16% in the below ground compartment. Trees contributed 80.3%, herbs 0.01%, shrubs 0.02%, and litter 3.7% to the total forest biomass. The total AGB of the forest including litter, herb and shrub components was 159.3 Mg ha⁻¹. The total ecosystem NPP of the forest was 18.4 Mg ha⁻¹ yr⁻¹. The leaf litter, twig, branch and miscellaneous parts contributed to 80.6, 12.4, 5.8 and 1.2% to the total litter production. The total ecosystem carbon content of the forest was 147.8 Mg C ha⁻¹. The soil organic carbon was 55.6 Mg C ha⁻¹ contributing 37.6% to the total ecosystem carbon. The above ground NPP of the forest contributed 87.5% to the total ecosystem NPP, while below ground NPP contribute only 12.5% (Table 6).

5. Discussion

The species diversity in the old-growth forest was higher than the regenerating forest as the former is an undisturbed primary forest and is well protected. Most species in both the forest types showed clumped distribution pattern (91.2-92.6% species) due to site heterogeneity and only 7.4-8.8% showed random distribution pattern. The clumped distribution pattern as exhibited by most species in the present study is in accordance with the findings of Richard *et al.* (1980) and Rao *et al.* (1990).

The amount of soil organic carbon in the old-growth forest was 83.2 Mg C ha⁻¹ compared to 55.6 Mg C ha⁻¹ in the regenerating forest. The value for old-growth forests is comparable with the findings (72-149 Mg C ha⁻¹) of Glaser *et al.* (2003) for the Amazonian rain forest near Belterra and of Lu *et al.* (2010) in the tropical seasonal forest of China (84 to 102 Mg C ha⁻¹).

The SOC values obtained in the present study are low compared with the values obtained by the earlier workers for other tropical forests. For example, Dixon *et al.* (1994) reported a value of 139 Mg C ha⁻¹ in the tropical forests of Asia and Glaser *et al.* (2003) reported a value of 147-506 Mg C ha⁻¹ in Amazonian rain forests near Manaus. IPCC (2000) reported an average SOC value of 86 Mg C ha⁻¹ for the tropical forests of the world which is very close to the present finding. The SOC values of regenerating forest is comparable with the findings of Sombroek *et al.* (1993) (34-56 Mg C ha⁻¹) for sandy to clay soil of Amazonian forests. Change in land-use and land management practices can have significant direct and indirect effects on soil organic

pools, due to changes in species community, primary productivity, litter quantity and quality and soil structure (Schwendenmann *et al.*, 2007).

The soil organic matter in the old-growth forest (143.5 Mg ha^{-1}) was higher than the regenerating forest (95.8 Mg ha^{-1}). The soil organic matter obtained in the present study was less than the reported value of 162 Mg ha^{-1} for tropical soils (Malhi *et al.*, 1999). The soil organic matter is a major factor in ecosystem functioning and determines the sinks or sources of carbon in the global carbon cycle (Brown and Lugo, 1982; Smithson *et al.*, 2002).

The MBC expressed as percentages of SOC gives estimates of the quantities of carbon present in the microbial biomass, substrate availability and organic matter dynamics in soils (Sparling, 1992). In the present study, the contribution of MBC to soil organic carbon in the surface soil layer during summer season (2% to 4.9%) was within the reported range for tropical forests. For example, Theng *et al.* (1989) and Luizao *et al.* (1992) reported a range of 1.5-5.3% for the tropical forests of central Amazon. Relatively denser plant canopy in the old-growth forest than in the regenerating forest had a greater accumulation of litter and fine roots in the understory region and might have favoured the growth of microbial populations and the accumulation of C in microbial biomass. Our results are consistent with previously reported studies (Arunachalam and Arunachalam, 2000; Sharma *et al.*, 2004; Wright *et al.*, 2005). The SOC showed a strong positive correlation with MBC ($R^2=0.9$, $p<0.001$).

The total annual litter fall obtained in the present study ($6.9\text{-}9.8 \text{ Mg ha}^{-1}$) was within the reported range for various tropical forests ($2.2\text{-}22.6 \text{ Mg ha}^{-1}$) (Vogt *et al.*, 1986). Cuevas and Medina (1986) reported a range of $2.4\text{-}10.3 \text{ Mg ha}^{-1}$ for the Amazonian tropical forest. Cornforth (1970) and Folster and Salas (1976) recorded the range of $6.8\text{-}10 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ for the humid tropical forest of West Africa. The values were, however, lower ($13\text{-}15 \text{ Mg ha}^{-1}$) than the moist deciduous forest of Indian Western Ghats (Swamy and Procter, 1994). The life span, size and weight of leaf play an important role in the litter production (Kamei *et al.* 2009). In the present study, the proportion of leaf (68.9-76.8%) in the litter fall was within the values reported by Meentemeyer *et al.* (1982) (70%) and for the tropical rainforest in Malaysia (71%) and Venezuela (74%) by Haase (1999).

The carbon sequestration potential of forests depends on the forest type, age of forest and size class of trees (Terakunpisut *et al.*, 2007). The observed AGB value of 323.7 Mg ha^{-1} in the old-growth forest is comparable with the findings of Ramachandran *et al.* (2007) who reported a value of 307 Mg ha^{-1} for the tropical evergreen forests of eastern coast of Tamil Nadu, India and Hase and

Foelster (1983) for the mature forests of West Venezuela (398 Mg ha^{-1}) and 362 Mg ha^{-1} for the tropical forests of Asia (Houghton, 2005). The present AGB values for the old-growth forest is within the reported range for the primary rainforests of Southeast Asia, which ranged from $300\text{-}500 \text{ Mg ha}^{-1}$ (Kato *et al.*, 1978; Kira and Shidei, 1967; Laumonier *et al.*, 2010; Yamakura *et al.*, 1986). The present value is however less than the AGB values of 468 Mg ha^{-1} reported for tropical wet evergreen forest and tropical semi-evergreen forest of Western Ghats of India by Swamy (1989). The AGB value was also close to those reported by Muller (1982) for the tropical forests of eastern hardwood region of USA (330 Mg ha^{-1}) and by Brown and Lugo (1982) for the tropical rain forests in Malaysia ($225\text{-}446 \text{ Mg ha}^{-1}$) and Cameroon ($238\text{-}341 \text{ Mg ha}^{-1}$). The value range of $153\text{-}221 \text{ Mg ha}^{-1}$ reported from Sri Lankan tropical rain forests (Brown and Lugo, 1982) was lower than the values found in the present study. Terakunpisut *et al.* (2007) reported an AGB value of $96\text{-}276 \text{ Mg ha}^{-1}$ for the tropical rain forests of Thailand which was also less than the present study. However, the AGB value obtained for this north-eastern Indian tropical forest was much lower than the highest AGB value reported so far i.e. $500\text{-}600 \text{ Mg ha}^{-1}$ for the undisturbed deciduous forest in the southern Appalachian Mountains (Whittaker, 1996).

The AGB of 159.3 Mg ha^{-1} obtained in the regenerating broad-leaved forest was higher than the 20 years (118 Mg ha^{-1}) and lower than 30 years old (177 Mg ha^{-1}) tropical secondary forest of Ecuador (Fehse *et al.*, 2002). The above ground biomass of regenerating broad-leaved forest (20-22 years) in the present study was within the range for various tropical secondary forests ($14\text{-}272 \text{ Mg ha}^{-1}$) of 15-20 years old (Hashimoto *et al.*, 2000; Marin-Spiotta *et al.*, 2008).

The amount of AGB carbon stored in the old-growth broad-leaved forest ($158.4 \text{ Mg C ha}^{-1}$) in the present study was greater than the tropical forests of Sri Lanka (77 Mg C ha^{-1}) as reported by Brown and Lugo (1982), the primary Amazon forest (110 Mg C ha^{-1}) by Phillips *et al.* (1998) and tropical forests of Asia (127 Mg C ha^{-1}) by Houghton (2005), but lower than the relatively undisturbed matured tropical rain forest of Malaysia (223 Mg C ha^{-1}) reported by Brown and Lugo (1982). The present value for old-growth forest is in conformity with the findings of Clark *et al.* (2001) for the tropical old-growth forest of Ivory Coast ($151.5\text{-}256.5 \text{ Mg C ha}^{-1}$) and $151\text{-}203 \text{ Mg C ha}^{-1}$ for Brazil. The values were however lower than the reported values of $324.5 \text{ Mg C ha}^{-1}$ for India by Clark *et al.* (2001), $123.5 \text{ Mg C ha}^{-1}$ for the Amazonian forest by Girardin *et al.* (2010), and $48\text{-}138 \text{ Mg ha}^{-1}$ for the tropical rain forests of Thailand by Terakunpisut *et al.* (2007). Ogawa *et al.* (1965) reported a carbon stock of 60 to 179 Mg C ha^{-1} in different tropical forest types of

Thailand. Flint and Richards (1996) estimated carbon sequestration in Southeast Asia including India, Thailand, Cambodia, Malaysia and Indonesia, and reported that the value ranged from 17 Mg C ha⁻¹ in severely degraded tropical dry forest to 350 Mg C ha⁻¹ in the undisturbed matured tropical rain forests. The AGB carbon in the regenerating broad-leaved forest (77.9 Mg C ha⁻¹) is comparable with the findings of Brown and Lugo (1982) in the disturbed tropical forests of Sri Lanka (77 Mg C ha⁻¹).

A higher proportion of AGB in the higher diameter classes in old-growth broad-leaved forest does indicate the importance of large trees in carbon storage, but does not undermine the role of small trees (<60 cm dbh) which would enhance the future carbon stock because of their high carbon sequestration potential. Beyond maturity, the trees generally have marginal carbon sequestration capability (Lal and Singh, 2000). The higher AGB in the old-growth forest than the regenerating forest may be attributed to the combination of site and stand factors and adopted management practices (Baishya *et al.*, 2009). Other factors responsible for such low total AGB in the regenerating forest are different stages of forest growth cycle, habitat and species variability, and varying tree density (Terakunpisut *et al.*, 2007).

The large trees (>60 cm dbh) in the old-growth forest contributed 43% to the total AGB in the forest. In contrast, the contribution of the smaller trees to total AGB in the regenerating forest was significantly higher (100%). The greater contribution of large trees to AGB in the old-growth forest was in conformity with the findings of earlier workers (Brown and Lugo, 1992; Brown *et al.*, 1995; Brown, 1996) who reported up to 50% contribution to AGB by the large trees (>70 cm dbh). On the other hand, Brown *et al.* (1997) reported that smaller trees contribute to most AGB in forests with <300 Mg ha⁻¹ above ground biomass. The distribution of biomass in large trees in the old-growth forest, therefore, could be an indicator of the presence or absence of past anthropogenic disturbance (Brown, 1996).

The ecosystem level carbon stock was higher in the old-growth forest (265.5 Mg C ha⁻¹) than the regenerating forest (147.8 Mg C ha⁻¹). The data on ecosystem level carbon pool in general are lacking. The only available ecosystem level biomass and NPP data are those of Tanabe *et al.* (2003) in the *Pinus densiflora* forest of Central Japan and Baishya and Barik (2011) in the *Pinus kesiya* forest of north-eastern India.

The regenerating forest with less AGB in the higher diameter class had greater potential to accumulate significant quantities of biomass, and thus sequestering more atmospheric C than the old-growth forest with more AGB in the higher diameter classes.

The total above ground NPP in the regenerating forest (16.1 Mg ha⁻¹ yr⁻¹) was higher than the old-growth forest (12.3 Mg ha⁻¹ yr⁻¹). The above ground NPP of the old-growth forest was in the range of above ground NPP reported by Clark *et al.* (2001) for Ivory Coast (9.9-14.3 Mg ha⁻¹ yr⁻¹). The above ground NPP in the regenerating forest (16.1 Mg ha⁻¹ yr⁻¹) was greater than the 18-year old mixed forest (5.2 Mg ha⁻¹ yr⁻¹) in Japan (Ohtsuka *et al.*, 2010). The values were however more than the reported values for India (3.3 Mg ha⁻¹ yr⁻¹) and for Brazil (6.4-7.6 Mg ha⁻¹ yr⁻¹) by Clark *et al.* (2001). The mean NPP for the two forest types (12.3 and 16.1 Mg ha⁻¹ yr⁻¹) is significantly greater than the value reported by Luyssaert *et al.* (2008) (8.64 Mg ha⁻¹ yr⁻¹) for 29 tropical humid evergreen forests of the world.

The net ecosystem NPP of the forest was higher in the regenerating broad-leaved forest (18.4 Mg ha⁻¹ yr⁻¹) than old-growth broadleaved forest (13.6 Mg ha⁻¹ yr⁻¹). The net ecosystem NPP values of the two forest types are comparable with the findings of Clark *et al.* (2001) with 3.1 to 21.7 Mg ha⁻¹ yr⁻¹ for the tropical forests of the world. The ecosystem level carbon sequestration values in the old-growth and regenerating forests were 265.5 and 147.7 Mg C ha⁻¹, respectively.

The present finding that old-growth forest contains very high ecosystem carbon is significant in north-eastern Indian context as very few such forests are left in the region (Barik *et al.* 1992). This underscores their conservation priority from carbon sequestration. The regenerating broad-leaved forest with higher ecosystem productivity signifies its higher carbon sequestration potential than the tropical old-growth broad-leaved forest. The management of regenerating forests is therefore of utmost importance as they have greater carbon sequestration potential in comparison to the old-growth forests which have marginal carbon sequestration capacity after maturity.

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References

- Allen, S.E., Grimshaw, H.M., Parkinson, J.A. and Quarmby, C. 1974. *Chemical Analysis of Ecological Materials*. Blackwell Scientific Publication, London.
- Anderson, J.M. and Ingram, J.S.I. 1993. *Tropical Soil Biology and Fertility*. A handbook of Methods. C.A.B. International Wallingford, U.K.
- Arunachalam, A. and Arunachalam, K. 2000. Influence of gap size and soil properties on microbial biomass in a subtropical humid forest of north-east India. *Plant and Soil* **223**:185-193.

- Baishya, R., Barik, S.K. and Upadhaya, K. 2009. Distribution pattern of above ground biomass in natural and plantation forests of humid tropics in northeast India. *Tropical Ecology* **50**:295-304.
- Baishya, R. and Barik, S.K. 2011. Estimation of tree biomass, carbon pool and net primary production of an old-growth *Pinus kesiya* Royle ex. Gordon forest in north-eastern India. *Annals of Forest Science* **68**:727-736.
- Barrio-Anta, M., Balboa-Murias, M.A., Castedo-Dorado, F., Dieguez-Aranda, U. and Alvarez-Gonzalez, J.A. 2006. An ecoregional model for estimating volume, biomass and carbon pools in maritime pine stands in Galicia (Northwestern Spain). *Forest Ecology and Management* **223**:24-34.
- Barik, S.K., Pandey, H.N., Tripathi, R.S. and Rao, P. 1992. Micro-environmental variability and species diversity in tree fall gaps in a sub-tropical broadleaved forest. *Vegetatio* **103**:31-40.
- Brown, I.F., Martinelli, L.A., Thomas, W.W., Moreira, M.Z., Ferreira, C.A.C. and Victoria, R.A. 1995. Uncertainty in the biomass of Amazonian forests: an example from Rondonia, Brazil. *Forest Ecology and Management* **75**:175-189.
- Brown, S. 1996. Tropical forests and the global carbon cycle: Estimating state and change in biomass density. In: Apps, M. and Price, D. (Eds.) *Forest Ecosystems, Forest Management and the Global Carbon Cycle*, NATO ASI Series, Springer-Verlag, pp. 135-144.
- Brown, S. 1997. Estimating biomass and biomass change of tropical forests: a primer. FAO Forestry Paper 134, Food and Agricultural Organization, Rome.
- Brown, S. and Iverson, L.R. 1992. Biomass estimates for tropical forests. *World Resource Review* **4**:366-384.
- Brown, S. and Lugo, A.E. 1982. The storage and production of organic matter in tropical forests and their role in the global carbon cycle. *Biotropica* **14**:161-187.
- Brown, S. and Lugo, A.E. 1990. Tropical secondary forests. *Journal of Tropical Ecology* **6**:1-32.
- Brown, S. and Lugo, A.E. 1992. Above ground biomass estimates for tropical moist forests of the Brazilian Amazon. *Interciencia* **17**:8-18.
- Brown, S., Gillespie, A. and Lugo, A. 1989. Biomass estimation methods for tropical forests with applications to forest inventory data. *Forest Science* **35**:881-902.
- Brown, S., Schroeder P. and Birdsey, R. 1997. Above ground biomass distribution of US eastern hardwood forests and the use of large trees as an indicator of forest development. *Forest Ecology and Management* **96**:37-47.
- Cairns, M.A., Brown, S., Helmer, E.H. and Baumgardner, G.A. 1997. Root biomass allocation in the world's upland forests. *Oecologia* **111**:1-11.
- Chambers, J.Q., dos Santos, J., Ribeiro, R.F. and Higuchi, N. 2001. Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest. *Forest Ecology and Management* **152**:73-84.
- Chave, J., Riéra, B. and Dubois, M.A. 2001. Estimation of biomass in a neotropical forest of French Guiana: Spatial and temporal variability. *Journal of Tropical Ecology* **17**:79-96.
- Clark, D.A. 2002. Are tropical forests an important carbon sink? Reanalysis of the long-term plot data. *Ecological Applications* **12**:3-7.
- Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R., Ni, J. and Holland, E.A. 2001. Net primary production in tropical forests: an evaluation and synthesis of existing field data. *Ecological Applications* **11**:371-384.
- Cornforth, I.S. 1970. Leaf fall in a tropical rain forest. *Journal of Applied Ecology* **7**:603-608.
- Cuevas, E. and Medina, E. 1986. Nutrient dynamics within Amazonian forest ecosystems. I. Nutrient flux in fine litterfall and efficiency of nutrient utilization. *Oecologia* **68**:466-472.
- Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Trexler, M.C. and Wisniewski, J. 1994. Carbon pools and flux of global forest ecosystems. *Science* **263**:185-190.
- Fang, J.Y. and Wang, Z.M. 2001. Forest biomass estimation at regional and global levels, with special reference to China's forest biomass. *Ecological Research* **16**:587-592.
- FAO 1988. *Interim report on the state of forest resources in the developing countries*. Food and Agriculture Organization, Rome.
- FAO 1997. *Estimating Biomass and Biomass Change of Tropical Forests: a Primer*. FAO Forestry Paper - 134. Food and Agriculture Organization, Rome.
- FAO 2005. *Global Forest Resources Assessment. Progress towards sustainable forest management*. FAO Forestry Paper. 147, Rome, pp. 320.
- Fehse, J., Hofstede, R., Aguirre, N., Paladines, C., Kooijman, A. and Sevink, J. 2002. High altitude tropical secondary forests: a competitive carbon sink? *Forest Ecology and Management* **163**:9-25.
- Flint, P.E. and Richards, J.F. 1996. Trends in carbon content of vegetation in South and Southeast Asia associated with change in land use. In: Dale, V.H. (Ed.) *Effects of Land-Use Change on Atmospheric CO₂ Concentrations, South and Southeast Asia as a Case Study*. Springer-Verlag, Berlin, pp. 201-300.
- Folster, H. and Salas, G. 1976. Litterfall and mineralization in three evergreen forest stands, Columbia. *Acto Cientifica Venezolana* **27**:196-202.
- Girardin, C.A.J., Malhi, Y., Aragao, L.E.O.C., Mamani, W.M., Huasco, W.H., Durand, L., Feeley, K.J., Rapps, J., Silva-Espejo, J.E., Silmans, M., Salinas, N. and Whittaker, R.J. 2010. Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. *Global Change Biology* **16**:3176-3192.
- Glaser, B., Guggenberger, G., Zech, W. and Ruivo, M.L. 2003. Soil organic matter stability in Amazonian Dark Earths. In: Lehmann J. et al. (Eds.) *Amazonian Dark Earths: Origin, Properties, Management*. The

- Netherlands: Kluwer Academic Publishers, pp. 141-158.
- Gurney, K.R., Law, R.M., Denning, A.S., Rayner, P.J., Baker, D., Bousquet, P., Bruhwiler, L., Chen, Y.H., Ciais, P., Fan, S., Fung, I.Y., Gloor, M., Heimann, M., Higuchi, K., John, J., Maki, T., Maksyutov, S., Masarie, K., Peylin, P., Prather, M., Pak, B.C., Randerson, J., Sarmiento, J., Taguchi, S., Takahashi, T. and Yuen, C.W. 2002. Towards robust regional estimates of CO₂ sources and sinks using atmospheric transport models. *Nature* **415**:626-630.
- Haase, R. 1999. Litterfall and nutrient return in seasonally flooded and non-flooded forest of the Pantanal, Mato Grosso, Brazil. *Forest Ecology and Management* **117**:129-147.
- Haridasan, K. and Rao, R.R. 1985-1987. *Forest Flora of Meghalaya*. Vol. I and II. Bishen Singh and Mahendrapal Singh, Dehra Dun, India, pp. 937.
- Harmon, M.E. 2001. Carbon sequestration in forests: addressing the scale question. *Journal of Forestry* **99**:24-29.
- Hase, H. and Foelster, H. 1983. Impact of plantation forestry with teak (*Tectona grandis*) on the nutrient status of young alluvial soils in West Venezuela. *Forest Ecology and Management* **6**:33-57.
- Hashimoto, T., Kojima, K., Tange, T. and Sasaki, S. 2000. Changes in carbon storage in fallow forests in the tropical lowlands of Borneo. *Forest Ecology and Management* **126**:331-337.
- Houghton, R.A. 1991. Tropical deforestation and atmospheric carbon dioxide. *Climatic Change* **19**:99-118.
- Houghton, R.A. 2005. Above ground forest biomass and the global carbon balance. *Global Change Biology* **11**:945-958.
- Hughes, R.F., Kauffman, J.B. and Jaramillo, V.J. 1999. Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. *Ecology* **80**:1892-1907.
- IPCC 2000. The carbon cycle and atmospheric carbon dioxide. In: Watson R.T. *et al.* (Eds.) *Land Use, Land-Use Change and Forestry: A Special Report of the International Panel on Climate Change*. Cambridge University Press, Cambridge.
- Isaev, A., Korovin, G., Zamolodehikov, D., Utkin, A. and Pryaznikov, A. 1995. Carbon stock and deposition in phytomass of the Russian forests. *Water Air Soil Pollution* **82**:247-256.
- Iverson, L.R., Brown, S., Grainger, A., Prasad, A. and Liu, D. 1993. Carbon sequestration in tropical Asia: an assessment of technically suitable forest lands using geographic information systems analysis. *Climate Research* **3**:23-38.
- Kamei, J., Barik, S.K. and Pandey, H.N. 2009. Inter-specific variation in leaf litter production, decomposition, and N and P mineralization in a humid subtropical forest ecosystem of north-east India. *Canadian Journal of Forest Research* **39**:1797-1805.
- Kanjilal, V.N., Kanjilal, P.C., Das, A., De, R.N. and Bor, N.L. 1934-1940. *Flora of Assam*. 5 vols. Government Press, Shillong, India.
- Kato, R., Tadaki, Y. and Ogawa, H. 1978. Plant biomass and growth increment studies in Pasoh Forest Reserve. *Malaysian National Journal* **30**:211-224.
- Kira, T. and Shidei, T. 1967. Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. *Japanese Journal of Ecology* **17**:70-87.
- Lal, M. and Singh, R. 2000. Carbon sequestration potential of Indian Forests. *Environmental Monitoring and Assessment* **60**:315-327.
- Laumonier, Y., Edin, A., Kanninen, M. and Munandar, A.W. 2010. Landscape-scale variation in the structure and biomass of the hill dipterocarp forest of Sumatra: implications for carbon stock assessments. *Forest Ecology and Management* **259**:505-513.
- Lu, X.T., Yin, X.Y., Jepsen, M.R. and Tang, J.W. 2010. Ecosystem carbon storage and partitioning in a tropical seasonal forest in Southwestern China. *Forest Ecology and Management* **260**:1798-1803.
- Luizao, R.C.C., Bonde, T.A. and Rosswall, T. 1992. Seasonal variation of soil microbial biomass- the effect of clear felling in a tropical rainforest and establishment of pasture in the central Amazon. *Soil Biology and Biochemistry* **24**:805-813.
- Luyssaert, S., Schulze, E.D., Börner, A., Knohl, A., Hessenmöller, D., Law, B.E., Ciais, P. and Grace, J. 2008. Old-growth forests as global carbon sinks. *Nature* **455**:213-215.
- Malhi, Y., Nobre, A.D., Grace, J., Kruijt, B., Pereira, M.G., Gulf, A. and Scott, S. 1998. Carbon dioxide transfer over a central Amazonian rain forest. *Journal of Geophysical Research* **103**:593-531.
- Malhi, Y., Baldocchi, D.D. and Jarvis, P.J. 1999. The carbon balance of tropical, temperate, and boreal forests. *Plant Cell and Environment* **22**:715-740.
- Marin-Spiotta, E., Cusack, D.F., Ostertag, R. and Silver, W.L. 2008. Trends in above and below ground carbon with forest regrowth after agricultural abandonment in the neotropics. In: Myster, R.W. (Ed.), *Post-agricultural Succession in the Neotropics*. Springer, New York, pp. 22-72.
- Meentemeyer, V., Box, E.O. and Thompson, R. 1982. World pattern and amounts of terrestrial plant litter production. *BioScience* **32**:125-128.
- Melillo, J.M., McGuire, A.D., Kicklighter, D.W., Vorosmarty, C.J. and Schloss, A.L. 1993. Global climate change and terrestrial net primary productivity. *Nature* **363**:234-240.
- Misra, R. 1968. *Ecology Work Book*. Oxford and IBH Publishing Company, New Delhi, pp. 244.
- Montero, G., Ruiz-Peinado, R. and Munoz, M. 2005. Producción de Biomasa y fijación de CO₂ por los bisques españoles. Monografías INIA: Serie Forestales, n°13. p. 270.
- Muller, R.N. 1982. Vegetation pattern in the mixed mesophytic forest of eastern Kentucky. *Ecology* **63**:1901-1917.
- Ogawa, H., Yoda, K., Ogino, K. and Kira, T. 1965. Comparative ecological studies on three main type of forest vegetation in Thailand II. Plant Biomass. *Nature and Life in Southeast Asia* **4**:49-80.
- Ohtsuka, T., Shizu, Y., Nishiwaki, A., Yashiro, Y. and Koizumi, H. 2010. Carbon cycling and net ecosystem production at an early stage of secondary succession in an abandoned coppice forest. *Journal of Plant Research* **123**:393-401.
- Pearson, T.R., Brown, S.L. and Birdsey, R.A. 2007. *Measurement guidelines for the sequestration of forest carbon*. U.S. Northern research Station, Department of Agriculture.
- Persson, H. 1978. Root dynamics in a young Scots Pine stand in Central Sweden. *Oikos* **30**:508-519.

- Phillips, O.L., Mahli, Y., Higuchi, N., Laurance, W.F., Nunez, P.V., Vasquez, R.M., Laurence, S.G., Ferreira, L.V., Stern, M., Brown, S. and Grace, J. 1998. Changes in the carbon balance of tropical forests: evidence from long-term plots. *Science* **282**:439-442.
- Pignard, G., Dupouey, J., Arrouays, D. and Loustau, D. 2004. Carbon stocks estimates for French forests. *Biotechnology, Agronomy, Society and Environment* **4**:285-289.
- Rao, P., Barik, S.K., Pandey, H.N. and Tripathi, R.S. 1990. Community composition and tree population structure in a subtropical broad-leaved forest along a disturbance gradient. *Vegetatio* **88**:151-162.
- Ramachandran, A., Jayakumar, S., Haroon, R.M., Bhaskaran, A. and Arockiasamy, D.I. 2007. Carbon sequestration: estimation of carbon stock in natural forests using geospatial technology in the Eastern Ghats of Tamil Nadu, India. *Current Science* **92**:323-331.
- Richard, T., Forman, T. and Hahn, D.C. 1980. Spatial patterns of trees in a Caribbean semievergreen forest. *Ecology* **61**:1267-1274.
- Roy, P.S. and Joshi, P.K. 2002. Forest cover assessment in north-east India-the potential of temporal wide swath satellite sensor data (IRS-1C WiFS). *International Journal of Remote Sensing* **23**:4881-4896.
- Salati, E. and Vose, P.B. 1984. Amazon basin: a system in equilibrium. *Science* **225**:129-138.
- Schlesinger, W.H. and Andrews, J.A. 2000. Soil respiration and the global carbon cycle. *Biogeochemistry* **48**:7-20.
- Schroeder, P., Brown, S., Mo, J., Birdsey, R. and Cieszewski, C. 1997. Biomass estimation for temperate broadleaf forests of the United States using inventory data. *Forest Science* **43**:424-434.
- Schulze, E.D., Wirth, C. and Heimann, M. 2000. Managing forest after Kyoto. *Science* **289**:2058-2059.
- Schwendenmann, L., Pendall, E. and Potwin, C. 2007. Surface soil organic carbon pools, mineralization and CO₂ efflux rates under different land-use types in Central Panama. In: Tschardtke, T. et al. (Eds.) *Stability of Tropical Rainforest Margins*, Springer, pp. 107-130.
- Sharma, P., Rai, S.C., Sharma, R. and Sharma, E. 2004. Effects of land-use change on soil microbial C, N and P in a Himalayan watershed. *Pedobiologia* **48**:83-92.
- Silver, W.L., Ostertag, R. and Lugo, A.E. 2000. The potential for carbon sequestration through reforestation of abandoned agricultural and pasture lands. *Restoration Ecology* **8**:394-407.
- Smithson, P., Addison, K. and Atkinson, K. 2002. Carbon sequestration in soils. In: *Fundamentals of the Physical Environment* 3rd edition, pp. 394-397.
- Sombroek, W.G., Nachtergaele, F.O. and Hebel, A. 1993. Amounts, dynamics and sequestering of carbon in tropical and subtropical soils. *Ambio* **22**:417-42.
- Soni, P. 2003. Climate change and restoration of tropical forests. *Indian Forester* **129**:865-873.
- Sparling, G.P. 1992. Ratio of microbial biomass carbon to soil organic carbon as a sensitive indicator of changes in soil organic matter. *Australian Journal of Soil Research* **30**:195-207.
- Swamy, H.R. and Proctor, J. 1994. Litterfall and nutrient cycling in four rainforests in the Sringeri area of the Indian Western Ghats. *Global Ecology and Biogeography Letters* **4**:155-165.
- Swamy, H.R. 1989. *Study of Organic Productivity, Nutrient Cycling and Small Watershed Hydrology in Natural Forests and in Monoculture Plantations in Chikamagalur District, Karnataka*, Final Report, Sri Jagadguru Chandrashekara Bharti Memorial College, Sringeri, India.
- Tanabe, H., Nakano, T., Mimura, M., Abe, Y. and Mariko, S. 2003. Biomass and net primary production of a *Pinus densiflora* forest established on a lava flow of Mt. Fuji in central Japan. *Journal of Forestry Research* **8**:247-252.
- Terakunpisut, J., Gajasen, N. and Ruankawe, N. 2007. Carbon sequestration potential in above ground biomass of Thong phaphun national forest, Thailand. *Applied Ecology and Environmental Research* **5**:93-102.
- Theng, B.K.G., Tate, K.R. and Sollins, P. 1989. Constituents of organic matter in temperate and tropical soils. In: Coleman, D.C. et al. (eds.), *Dynamics of Soils Organic Matter in Tropical Ecosystems*. University of Hawaii Press, Honolulu, pp. 5-32.
- Vance, E.D., Brookes, P.C. and Jenkinson, D.S. 1987. An extraction method for measuring soil microbial biomass. *Soil Biology and Biochemistry* **19**:703-707.
- Vogt, K.A., Grier, C.C. and Vogt, D.J. 1986. Production, turnover, and nutrient dynamics of above- and below ground detritus of world forests. *Advances in Ecological Research* **15**:303-377.
- Whittaker, R.H. 1996. Forest dimensions and production in the Great Smoke Mountains. *Ecology* **44**:233-252.
- Wright, A.L., Hons, F.M. and Jr-Matocha, J.E. 2005. Tillage impacts on microbial biomass and soil carbon and nitrogen dynamics of corn and cotton rotations. *Applied Soil Ecology* **29**:85-92.
- Yamakura, T., Hagihara, A., Sukardjo, S. and Ogawa, H. 1986. Above ground biomass of tropical rain forest stands in Indonesian Borneo. *Vegetation* **68**:71-82.