ORIGINAL PAPER

Estimation of tree biomass, carbon pool and net primary production of an old-growth *Pinus kesiya* Royle ex. Gordon forest in north-eastern India

Ratul Baishya · Saroj Kanta Barik

Abstract

· **Background** The data on carbon pool and biomass distribution pattern of old-growth *Pinus kesiya* Royle ex. Gordon forests are not available.

· **Methods** The forest carbon pool and annual net primary production (NPP) were assessed in three old-growth *P. kesiya* forest stands in north-eastern India, using biomass equations developed from 40 harvested trees between 9 and 63 cm in diameter at breast height (DBH) range.

· **Results** Regression models of the form Log(Y)=a + b logD+c (logD)^2+d (logD)^3 were the best fits for biomass estimation of total tree and its various components. The total forest biomass (which includes live and dead compartments of trees, shrubs, and herbs) was 460.5 Mg ha^{-1}, of which 91.2% was in the aboveground and 8.8% in the belowground compartment. *P. kesiya* contributed 77%, broad-leaved tree species 13.5%, shrubs 0.12%, herbs 0.03% and litter 0.5% to the total forest biomass. The total ecosystem carbon content of the forest including soil organic carbon pool was 283.1 Mg C ha^{-1}. The annual net primary production (NPP) of the forest was 17.5 Mg ha^{-1} yr^{-1}.

· **Conclusion** The estimated total forest biomass and carbon pool of the *P. kesiya* forest were greater than for the other pine forests studied world-wide.

R. Baishya
Department of Botany, University of Delhi,
Delhi 110007, India

S. K. Barik (✉)
Centre for Advanced Studies in Botany, School of Life Sciences,
North-Eastern Hill University,
Shillong 793022 Meghalaya, India
e-mail: sarojkbarik@gmail.com

1 Introduction

The carbon pool of a forest ecosystem varies with age (Clark et al. 2004; Kurz and Apps 1995). While young and middle-aged forest stands act as active carbon sinks (Valentini et al. 2000), old stands are moderate to small C sinks or even C sources, depending on the forest type and species composition (Desai et al. 2005; Knohl et al. 2003; Law et al. 2003; Malhi et al. 1999). However, most NPP studies world-wide have been carried out in relatively younger stands, and data on carbon content and NPP in old-growth pine forests are limited (Delrio et al. 2008).

Determination of carbon sequestration potential in terrestrial ecosystems through biomass estimation has been the most widely followed and appropriate approach (Brown 1997; Brown et al. 1989; Chambers et al. 2001). Regression models are used for biomass estimation because of their relative simplicity and ease for converting inventory data into a biomass estimate. Although it is difficult and tedious at the initial stage to develop the best-fit models, tree dimension values as the input data requirement for subsequent estimations have made the regression-based biomass estimation method extremely popular (Brown 1997). Several regression models have been developed to estimate biomass or biomass-related parameters (Brown et al. 1989; Schmidt et al. 2009), which are being used to prepare volume tables for several forestry species (Li and Weiskittel 2010) and to estimate carbon in tropical, temperate, boreal, and semi-arid forest ecosystems (Schroeder et al. 1997). The total biomass data obtained

from such models are then converted into carbon content for estimating carbon pools in different compartments, by multiplying by a conversion factor of 0.5 on the assumption that the tree biomass contains 50% carbon (Ravindranath et al. 1997; Richter et al. 1995).

Although several workers have used tree height, trunk diameter [i.e., diameter at breast height (DBH)] and wood density as independent variables for estimating tree above-ground biomass (AGB), the allometric relationship between AGB and DBH has been proved to be the best fit for tree biomass estimation in several forests (Brown 1997; Brown et al. 1989). The carbon present in other compartments of the ecosystem such as shrub, herb, litter, woody debris, root, and soil is added to the tree carbon data to obtain the size of the total carbon pool in a forest ecosystem. Since AGB of trees contains a large fraction of the total forest carbon stock, most studies on forest carbon budget have focused only on tree AGB estimation. Although these studies do provide empirical data on the major carbon pool of the forest, total ecosystem level carbon data for most ecosystems is lacking.

Net primary productivity (NPP), the balance between the light energy fixed through photosynthesis and respiratory loss and mortality, represents the net carbon input from the atmosphere to terrestrial vegetation (Melillo et al. 1993). It is the net organic matter produced by live plants at the end of a specific time interval (Clark et al. 2001). It is an important index for estimating carbon budget and evaluating the patterns, processes and dynamics of carbon cycling in forest ecosystems at local, regional and global scales (Luo et al. 2002). Most studies on NPP estimation consider only the increment in AGB and litterfall, and completely ignore the belowground component. Cairns et al. (1997) argued that the approach of allometric modeling should be more realistic than root/shoot ratio for estimating tree belowground biomass (BGB). For estimating ecosystem level NPP of a forest, time-series biomass data for tree, shrub, herb, and litter components are pre-requisites. However, such data for different components other than tree are not available easily, and therefore studies on total ecosystem level NPP estimation are limited.

The natural forests of *Pinus kesiya* Royle ex. Gordon are found throughout north-eastern India at an elevation range of 800–2,000 ma.s.l., and extend up to the Philippines through Myanmar and Vietnam (Changala and Gibson 1984). Plantation forests of the species have been reported from such far-off places as Kenya, Zimbabwe, and Tanzania, indicating its global importance. *P. kesiya* has been invading the montane subtropical broad-leaved forest areas of north-eastern India once the primary broad-leaved forest species are cleared (Barik et al. 1996). Therefore, *P. kesiya* forest is very important for north-eastern India as a carbon sink. Although the AGB and NPP of a *P. kesiya* plantation forest were studied by Das and Ramakrishnan (1987) along an age series of 1–22 years through

developing an allometric model, the model did not fit well to the old-growth forests. As such, the total as well as compartment-wise carbon pool, and NPP of natural old-growth *P. kesiya* forests have not been studied. Therefore, the present study was undertaken (i) to develop regression models for biomass estimation of *Pinus kesiya* and broad-leaved trees, and (ii) to estimate carbon pools in different compartments, and (iii) net primary productivity of an old-growth *Pinus kesiya* forest ecosystem.

2 Materials and methods

2.1 Study site and climate

The study was conducted in Riat Laban reserved forest (latitude 25°55′N, longitude 91°88′E, elevation 1,643 m a.s.l, area 2.0 sq. km), and its adjoining Laitkor (latitude 25°56′N, longitude 91°89′E, elevation 1,660 ma.s.l., area 3.2 sq. km) and Upper Shillong (latitude 25°56′N, longitude 91°85′E, elevation 1,655 ma.s.l., area 7.9 sq. km) community forests in Meghalaya during 2005–2007. The forest stands are natural, continuous, well-protected, 65–80 years old and are dominated by *Pinus kesiya*. The forest is classified as Assam sub-tropical pine forest (Champion and Seth 1968). The study site received an average annual rainfall of 2466.2 mm during the study period. The average monthly temperature varied from a maximum of 22.9°C in the month of July to a minimum of 1.8°C in December.

The density of *P. kesiya* contributed to 71–73% of the total tree density in the forest. *Lyonia ovalifolia* Hort., with density ranging between 6 and 159 trees ha^{-1}, was the dominant sub-canopy tree species in all the three stands. The other associated tree species were *Alnus nepalensis* D. Don, *Lithocarpus dealbatus* Rehder, *Lyonia ovalifolia* Hort., *Myrica esculenta* Buch.-Ham. ex D. Don, *Rhododendron arboretum* Sm., and *Schima wallichii* Choisy. The shrub layer was dominated by *Eupatorium adenophorum* Spreng and *Lantana camara* L. Some of the herbaceous species were *Arundinella benghalensis* Druce, *Duchesnea indica* Focke, *Eupatorium riparium* Regel, *Gnaphalium luteo-album* L., *Imperata cylindrica* Beauv., *Paspalam dilatatum* Poir, *Plantago major* L., *Pouzolzia hirta* Hassk, *Potentilla fulgens* Wall. ex Hook., and *Rananculus scleratoides* Perf. ex Ovczinn. *Aeginetia indica* L. was the dominant herb on decomposing litter. *Smilax aspera* DC. and *S. ovalifolia* A. DC. were the dominant climbers in the forest.

2.2 Determination of forest age and analysis of tree population structure

Six permanent plots of 250 m × 20 m size were laid in the three stands. In each plot, all trees with ≥ 5 cm DBH were

tagged, measured, and identified. The girth of each individual tree was measured. The tree species other than *P. kesiya* were identified with the help of regional flora (Haridasan and Rao 1985–1987). The ASSAM herbarium at Botanical Survey of India, Shillong was consulted for confirmation. The density and basal area were calculated following Misra (1968). For depicting tree population structure of the forest, all trees including broad-leaved species were grouped into eight diameter classes i.e.: >5–9.9, 10–19.9, 20–29.9, 30–39.9, 40–49.9, 50–59.9, 60–69.9 and 70–79.9 cm. The diameter–density distribution of *P. kesiya* was presented.

2.3 Estimation of total biomass and carbon of the forest

The total forest biomass was estimated by adding the biomass of the following components: (i) *P. kesiya* trees, (ii) broad-leaved trees, (iii) litter, and (iv) shrubs and herbs. Since biomass models for *P. kesiya*, particularly in old-growth forests, were not available, allometric biomass equations were developed for AGB and BGB estimation. The existing biomass models for broad-leaved species (Cairns et al. 1997; Chambers et al. 2001) were used to estimate the BGB and AGB of broad-leaved trees in the forest. The biomass of shrubs and herbs were directly estimated through a harvest method following Misra (1968). The mean biomass values calculated from the six permanent plots in the three sites were presented. Carbon content of each component was calculated as 50% of the ash-free mass. Ash content was determined by igniting the oven-dried plant materials at 550°C for 6 hours in a muffle furnace.

2.4 Estimation of *P. kesiya* tree biomass for model development

Forty trees of *P. kesiya* were randomly selected for felling from the three forest stands. The trees selected for the Riat Laban reserved forest stand were from the adjacent community forest area, which is continuous with the reserve, since felling of tree is banned inside the reserve. The trees selected in the two community forest stands were from the peripheral areas of the stands. Five to six trees were selected from each of the seven diameter classes of *P. kesiya* i.e.: >5–9.9, 10–19.9, 20–29.9, 30–39.9, 40–49.9, 50–59.9 and 60–69.9 cm, which represented the minimum and maximum diameter range of the species in the forest. The DBH of the felled trees was measured. The age of the pine forest was determined by counting the annual growth rings in circular sections taken from the above mentioned 40 sample trees. The counting of the rings was done in sections taken at 30 cm from the base of the tree. The mean value represented the age of the forest stand. The trees were separated into stem, branch, twig, needle, reproductive part,

and root components, and the fresh weight of each component was taken. Three replicate samples of 2 kg each for each component were oven-dried at 80°C till constant weight was achieved. For estimation of BGB, the roots of each cut tree were excavated as completely as possible, and separated into fine roots (<2 mm diameter) and coarse roots (>2 mm diameter). Both the coarse and fine roots of each cut tree were weighed in the field. The portion of the tree stump that remains underground was treated as a part of the coarse root. The root samples in triplicate were brought to the laboratory and oven-dried at 80°C till constant weight was achieved.

2.5 Development and evaluation of allometric models

Regression models were developed considering tree DBH as independent variable, and stem, branch, twig, needle, reproductive part, root, total aboveground, and total tree biomass as dependent variables. The DBH and dry weight values were log-transformed, and nonlinear regression models were fitted for different tree components, as well as for total tree biomass. For selecting the best-fit models, the coefficient of determination (R^2), standard deviation (SD), sum of square error (SSE), mean square error (MSE) and root mean square error (RMSE) of the allometric equations were compared with those of existing models developed by earlier workers (Brown 1997; Delrio et al. 2008; Ter-Mikaelian and Korzukhin 1997) for *Pinus* spp.

The models developed by Chambers et al. (2001) for AGB and Cairns et al. (1997) for BGB estimation were used for determining broad-leaved tree biomass. The allometric model for the aboveground component (Y_1) is: $\ln(Y_1) = -0.37 + 0.333 \ln D + 0.933 [\ln(D)]^2 - 0.122 [\ln(D)]^3$, and that for belowground component (Y_2) is: $Y_2 = \text{Exp} [-1.085 + 0.9256 (\ln AGB)]$. These two models were selected based on R^2, SD, SSE, MSE, and RMSE values.

2.6 Litter

Litterfall was estimated at monthly interval over a period of 2 years from September, 2005 to August, 2007. Five traps of 1 m × 1 m × 0.15 m (length × breadth × height) were placed within each permanent plot ($n=120$). The litter components were segregated into five fractions, viz., leaf, twig, branch, cone, and reproductive parts. The biomass of each component was determined after oven-drying the samples at 80°C till constant weight was achieved.

2.7 Analysis of soil organic carbon

Composite soil samples were collected from each of the six permanent plots up to 1 m depth from the surface. Soil samples were collected during each of the four seasons of

the year 2005, and analysis for determination of soil organic carbon content was done after air-drying and sieving the soil samples through a 2-mm mesh sieve. Soil organic carbon was estimated following the colorimetric method described by Anderson and Ingram (1993).

2.8 Estimation of NPP

The NPP of the forest was determined from the NPP estimates for each component, i.e., tree, shrub, herb, and litter in the six permanent sample plots. The NPP was estimated for all these components for 2 consecutive years (i.e., 2006 and 2007), and the mean values were presented. The biomass for *P. kesiya* was estimated by applying the allometric equations developed in this study, and for other broad-leaved tree species it was estimated using the equations of Chambers et al. (2001) for AGB and Cairns et al. (1997) for BGB. The standing tree biomass component of NPP was estimated by subtracting biomass estimated for September 2005 from that of August 2006, and biomass for September 2006 from that of August 2007, for the years 2006 and 2007 respectively. The aboveground NPP was determined by summing the tree biomass component of NPP and annual litter production measured at the same time interval (Kira and Shidei 1967). The annual root production was measured by sampling roots using a soil augur in 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 in 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.

3 Results

3.1 Allometric biomass models for *P. kesiya*

The aboveground biomass data for 40 trees (Table 1) were regressed against the DBH using the regression models developed by the earlier workers for pine species. None of these models yielded a satisfactory coefficient of determination (R^2), MSE and RMSE. Hence, the following form of model was developed by log transforming the data of each tree component, which yielded greater R^2 and lower MSE, SSE and RMSE than the earlier models —

$$Log(Y) = a + b \log D + c (\log D)^2 + d (\log D)^3 \qquad (1)$$

where Y=AGB (kg/tree), a, b, c, and d are regression coefficients, and D is the stem diameter at breast height. All the measures of coefficients of the models for tree components were statistically significant ($P<0.001$) (Fig. 1).

3.2 Density of trees, shrubs and herbs

The density of trees in the forest ranged between 628 and 947 trees ha^{-1}. The density of *P. kesiya* ranged between 454 and 677 trees ha^{-1}. The total tree basal areas of the three forest stands were 70.6, 66 and 126 m^2 ha^{-1} respectively. *P. kesiya* contributed to 97.4, 96.5 and 74% of the total basal area in the three stands. The total shrub density of the forest was 4,400 plants ha^{-1}, and that for herb was 385,000 plants ha^{-1}.

3.3 Estimation of total forest biomass and NPP

The total biomass of the forest was 460.5 Mg ha^{-1}, of which 91.2% was in the aboveground compartment and 8.8% in the belowground compartment. *P. kesiya* contributed 77%, broad-leaved tree species 13.5%, shrubs 0.12%, herbs 0.03% and litter 0.5% to the total forest biomass (Table 2). The total AGB of pine including litter, herb and shrub components was 357.6 Mg ha^{-1}. The tree AGB and BGB were 419.7 and 40.8 Mg ha^{-1} respectively. While *P. kesiya* had 354.6 Mg ha^{-1} as AGB and 31.8 Mg ha^{-1} as BGB, the corresponding figures for the broad-leaved species were only 62.2 and 9.0 Mg ha^{-1} respectively (Table 2). The needles, twigs, branches, and reproductive parts accounted for 44.9, 31.3, 4.8, and 18.9% respectively to the total litterfall. The fine and coarse root biomass of *P. kesiya* were 0.5 and 6.4% of the total forest biomass and constituted 6% and 72% of the total BGB, respectively. The BGB of broad-leaved species was only 1.9% of the total forest ecosystem biomass and 22% of the total BGB. The total ecosystem NPP of the forest was 17.5 Mg ha^{-1} yr^{-1}. The leaf litter, twig, branch, and reproductive parts contributed to 42.6, 14.9, 10.6, and 31.9% of the total litter production. The stem (55%), branches (8.6%), and twigs, needles, and reproductive parts (8.6%) of *P. kesiya* were the major contributors to the total ecosystem NPP. The total ecosystem carbon content of the forest was 283.1 Mg C ha^{-1} (Table 2). The soil organic carbon was 58.7 Mg ha^{-1}, contributing 20.7% to the total ecosystem carbon. The DBH class 50–59.9 cm had the highest tree density among all the DBH classes, and hence contributed maximum biomass of 115.9 Mg ha^{-1}, which accounted for 27.8 % of the total AGB of the forest (Fig. 2).

4 Discussion

In most allometric models that relate biomass with DBH, the variability in untransformed data increases with increase

Table 1 Dry weight (kg) of different components of *Pinus kesiya* tree used for developing regression models

DBH (cm)	Stem	Branch	Twig	Needle	Cone	Fine root	Coarse root	Total root	Total AGB	Total tree
9.01	15.18	4.99	3.27	1.53	0.42	0.31	2.22	2.53	25.38	27.90
9.20	15.57	6.28	3.83	1.97	0.44	0.98	2.54	3.52	28.08	31.60
11.28	19.61	8.13	3.96	1.88	0.90	0.26	3.18	3.44	34.46	37.90
11.41	20.12	8.51	3.40	2.00	0.97	0.29	3.61	3.90	35.01	38.91
12.37	22.19	9.72	3.53	2.13	0.82	0.55	6.76	7.31	38.38	45.69
13.94	32.51	12.99	3.27	4.97	2.22	0.95	11.65	12.61	55.96	68.56
14.33	48.25	14.02	3.40	4.66	2.38	1.05	12.81	13.85	72.70	86.55
15.96	41.11	19.61	4.56	5.49	2.33	1.43	17.50	18.93	73.09	92.02
16.12	63.08	23.91	5.42	4.76	2.60	1.46	17.94	19.41	99.76	119.17
17.12	81.36	28.34	6.71	5.34	2.51	1.68	20.62	22.31	124.24	146.55
18.11	88.84	35.52	8.15	5.01	3.25	1.89	23.19	25.08	140.77	165.85
19.29	72.93	22.49	9.72	6.67	2.58	2.13	26.10	28.23	114.39	142.62
22.60	121.52	37.20	8.28	5.40	3.27	2.73	33.40	36.13	175.67	211.80
23.15	133.86	48.29	9.61	6.12	3.07	2.82	34.52	37.33	200.94	238.28
27.76	287.37	83.95	10.99	6.48	2.66	3.47	42.60	46.08	391.44	437.52
28.59	287.37	83.91	10.99	6.48	3.37	3.58	43.85	47.43	392.12	439.55
32.76	354.54	86.06	11.72	6.41	3.27	4.01	49.22	53.23	462.01	515.24
35.03	376.52	80.57	11.52	6.22	5.83	4.20	51.56	55.76	480.66	536.42
37.12	425.53	82.26	11.87	6.55	7.20	4.35	53.38	57.73	533.40	591.13
38.11	478.43	84.99	11.33	7.29	4.77	4.41	54.14	58.55	586.80	645.35
39.29	502.51	90.58	14.06	8.15	5.16	4.48	54.96	59.44	620.46	679.89
40.61	578.48	88.92	14.02	7.38	3.95	4.54	55.77	60.31	692.75	753.07
43.47	640.42	93.03	13.91	7.52	4.65	4.66	57.19	61.84	759.54	821.39
47.53	722.25	105.93	15.20	8.38	9.88	4.76	58.48	63.24	861.65	924.89
48.27	730.40	101.70	15.57	7.09	5.15	4.77	58.63	63.40	859.90	923.30
49.23	739.84	106.12	14.04	8.16	8.38	4.78	58.80	63.58	876.53	940.11
49.74	750.93	102.00	13.14	7.92	6.39	4.79	58.87	63.66	880.38	944.04
51.41	769.36	110.38	15.70	8.43	4.18	4.80	59.05	63.86	908.04	971.89
52.95	799.52	114.25	15.10	8.37	6.39	4.81	59.14	63.94	943.63	1,007.57
53.59	815.11	105.93	17.01	9.12	7.13	4.81	59.15	63.96	954.31	1,018.27
54.58	836.39	124.40	16.94	7.57	7.88	4.81	59.15	63.95	993.18	1,057.14
56.70	961.72	115.52	13.81	7.71	5.62	4.80	59.06	63.86	1,104.37	1,168.23
57.44	1,000.33	114.43	15.63	8.46	6.65	4.79	59.01	63.81	1,145.50	1,209.31
59.49	1,046.02	93.03	14.04	8.16	8.77	4.78	58.82	63.59	1,170.02	1,233.61
59.90	1,056.21	101.31	13.14	8.38	9.88	4.77	58.77	63.54	1,188.93	1,252.47
60.10	1,080.29	105.93	15.70	7.09	5.15	4.77	58.75	63.52	1,214.16	1,277.68
61.28	1,085.15	101.70	15.10	8.16	8.38	4.76	58.60	63.36	1,218.48	1,281.84
61.28	1,104.67	106.12	17.01	7.92	6.39	4.76	58.60	63.36	1,242.10	1,305.45
62.37	1,142.38	102.00	16.94	8.43	4.18	4.74	58.45	63.20	1,273.93	1,337.13
62.69	1,184.05	110.38	13.81	8.37	6.39	4.74	58.41	63.15	1,323.00	1,386.14

in diameter (Beauchamp and Olson 1973). The log transformation brings the variance down to uniformity by stretching the smaller values and compressing the larger values. The actual biomass values are obtained from the model-derived values through antilog transformation (Ovington and Olson 1970). The log-transformed DBH data of the harvested trees used for the model development yielded lower variance (0.074), standard deviation (0.272) and standard error (0.043) than the untransformed DBH. The variance (0.056–0.076), standard deviation (0.238–0.275) and standard error (0.008–0.009) of the log-transformed DBH data in the three pine forest stands, used for estimating total forest biomass, were also low. Several authors (Baskerville 1972; Beauchamp and Olson 1973)

Fig. 1 Regression analyses between tree diameter at breast height (cm), and biomass of different tree components, above ground biomass and total tree biomass of *Pinus kesiya*
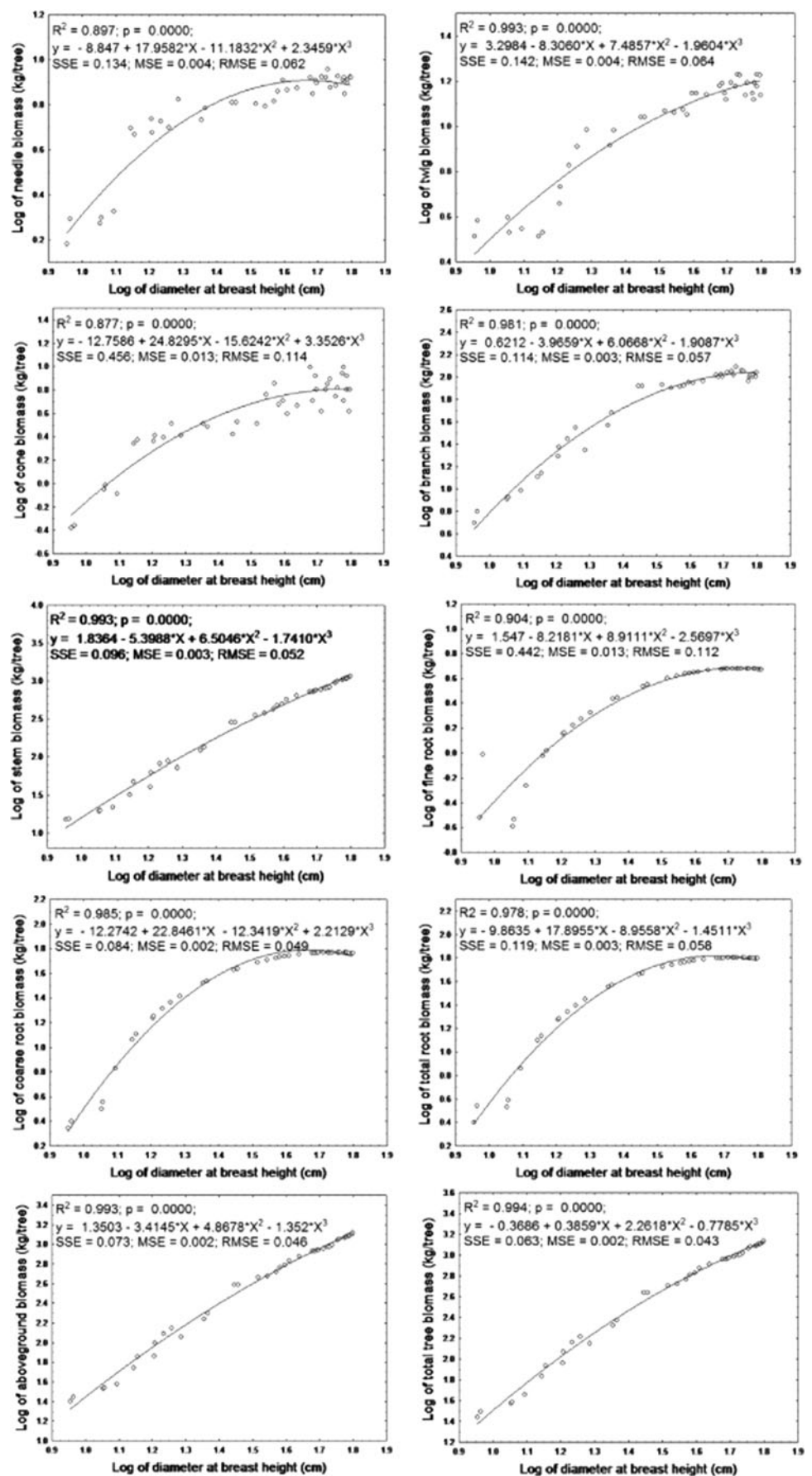
Table 2 Total ecosystem, above- and belowground biomass, carbon content and net primary production of an old-growth *Pinus kesiya* forest in north-eastern India

| Component	Biomass (Mg ha^{-1})	Carbon (Mg C ha^{-1})	% contribution	Net primary production (Mg ha^{-1}yr^{-1})	% contribution
Aboveground biomass of *Pinus kesiya*					
- Stem	291.8±33.0	143.0	63.4	9.8	56.0
- Branch	48.2±2.0	23.6	10.5	1.5	8.6
- Twig	7.3±0.5	3.6	1.6	0.7	4.0
- Needle	4.3±0.4	2.1	0.9	0.5	2.9
- Reproductive parts	3.1±0.2	1.5	0.7	0.3	1.7
Aboveground biomass of broad-leaved species	62.2±40.3	30.5	13.5	3.2	18.3
Herbs	0.1±2.5	0.1	0.03	0.0	0.0
Shrubs	0.6±4.6	0.3	0.12	0.0	0.0
Detrital biomass					
- Needle	1.0±1.6	0.5	0.2	0.0	0.2
- Twig	0.7±2.4	0.3	0.2	0.0	0.1
- Branch	0.1±1.4	0.1	0.0	0.0	0.1
- Reproductive parts	0.4±2.2	0.2	0.1	0.0	0.2
- Total detrital biomass	2.3±7.6	1.1	0.5	0.1	0.5
Total aboveground biomass	419.7	205.7	91.2	16.1	92.0
Belowground biomass of *Pinus kesiya*					
- Fine roots (<2 mm)	2.4±4.7	1.1	0.5	0.3	1.7
- Coarse roots (>2 mm)	29.4±7.2	13.5	6.4	0.7	4.1
Belowground biomass of others species	9.0±1.7	4.1	1.9	0.4	2.2
- Total forest	460.5	224.4	100.0		
- Total soil organic carbon		58.7			
Total ecosystem	460.5	283.1	100.0	17.5	100.0
BNPP				0.1	8.0
ANPP				0.9	92.0

have argued that log-transformed nonlinear regression models produce up to 20% error for certain components if they are back-transformed into linear form. The back transformation is acceptable if MSE is not too large (Baskerville 1972). In this study, the MSE and RMSE values for different tree components are extremely low.

The AGB in this old-growth *Pinus kesiya* forest (419.7 Mg ha^{-1}) was about 36% greater than that of the 22-year-old young forest studied by Das and Ramakrishnan (1987) (308.7 Mg ha^{-1}). Increase in AGB with age was also depicted through the studies conducted by Ovington and Madgwick (1959), and Delrio et al. (2008) for *Pinus sylvestris* L. for young- and old-growth forests respectively. A similar increase was also noted from the studies of Karizumi (1974) and Tanabe et al. (2003) for *Pinus densiflora* Sieb. et Zucc. The AGB obtained in this study is comparable with a 41–80-year-old *P. sylvestris* forest in Spain (359.7–456.9 Mg ha^{-1}) (Delrio et al. 2008). However, it is much greater than that of a 71–80-year-old *Pinus*

koraiensis Sieb. et Zucc. forest of Japan (317.9 Mg ha^{-1}) (Son et al. 2001). The AGB obtained in the present study was also greater than that of most tropical forests studied. Muller (1982) obtained an AGB of 330 Mg ha^{-1} for the tropical broad-leaved forests of the eastern hardwood region of USA, and Brown et al. (1989) reported 238–341 Mg ha^{-1} for Cameroon and 153–221 Mg ha^{-1} for Sri Lanka. However, the AGB of the present study is comparable with the findings of Brown et al. (1989) for the tropical rain forests of Malaysia (225–446 Mg ha^{-1}).

The 50–60 cm tree diameter class contributed 27.8% to the total tree AGB, indicating the important role of this diameter class in carbon storage. The larger trees (>60 cm DBH) contributed 15.8% to the total aboveground biomass. Thus, the large trees together accounted for more than 43% of the total carbon in the tree component. The greater contribution of large trees to AGB is in conformity with the findings of earlier workers (Baishya et al. 2009; Brown 1996; Brown and Lugo 1992), who had found that large

Fig. 2 Diameter–density distribution of *Pinus kesiya* in an old-growth pine forest of north-eastern India. *Bars* show standard error
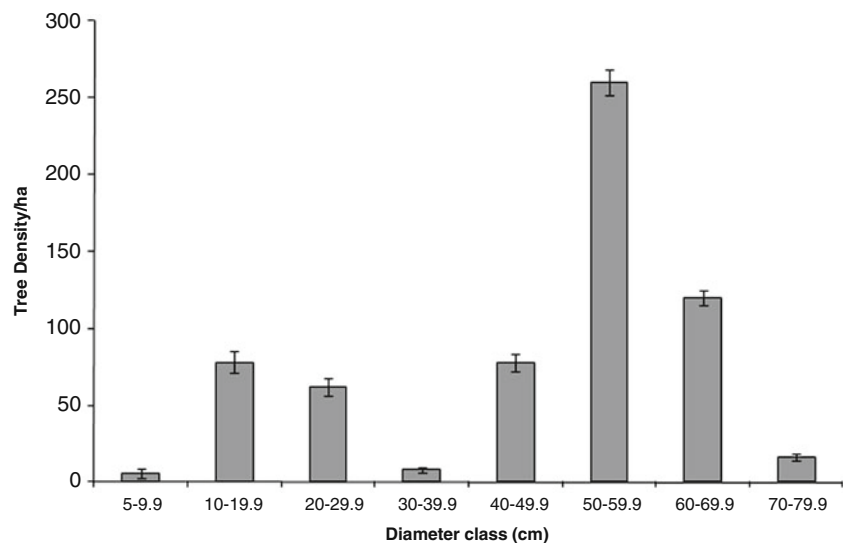
trees contributed up to 50% of the aboveground biomass. The smaller diameter trees thus had about 57% of the total tree carbon in this forest, indicating their importance in carbon storage.

The annual litterfall in this old-growth *P. kesiya* forest (2.3 Mg ha^{-1}) was greater than that in the 22-year-old forest (1.5 Mg ha^{-1}) reported by Arunachalam et al. (1996). The amount of annual litter fall is within the reported range of 2.2–22.6 Mg ha^{-1} for various tropical and subtropical forests (Vogt et al. 1986). The proportion of leaf litter in the total litter was 42.6%, and the twigs, branches, and reproductive parts accounted for 14.9%, 10.6%, and 31.9% respectively. Arunachalam et al. (1996) reported that leaf litter constituted as high as 75% of the total litter in the young 22-year-old *P. kesiya* forest stand. Therefore, it is evident that with increasing age of a *P. kesiya* forest, the relative proportion of leaf litter in the litter decreases.

Fine and coarse root biomass of *P. kesiya* contributed 6% and 72% to the total root biomass respectively. The fine root biomass was lower (2.4 Mg ha^{-1}) than the values reported by Arunachalam et al. (1996) (3.4–5.1 Mg ha^{-1}) and by John et al. (2001) (4.6 Mg ha^{-1}) in a 22-year-old and 23-year-old *P. kesiya* plantation forest, indicating the reduction of fine root production in old-growth forest. The fine root biomass obtained in the present study was also lower than the global range of 1.0–17.7 Mg ha^{-1} for various ecosystems (Vogt et al. 1986). Low availability of soil nutrients and water has been reported to promote high production and accumulation of fine roots (Vogt et al. 1986).

The BGB in this forest was 8.9% of the total tree biomass, which is within the range reported by earlier workers. Cairns et al. (1997) concluded that the BGB of an ecosystem can reach up to 25% of the total tree biomass. The contribution of shrub and herb components to the total forest biomass was negligible (0.15%). Brown (1997)

concluded that shrubs and herbs can contribute up to 3% of the total forest AGB.

The total NPP of the forest was high, which may be attributed to relatively higher soil NPK content and moisture regime in this pine forest. Gower et al. (1994) reported that N fertilization increases NPP of forest, and carbon allocation to belowground components decreases with increase in soil N availability (Haynes and Gower 1995). The extremely low BGB (40.8 Mg ha^{-1}) obtained in this study may be attributed to this reason. Vogt et al. (1996) reported that root NPP does not depend only on nutrient availability for many pine species. Relatively low root NPP as observed in this study (1.4 Mg ha^{-1} yr^{-1}) in comparison to other studies (Karizumi 1974) supports this argument.

The total aboveground NPP in this old-growth forest (16.1 Mg ha^{-1} yr^{-1}) was lower than the younger (5–22-year-old) *P. kesiya* forest (30.1–20.1 Mg ha^{-1} yr^{-1}) reported by Das and Ramakrishnan (1987). The total aboveground NPP was higher than most pine forests around the world. For example, Chaturvedi and Singh (1982, 1987) and Rana et al. (1989) calculated the aboveground NPP for *Pinus roxburghii* forest (6.1–15.6 Mg ha^{-1} yr^{-1}) in the central Himalayas of India. Ma (1988) reported NPP of 3.5–17.5 Mg ha^{-1} yr^{-1} for 33–70-year-old *Pinus tabulaeformis* forest from China. The high productivity of *P. kesiya* may be attributed to high net assimilation rate due to prolonged photosynthetic activity, and higher uptake of nutrients due to rapid turnover of nutrients (Das and Ramakrishnan 1987). The potential of a forest to sequester carbon depends on the forest type, age of forest and size class of trees (Terakunpisut et al. 2007). Considering the NPP level, tree diameter distribution, species composition and the age of the forest, it can be concluded that the forest is yet to fully mature and has the potential to store additional carbon in the future.

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