Structure and Function of Shisham Forests in Central Himalaya, India: Dry Matter Dynamics

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The biomass and net primary productivity (NPP) of 5- to 15-year-old Shisham (*Dalbergia sissoo* Roxb.) forests growing in central Himalaya were estimated. Allometric equations were developed for all above- and below-ground components of trees and shrubs for each stand. Understorey forest floor biomass and litter fall were also estimated in forest stands. The biomass (dry matter), forest floor biomass (standing crop litter), tree litter fall and NPP of trees and shrubs increased with increasing age of the forest stand, whereas the dry matter and herb NPP decreased significantly ($P < 0.001$) with increasing age of the forest. Total forest biomass and NPP ranged from 58·7 (5-year-old stand) to 136·1 t ha^{-1} (15-year-old stand) and 12·6 (5-year-old stand) to 20·3 t ha^{-1} year^{-1} (15-year-old stand), respectively. Of these values, tree biomass accounted for 85·7 (5-year-old stand) to 90·1 % (15-year-old) of total forest biomass, and tree NPP for 72·2 (5-year-old) to 82·3 % (15-year-old) of total forest NPP. The biomass accumulation ratio (BAR) of the bole component (bole wood + bole bark) increased with increasing age of the forest stand. The bole BAR was 5·8 (5-year-old stand) to 7·9 (15-year-old stand). However, total BAR of the forest stand ranged from 5·5 (5-year-old) to 7·5 (15-year-old).

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Key words: *Dalbergia sissoo* Roxb, biomass, net primary productivity, litter input, forest floor biomass, turnover rate, Tarai belt, Central Himalaya, India.

INTRODUCTION

Shisham (*Dalbergia sissoo* Roxb.) is an important tree species belonging to the family Papilionaceae. It is a medium- to large-sized, gregarious deciduous tree, attaining a height of approx. 30 m and a girth of approx. 2·5 m in a favourable climate (sub-tropical and tropical zones). According to Champion and Seth (1968), the Shisham tree is a characteristic species of Khair–Sissoo (*Acacia catechu–Dalbergia sissoo*) primary seral type forest. Shisham occurs naturally throughout the sub-Himalayan tract and outer Himalayan valley from the Indus to Assam, usually at elevations of about 900 m, but sometimes occurring up to 1500 m. Shisham is found either in a pure forest stand or together with other species, commonly Khair (*Acacia catechu*). Shisham is a good example of a pioneer species in the riverain succession of the Gangetic alluvial plains in India. Shisham usually regenerates naturally on recently laid down terraces of rivers, on freshly exposed soils, road cuttings, fresh embankment and landslips where drainage is good and there is sufficient soil aeration. However, Shisham shows remarkable variation in growth pattern and yield per unit area because it is adapted to a wide range of ecological habitats which thus influence its dry matter production.

Shisham is a very hardy species and produces valuable timber. Trees shed leaves from October to February; new leaves appear between February and April. Shisham can be propagated both by seeds and vegetative parts. Stump planting of Shisham (i.e. planting approx. 5 cm of stem and 20 cm of root) is known to be the best method of artificial regeneration.

Shisham is amongst the principal tree species commonly recommended for plantation programmes in dry regions for soil and water conservation as well as for fuel wood production. This species can survive at sites where nitrogen levels are low and also on saline and alkaline soils. Its adaptability, drought resistance, hardiness and nitrogen-fixing properties, as well as its multipurpose nature, make it suitable for afforestation and reforestation in many parts of the country. Thus, this species is environmentally and socio-economically acceptable to the people of India.

Leith and Whittaker (1975) pointed out that if forest biomass is measured and analysed in its proper context as part of production, an overall picture of ecosystem functioning can be gained. However, the biomass and productivity of tree species varies from place to place due to variation in climate, soil, temperature and rainfall. Biomass and net primary productivity (NPP) have been studied in temperate and tropical forest vegetation types (Ogawa *et al.*, 1965; Ovington, 1965; Whittaker, 1966; Newbould, 1967; Attiwill and Ovington, 1968; Satoo, 1968; Whittaker and Woodwell, 1968; Whittaker and Likens, 1975; Chaturvedi *et al.*, 1984; Gurumurti *et al.*, 1987; Sharma *et al.*, 1988; Swaminath, 1988; Pal and Raturi, 1990). Bargali *et al.* (1992), Lodhiyal *et al.* (1995) and Lodhiyal and Lodhiyal (1997) have made detailed studies of the biomass and
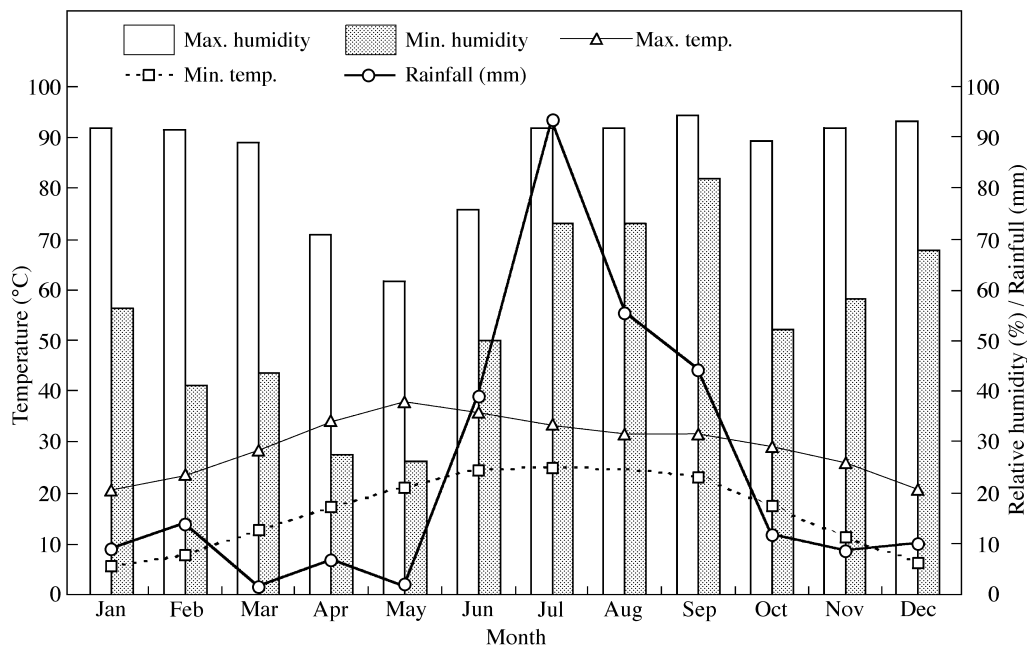
FIG. 1. Ombrothermic diagram based on meteorological data for 1996 and 1997 for the study area.

productivity of exotic plantations in the central Himalayan Tarai belt (Tarai is a region of high water and nutrient availability). Teller (1968) pointed out that forest floor biomass plays a significant role in the structure and functioning of forest ecosystems by acting as a nutrient reservoir for the intra-system cycling processes and improves the infiltration rate and water holding capacity of soils. Litter fall is another important component of nutrient recycling in a forest, and its inputs depend on a variety of factors such as species, age groups, canopy cover, weather conditions and biotic factors. Observations on litter input in different forests have been made by Carlisle *et al.* (1966), Attiwill *et al.* (1978), Merriam *et al.* (1982), Rawat and Singh (1988) and Lodhiyal and Lodhiyal (1997), but there is no detailed information about the structure and function of Shisham forests in relation to annual productivity and dry matter transfer in the Tarai belt of the central Himalayan mountains.

The main objectives of this study were: (1) to determine the biomass and net annual (primary) productivity in Shisham forests of different ages; and (2) to assess whether these forests perform better than conventional exotic plantations (i.e. poplar and eucalypt) and natural forests of the region. In this respect we adopted an ecological approach by considering dry matter flows in terms of quantity and seasonal periodicity.

MATERIALS AND METHODS

Description of study sites

The three study sites were located between 28°43′ and 29°37′N, and 79°20′ and 79°23′E at an altitude of 250 m in Tarai in the district of Udham Singh Nagar (about 80 km from Kumaun University, Nainital) of the Indo-Gangetic plains in the south of the Outer Shiwalik range of central Himalaya, India.

The climate of the study area is sub-tropical and monsoonal. There are three seasons per year: winter (November to February), summer (April to mid-June), and a rainy season (mid-June to mid-September). The months of October and March are transitional periods and are known as autumn and spring, respectively. The average monthly rainfall ranges from 0·5 mm in February (minimum) to 109·9 mm in July (maximum) (Fig. 1). The average minimum and maximum temperatures range from 4·5 °C (January) to 25·4 °C (July), and from 17·3 °C (December) to 37·0 °C (May), respectively (Fig. 1).

The slope of the Tarai area is not less than 2·5 m per km. The fertile soil is fine-textured, alluvial, loamy and free from boulders. Because the Tarai is recharged by water seepage from higher elevations it has a high water table and thus a high moisture and nutrient content, contributing to the high productivity of the site.

The Tarai belt is rich in natural resources. The natural vegetation in this region is mainly alluvial savannah woodland type 3/I51, with some pockets of the moist Tarai sal forest type 3C/C2c (Champion and Seth, 1968). The area consists of luxuriant growth of tall grasses with scattered growth of deciduous forest trees.

The total area planted with Shisham trees was 47 ha. Of this area, 5-, 10- and 15-year-old forest stands occupied 14, 16 and 17 ha, respectively. These 5-, 10- and 15-year-old forests were planted in 1991, 1986 and 1981, respectively, after clear felling of species indigenous to the area.

Biomass

Sampling design. In all three stands trees were similarly spaced (4 m × 4 m), giving a density of 625 trees ha^{-1}. A 1 ha plot was sampled in each forest stand. The sample plot was divided into four replicate sub-plots of 50 × 50 m^2 (0·25 ha), and 100 trees in each sub-plot (total of 400 trees in each forest stand) were measured. The height and diameter [diameter at breast height (dbh), 1·37 m] of trees were measured by Ravi's Multimeter and Tree Callipers, respectively. All the trees measured in each forest stand were divided into three diameter classes: 10·0–15·0, 16·0–21·0 and 22·0–27·0 cm in 5-year-old stands; 15·0–19·0, 20·0–24·0 and 25·0–29·0 cm in 10-year-old stands; and 21·0–24·0, 25·0–28·0 and 29·0–32·0 cm in 15-year-old forest stands. The average height of trees and of four shrubs (*Lantana camara*, *Murraya koenighii*, *Clerodendrum viscosum* and *Pogostemone benghalense*; 25 individuals of each shrub giving a total of 100 individuals of all four shrub species from each sub-plot) was 8·0, 12·0 and 18·0 m and 2·3, 2·5 and 2·6 m, respectively, in 5-, 10- and 15-year-old forest stands.

Individual trees and shrubs were selected at random from each sub-plot of each forest stand. To estimate understorey density, shrub and herb individuals were sampled in 50 quadrats of 2 × 2 m and 1 × 1 m, respectively in each forest stand.

To estimate the biomass of Shisham forest, the selective harvest technique was adopted (Ovington, 1962; Newbould, 1967). Twelve trees in each forest stand (three trees in each sub-plot, four from each dbh class) were harvested. Harvested trees were cut into 1–2 m logs. Above- (bole wood, bole bark, branches, twigs, leaves and reproductive parts, i.e. inflorescences, flowers and fruits) and below-ground (stump root, lateral roots and fine roots) components were assessed. The roots (stump root and lateral roots) were excavated from a 2 m^3 volume of soil for each harvested tree in each forest stand. The fine roots (roots < 5 mm diameter) and associated mycorrhizae were sampled by removing three randomly distributed 25 × 25 × 25 cm blocks of soil around harvested trees in each dbh class of each sub-plot (total of 12 from each forest stand).

The fresh weight of all components was determined in the field using a heavy weight spring balance and pan balance. Samples of approx. 500 g (fresh weight) of each tree component from each forest stand were taken separately to the laboratory and oven-dried at 60 °C to constant weight. Using the fresh/dry weight ratio, the dry weight of each tree was estimated. Regression equations were developed for different tree components. The data were subjected to regression in the form $Y = a + bX$, where Y is the dry weight of a component (kg), and X is the dbh above ground level (cm). The mean diameter value for each diameter class was used in the regression equation of the different components to obtain an estimate of mean biomass. This value was then multiplied by tree density in that diameter class. The total biomass of trees for each forest stand was calculated by summing the biomass of each diameter class.

Ten individuals of each shrub species differing in height and diameter were harvested and roots were recovered to a depth of 50 cm. The harvested material was separated into foliage, stem and roots. A regression equation was developed for each component to estimate shrub biomass. For herbaceous biomass, herbs were harvested at their peak (in the rainy season; September 1997) from ten 50 × 50 cm quadrats. The harvested material was divided into above- and below-ground components. Fresh and dry weights were determined for each shrub and herb component.

The total vegetation biomass was obtained by summing biomass values of trees, shrubs and herbs for each forest stand.

Net primary productivity

After the selecting a permanent sample plot (area: 1 ha) in each forest stand, 100 trees in each sub-plot were marked with white paint (at breast height, 1·37 m from the base) in September 1996 to assess diameter and height increments at annual intervals. The height and diameter of marked trees were measured again in September 1997. The mean diameter and height increments for each diameter class were then calculated.

The net primary productivity of the different tree components [bole wood, bole bark, branches, twigs, leaves and reproductive parts (above-ground parts), and stump root, lateral roots and fine roots (below-ground parts)] was calculated for each forest stand using the allometric equations of Rawat and Singh (1988) and Lodhiyal and Lodhiyal (1997).

The net increase in biomass ($\Delta B = B2 - B1$) yielded annual biomass accumulation. The sum of the ΔB values for the different components yielded net biomass accretion in the trees. Values for litter fall in the forests were added to the respective components (leaf and twigs). Considerable mortality of fine roots occurs in actively growing trees. However, a basic knowledge of the control of fine root production requires a better understanding of soil ecosystems (Nadelhoffer and Raich, 1992). The biomass of fine roots could not be estimated repeatedly during the course of the present study so we followed the methods of Kalela (1954), Orlov (1968) and Ogino (1977). We assumed that fine root mortality was equivalent to one-fifth of leaf litter fall; but present estimates of fine root production may be a gross underestimation (Harris *et al.*, 1980; Vogt *et al.*, 1982, 1986; Fogel, 1983; Lodhiyal *et al.*, 1995; Lodhiyal and Lodhiyal, 1997), and may differ from the real value as Nadelhoffer and Raich (1992) found no correlation between fine root production and leaf litter fall for a large data set. However, it must be pointed out that all methods, including those based on related biomass estimations of fine roots, are subject to uncertainties and possible biases (Lauenroth *et al.*, 1986; Sala *et al.*, 1988).

The net production value of each component was summed across diameter classes to give total net production of trees in each forest stand.

Twenty individuals of each dominant shrub species (*Lantana camara*, *Murraya koenighii*, *Clerodendrum viscosum* and *Pogostemone benghalense*) differing in height and diameter were marked with white paint and their basal diameter was measured in September 1996. After 1 year the

TABLE 1. *Stand structure and soil characteristics of Shisham (*Dalbergia sissoo *Roxb.) forests of different ages in central Himalaya*

Parameters	Age of Shisham forests (years)		
	5	10	15
Altitude (m)	250	250	250
Area of forest stand (ha)	14	16	17
Tree density (ha⁻¹)	625	625	625
Basal area (m^2 ha⁻¹)	16·9	23·3	34·7
Bulk density of soil (g cm⁻³)	1·02	1·06	1·11
Soil texture (%, in 0–30 cm)			
Sand	25·2	24·3	23·1
Silt	38·1	40·0	41·9
Clay	36·7	35·7	35·0
Porosity (%, in 0–30 cm)	62	61	58
Soil moisture (%, in 0–30 cm)			
Rainy season	28·4	27·0	26·5
Winter	17·5	16·5	15·2
Summer	11·8	12·5	12·8
Water holding capacity (%, in 0–30 cm)	86·7	87·1	87·6
Soil pH	6·6	6·5	6·4
Nutrient conc. of soil (%)			
N	0·155 ± 0·30	0·155 ± 0·31	0·151 ± 0·43
P	0·019 ± 0·26	0·013 ± 0·26	0·012 ± 0·39
K	0·064 ± 0·38	0·061 ± 0·32	0·056 ± 0·40

marked individuals were re-measured. Increases in biomass of these shrubs were calculated using regression equations, and to this value was added the foliage biomass (assuming 100 % turnover of leaves in 1 year) to obtain net annual production. The average production of a species multiplied by density yielded the total production of that species. Summing net production values for all species gave total shrub production for a site.

The biomass (above- and below-ground) of herbs at all sites was determined during their peak growth period in September 1996. This value was assumed to equal to net herb production. The sum of net production values of trees, shrubs and herbs yielded the total net primary productivity of vegetation in each Shisham forest stand.

Litter fall

Litter fall was studied for a 1 year period from July 1996 to June 1997. The litter input was measured by randomly placing 20 litter traps (five litter traps for each dbh class in each sub-plot) on the forest floor in each forest stand. Each trap was 50×50 cm with 15 cm high wooden sides fitted with a nylon net bottom. Litter was collected at monthly intervals on each sampling date and taken to the laboratory in polyethylene bags. Samples were then sorted into leaf, wood, reproductive parts and other components. The wood component comprised bark and twigs. Samples of separated components were cleaned and weighed after oven drying at 60 °C to constant weight. After weighing, the litter components were ground and retained for nutrient analysis.

Forest floor biomass

Forest floor litter data were collected using 15 quadrats (1 m × 1 m) placed randomly in each forest stand once in

each season, i.e. rainy, winter and summer. In each quadrat, all components were categorized into: (*a*) fresh leaf litter; (*b*) partially and decomposed litter; (*c*) wood litter (including twigs, bark and branches); (*d*) miscellaneous litter (consisting of inflorescences, flowers and fruits, litter parts of shrubs); and (*e*) herbaceous litter (living and dead), following Rawat and Singh (1988), Lodhiyal (1990), Bargali *et al*. (1992), Lodhiyal *et al*. (1995) and Lodhiyal and Lodhiyal (1997). In each quadrat all herbaceous standing shoots (alive and dead) were harvested at ground level (Green, 1959; Line, 1959; Lodhiyal, 1990; Lodhiyal *et al*., 1995; Lodhiyal and Lodhiyal, 1997). Forest floor material was collected carefully to avoid soil contamination. Collected material was taken to the laboratory in polyethylene bags, cleaned of soil particles, and weighed after oven drying at 60 °C to constant weight.

Turnover of litter

The turnover rate (K) of litter was calculated following Jenny *et al*. (1949), Olson (1963) and Lodhiyal and Lodhiyal (1997): $K = A/(A + F)$ where A is the annual increment of litter (i.e. annual litter fall) and F is the biomass of the litter at steady state. Turnover time (t, years) is the reciprocal of turnover rate and is expressed as $t = 1/K$. In the present study, F was the standing crop of partially and decomposed litter during the winter season and A was the annual tree litter fall plus shrub litter (equal to foliage biomass) plus herb litter (equal to peak above-ground herb biomass).

Soil samples were collected in September 1996, January 1997 and May 1997 from each forest stand (nine samples in each sub-plot, three samples from each depth class) using a soil corer placed randomly at three depths 0–10, 10–20 and 20–30 cm. Soil texture, bulk density, moisture content,

TABLE 2. *Relationship between the biomass of tree components (Y, kg per tree) and diameter at breast height (X, cm) for Shisham (*Dalbergia sissoo *Roxb.) forests*

Components		Age of Shisham forests (years)		
		5	10	15
Bole wood	a	−0·5672	1·6532	−4·9071
	b	2·3707	3·7616	4·3190
	r^2	0·995	0·994	0·981
Bole bark	a	−0·1147	0·3029	−0·8850
	b	0·4725	0·7095	0·7716
	r^2	0·995	0·994	0·982
Branch	a	−0·0777	0·2397	−0·7306
	b	0·3435	0·5402	0·6476
	r^2	0·993	0·994	0·981
Twig†	a	−0·0463	0·1102	−0·3821
	b	0·1593	0·2568	0·3245
	r^2	0·994	0·994	0·981
Leaf‡	a	−0·1231	0·1475	−0·4092
	b	0·2862	0·3377	0·3245
	r^2	0·994	0·994	0·940
Reproductive parts§	a	−0·0154	0·0195	−0·9809
	b	0·0357	0·0680	0·1296
	r^2	0·996	0·993	0·827*
Stump root¶	a	−0·1121	0·2963	−0·6018
	b	0·4985	0·6754	0·7163
	r^2	0·995	0·994	0·986
Lateral roots‖	a	−0·0432	−0·3068	−0·1004
	b	0·1854	0·3154	0·3573
	r^2	0·994	0·981	0·979
Fine roots**	a	−0·0288	0·0338	−0·5149
	b	0·0671	0·1087	0·1534
	r^2	0·994	0·993	0·941

The equation used was $Y = a + bX$. All equations are significant at $P < 0·01$ except those denoted by an asterisk which are significant at $P < 0·05$.
† Shoots of larger dimension without leaves.
‡ Current shoots bearing leaves.
§ Includes flowers and fruits.
¶ Main root bearing 30 cm above-ground stem part.
‖ Lateral branches of stump root (main root) with a diameter > 5 mm.
** Root originates from lateral roots with a diameter < 5 mm and associated mycorrhizae.

water holding capacity and soil porosity were determined according to Misra (1968). The pH of each soil sample was determined using a digital pH meter, the nitrogen concentration using a micro-Kjeldahl technique (Peach and Tracy, 1956), phosphorus by spectrophotometry and potassium by flame photometry (Jackson, 1958).

RESULTS AND DISCUSSION

Stand structure and soil characteristics

Table 1 summarizes stand structure and physicochemical properties of the soil studied in the three Shisham forest stands. The basal area increased significantly ($P < 0·01$) from 16·9 (5-year-old stand) to 34·7 m^2 ha^{-1} (15-year-old stand) with age of the forest stand. The soil parameters such as sand, clay, porosity, moisture percentage (in rainy and winter seasons), soil pH and soil nutrient (NPK) concentration decreased (the last not significantly); however, other soil parameters increased with increasing age of the forest (Table 1).

Biomass

The allometric equations, variables and parameters relating biomass of different tree components to dbh are presented in Table 2, while the allometric equations developed for estimating biomass of the different shrub components based on basal diameter are given in Table 3. Diameter at breast height was selected as the independent variable because of the ease and accuracy involved in making these measurements.

As evident from r^2-values in Table 2, the relationships between biomass and dbh were found to be quite satisfactory. Biomass was not calculated using the $X^2 h$ method (where h is height) because the resulting r^2-values were not significantly better than those obtained using dbh (X). Therefore, the regression model $Y = a + bX$ was used for computation of forest biomass.

Total biomass of trees ranged from 50·3 ± 2·46 (5-year-old stand) to 122·7 ± 3·14 t ha^{-1} (15-year-old stand), of which above- and below-ground parts represented 83–84 and 16–17 %, respectively (Table 4). Shrub biomass ranged from 5·6 ± 1·54 (5-year-old stand) to 11·0 ± 2·04 t ha^{-1}

TABLE 3. *Allometric relationship between biomass of shrub components* (Y, *kg per tree) and basal diameter (*D, *cm) for four shrub species under Shisham (*Dalbergia sissoo) *forests in the Tarai belt of central Himalaya*

Species	Components	Intercept (a)	Slope (b)	r^2
5-year-old stand				
Lantana	Foliage	1·8624	1·0542	0·970
camara	Stem	1·7506	3·1195	0·995
	Roots	1·7608	2·1074	0·997
Murraya	Foliage	1·2647	1·6441	0·998
koenighii	Stem	1·2448	6·6278	0·996
	Roots	1·2700	3·9169	0·998
Clerodendrum	Foliage	1·0662	3·4817	0·982
viscosum	Stem	1·1838	12·6674	0·981
	Roots	1·0561	6·2988	0·993
Pogostemone	Foliage	1·4407	1·8659	0·996
benghalense	Stem	1·4574	5·4921	0·993
	Roots	1·4574	3·5306	0·993
10-year-old stand				
Lantana	Foliage	1·6972	1·3303	0·992
camara	Stem	1·4594	5·0578	0·865*
	Roots	1·7222	1·8654	0·991
Murraya	Foliage	1·2557	1·5577	0·988
koenighii	Stem	1·2719	7·7734	0·969
	Roots	1·8716	0·8279	0·434 n.s.
Clerodendrum	Foliage	1·1549	2·6947	0·970
viscosum	Stem	1·1783	14·9055	0·966
	Roots	1·4324	2·1308	0·916
Pogostemone	Foliage	1·3724	2·0368	0·982
benghalense	Stem	1·3204	9·3897	0·981
	Roots	1·3575	3·3033	0·987
15-year-old stand				
Lantana	Foliage	1·6782	1·4005	0·988
camara	Stem	1·7844	3·8373	0·957
	Roots	1·6285	2·1831	0·927
Murraya	Foliage	1·3247	1·5179	0·977
koenighii	Stem	1·2685	7·3875	0·955
	Roots	0·6652	4·8477	0·845*
Clerodendrum	Foliage	1·1080	2·9784	0·959
viscosum	Stem	1·1938	12·1948	0·928
	Roots	1·1391	4·3298	0·956
Pogostemone	Foliage	1·5405	1·6191	0·935
benghalense	Stem	1·5586	7·2454	0·975
	Roots	1·7561	1·9661	0·824*

All equations are significant at $P < 0.01$ except those with an asterisk which are significant at $P < 0.05$. n.s., Not significant.

(15-year-old stand), of which stem, foliage and roots accounted for about 54–61, 13–15 and 26–30 %, respectively (Table 4). The herb biomass ranged from 2·4 ± 2·44 (15-year-old stand) to 2·8 ± 1·76 t ha^{-1} (5-year-old stand). Of this, the above-ground component accounted for 76–79 %. Herb biomass decreased with increasing age of the forest stand (Table 4). The vegetation biomass ranged from 58·7 ± 1·92 (5-year-old stand) to 136·1 ± 2·54 t ha^{-1} (15-year-old stand). Of this, the tree layer accounted for 86–90 %, shrubs for 8–10 % and herbs for 2–5 % (Table 4).

Values for above-ground biomass in the present study are comparable with those of aspen–maple–birch, Sal, Shisham, eucalypt and poplar forest stands studied elsewhere (Crow, 1978; Singh, 1979; Sharma *et al.*, 1988; Raizada and Srivastava, 1989; Lodhiyal, 1990; Lodhiyal and Lodhiyal, 1997) (Table 5). The present values fall within the range

reported for eucalypt stands (54–319 t ha^{-1}; Attiwill, 1979; Frederick *et al.*, 1985a, b; Tandon *et al.*, 1988; Bargali *et al.*, 1992), for 30-year-old stands of Shisham forest (141–172 t ha^{-1}; Lodhiyal, 2000), for 9- to 10-year-old *Populus deltoides* plantations (105–152 t ha^{-1}; Singh, 1989), for 8-year-old poplar plantations (134 t ha^{-1}; Lodhiyal *et al.*, 1995), and for *Pinus roxburghii* forests (113–283 t ha^{-1}; Chaturvedi, 1983), but are much lower than values reported for 100+-year-old oak forests (263–301 t ha^{-1}; Negi *et al.*, 1983; Rawat, 1983) (Table 5). Biomass production is higher in young Shisham forests than in older natural forests of the region.

The proportion of total biomass found in roots was 16–17 %, which is lower than values reported for *Populus deltoides* plantations (19–21 %; Lodhiyal *et al.*, 1995) and *Eucalyptus signata* and *E. umbra* forests (43 %; Westman and Rogers, 1977), but is higher than values reported for temperate forests (8–15 %; Whittaker and Woodwell, 1971; Nihlgard, 1972; Larsen *et al.*, 1976) and the 10–12 % reported for eucalypt forests (Feller, 1980). The differences in root contribution may be related to the method of estimating root biomass, which presents great sampling difficulty (Lodhiyal *et al.*, 1995) and is often omitted in biomass studies.

Analysis of variance showed significant ($P < 0.01$) variations in total tree biomass and its components among plantations of different ages. The contribution of bole wood, branches, twigs, reproductive parts, lateral roots and fine roots increased with age while that of the remaining parts decreased.

Forest floor biomass

Turnover rate ranged from 0·77 (15-year-old stand) to 0·81 kg year^{-1} (5-year-old stand), while turnover time was 1·23 (5-year-old stand) to 1·29 years (15-year-old stand) (Table 6). The replacement of litter from forest floor was 77–81 % each year. The turnover time increased with increasing age of the stand (Table 6). The turnover time of litter on the forest floor was greater than 1 year.

The biomass of litter on the forest floor increased with age of the forest stand. However, the herbaceous biomass (both alive and dead) showed the reverse trend. The same trend was observed for *Populus deltoides* plantations (Lodhiyal *et al.*, 1995) and *Eucalyptus* hybrid plantations (Bargali *et al.*, 1992). In the present study, forest floor biomass was lower than that reported for *Pinus* stands (13–110 t ha^{-1}; Ovington, 1965), oak forests (9·6–12·6 t ha^{-1}; Monk *et al.*, 1970; Reiners and Reiners, 1970), *Eucalyptus saligna* (12·4 t ha^{-1}; Richards and Charley, 1977), *Eucalyptus obliqua* (18·3 t ha^{-1}; Attiwill *et al.*, 1978), *Eucalyptus regnans* (47·5 t ha^{-1}; Feller, 1980) and *Pinus roxburghii* forests (9·6–13·6 t ha^{-1}; Chaturvedi and Singh, 1987a) but is within the range reported for 1- to 30-year-old *Dalbergia sissoo* forests (2·5–7·3 t ha^{-1}; Lodhiyal, 2000), tropical deciduous forests (1·5–8·9 t ha^{-1}; Singh and Misra, 1978; Singh, 1979) and eucalypt plantations (Bradstock, 1981; Frederick *et al.*, 1985b), and close to values reported for *Populus deltoides* plantations (2·8–6·4 t ha^{-1}; Lodhiyal, 1990), *Eucalyptus* hybrid plantations (4·0–6·7 t ha^{-1}; Bargali

TABLE 4. *Component-wise biomass (t ha⁻¹) in tree, shrub and herb layers at different ages of Tarai Shisham forests in Central Himalaya*

	Age of Shisham forests (years)		
Vegetation	5	10	15
Tree layer	50·3 ± 2·46	93·8 ± 2·92	122·7 ± 3·14
% Allocation in			
bole*	64·3	66·0	66·0
branch†	11·4	11·8	12·6
leaf	6·4	5·0	4·2
reproductive part	0·8	1·0	1·2
coarse roots‡	15·5	14·6	14·2
fine roots	1·6	1·6	1·8
Shrub layer	5·6 ± 1·54	9·7 ± 1·98	11·0 ± 2·04
% Allocation in			
above-ground parts§	69·7	74·2	72·7
below-ground parts	30·3	25·8	27·3
Herb layer	2·8 ± 1·76	2·6 ± 2·14	2·4 ± 2·44
% Allocation in			
above-ground parts	78·9	78·1	75·8
below-ground parts	21·1	21·8	24·2
Total vegetation	58·7 ± 1·92	106·1 ± 2·35	136·1 ± 2·54

* Bole wood + bole bark, which accounted for 10·0–10·7 % of the values.

† Branch + twig, which accounted for 3·6–4·2 % of the values.

‡ Stump root (main root) + lateral roots (lateral branches of main root), which accounted for 4·2–4·8 % of the values.

§ Stem + foliage, which accounted for 13·4–16·1 % of the values.

TABLE 5. *Comparisons of biomass distribution (%) in above-ground tree components of certain forests and plantations around the world*

					% Allocation					
Vegetation	Location	Age (years)	Density	Above-ground biomass (t ha⁻¹)	Bole	Branch	Twig	Foliage	Reproductive parts	References
Shorea robusta	India	>100	–	70·2	43·9	51·0	–	5·1	–	Singh (1979)
Aspen–maple–birch	USA	–	–	95·4	79·5	17·6	–	2·9	–	Crow (1978)
Oak forest	India	>100	–	301·5	51·0	44·4	–	4·6	–	Rawat (1983)
Oak forest	India	>100	–	263·2	51·7	40·5	–	7·8	–	Negi *et al.* (1983)
Eucalyptus obliqua	Australia	51	865	298·2	91·2	6·5	–	2·3	–	Attiwill (1979)
E. grandis	India	5	1650	97·6	83·8	6·8	4·6	4·6	–	Tandon *et al.* (1988)
E. grandis	India	10	689	275·1	92·0	3·9	2·0	2·0	–	Tandon *et al.* (1988)
E. saligna	Australia	8	829	129·8	80·9	13·4	1·2	4·4	0·08	Frederick *et al.* (1985*b*)
E. regnans	Australia	10	1075	319·0	82·1	13·0	–	4·8	–	Frederick *et al.* (1985*a*)
Pinus roxburghii	India	–	–	113·0–283·0	76·1	19·4	–	4·5	–	Chaturvedi (1983)
Eucalyptus hybrid	India	10	1223	21·9	62·1	15·4	8·8	13·7	–	Pandey *et al.* (1987)
Eucalyptus hybrid	India	1	2000	0·5	50·0	10·4	2·1	35·4	–	Bargali *et al.* (1992)
Eucalyptus hybrid	India	2	2000	3·2	75·2	5·6	1·9	17·2	–	Bargali *et al.* (1992)
Eucalyptus. hybrid	India	3	2000	18·5	77·7	7·0	1·8	14·5	–	Bargali *et al.* (1992)
Eucalyptus hybrid	India	5	2000	54·1	80·8	6·6	1·6	10·2	0·7	Bargali *et al.* (1992)
Populus deltoides Marsh	India	14	–	44·5	69·9	13·7	–	7·4	–	Raizada and Srivastava (1989)
P. deltoides (I C)	India	10	–	105·4	74·4	13·0	–	12·6	–	Singh (1989)
P. deltoides Marsh	India	9	–	151·6	71·9	16·0	–	12·1	–	Singh (1989)
P. deltoides Marsh	India	1	666	7·4	56·7	17·6	5·4	20·3	–	Lodhiyal and Lodhiyal (1997)
P. deltoides Marsh	India	2	666	28·0	59·6	18·6	6·1	15·7	–	Lodhiyal and Lodhiyal (1997)
P. deltoides Marsh	India	3	666	49·4	65·2	16·0	5·9	12·9	–	Lodhiyal and Lodhiyal (1997)
P. deltoides Marsh	India	4	666	89·3	67·2	15·2	5·4	12·2	–	Lodhiyal and Lodhiyal (1997)
P. deltoides Marsh	India	5	400	67·6	69·4	14·8	4·3	11·5	–	Lodhiyal *et al.* (1995)
P. deltoides Marsh	India	8	400	134·3	74·7	12·6	4·0	8·6	–	Lodhiyal *et al.* (1995)
Dalbergia sissoo	India	3	10000	41·39	38·6	29·2	12·0	–	–	Tewari (1994)
D. sissoo	India	5	–	82·0	40·6	34·9	–	6·5	–	Sharma *et al.* (1988)
D. sissoo	India	24	467	16·16	65·5	14·2	2·6	–	–	Sharma *et al.* (1988)
Tarai Shisham	Uttaranchal (India)	5	625	41·8	64·4	7·8	3·6	6·4	0·8	Present study
(*D. sissoo*) forests	Uttaranchal (India)	10	625	78·6	66·1	8·0	3·8	4·9	1·0	Present study
(*D. sissoo*) forests	Uttaranchal (India)	15	625	103·1	66·0	8·4	4·2	4·2	1·2	Present study

TABLE 6. *The average forest floor biomass (t ha⁻¹, across seasons) and turnover of litter (rate and time) in Shisham forests of different ages in central Himalaya*

Components	Age of Shisham forests (years)		
	5	10	15
Forest floor litter (t ha⁻¹)	4·8 ± 2·69	5·6 ± 3·01	6·6 ± 3·37
% Allocation in fresh leaf litter	8·9	9·3	9·8
Partially and more decomposed litter	22·9	27·8	30·0
Wood litter	6·5	12·5	18·8
Miscellaneous litter*	24·6	21·1	19·1
Herbaceous litter†	37·0	29·2	22·3
Turnover rate (kg year⁻¹)	0·81	0·78	0·77
Turnover time (t, year)	1·23	1·28	1·29

* Includes reproductive parts of trees and litter parts of shrubs.

† Includes living and dead herbaceous material, which accounted for 3·8–6·4 % of the values.

TABLE 7. *Litter production (t ha⁻¹ year⁻¹) in Shisham (*Dalbergia sissoo*) forests of Tarai area of central Himalaya*

Litter components	Age of Shisham forests (years)		
	5	10	15
Leaf litter	2·02 (74·3)	3·04 (72·0)	3·44 (66·9)
Wood litter*	0·09 (3·3)	0·21 (5·0)	0·36 (7·0)
Reproductive litter†	0·03 (1·1)	0·09 (2·1)	0·18 (3·5)
Other litter‡	0·58 (21·3)	0·88 (20·9)	1·16 (22·6)
Total	2·72 (100)	4·22 (100)	5·14 (100)

* Includes barks, twigs and branches.

† Includes inflorescences, pods and fruits of trees and shrubs.

‡ Includes the leaf litter of shrubs and herbs.

TABLE 8. *Component wise net primary productivity (t ha⁻¹ year⁻¹) in trees, shrubs and herbs of Shisham forests in central Himalaya*

Vegetation	Age of Shisham forests (years)		
	5	10	15
Tree layer	9·1 ± 1·25	12·5 ± 1·76	16·7 ± 2·02
% Allocation in			
bole*	61·5	63·2	60·4
branch†	11·1	11·2	11·4
leaf	6·6	4·8	4·8
reproductive part	1·0	1·6	1·8
coarse roots‡	14·3	12·8	15·6
fine roots	5·5	6·4	6·0
Shrub layer	0·7 ± 0·74	1·2 ± 0·85	1·3 ± 0·98
% Allocation			
above-ground§	71·4	75·0	69·2
below-ground	28·6	25·0	30·8
Herb layer	2·8 ± 1·42	2·6 ± 1·68	2·4 ± 1·92
% Allocation			
above-ground	78·9	78·1	75·8
below-ground	21·1	21·9	24·2
Total vegetation	12·6 ± 1·14	16·3 ± 1·43	20·3 ± 1·64

* Bole wood + bark, which accounted for 8·9–10·4 % of the values.

† Branch + twigs (current shoots bearing leaves), which accounted for 3·3–4·0 % of the values.

‡ Stump root (main root) + lateral roots (lateral branches of main root), which accounted for 3·2–7·2 % of the values.

§ Stem + foliage, which accounted for 14·3–16·7 % of the values.

et al., 1992) and oak forest (Rawat and Singh, 1988) in adjacent areas. The smaller biomass on the forest floor indicates a high rate of decomposition under the warm and humid conditions. Similar findings were also reported for deciduous poplar plantations in adjacent areas (Lodhiyal et al., 1995; Lodhiyal and Lodhiyal, 1997).

The turnover rate of forest floor litter biomass in the present study sites is higher than values reported for *Cassia siamea*, *Dalbergia sissoo* and *Gmelina arborea* forests (0·58, 0·60 and 0·73, respectively; Pacholi, 1997). The turnover time of litter is close to the value of 1·25 years reported for *Eucalyptus grandis* (Turner and Lambert, 1983). The present values are lower than the 2·7–14·3 years reported for temperate forests (Reiners and Reiners, 1970; Gosz et al., 1972; Rochow, 1975), 3·5 years for *Eucalyptus obliqua* (Attiwill et al., 1978) and 1·4–1·5 years for central Himalayan forests (Rawat and Singh, 1988). Thus, present findings show that Shisham forest floor litter biomass is more dynamic than that of temperate deciduous forests, exotic eucalypt plantations and central Himalayan oak forests.

Litter input

Leaves are a major component of the total litter input. Leaf fall began in October and culminated in January the following year. Total litter fall ranged from 2·7 (5-year-old stand) to 5·1 t ha⁻¹ year⁻¹ (15-year-old stand) (Table 7). Of this, leaf litter accounted for 67–74 %, within the range reported for natural forests of central Himalaya (60–80 %; Singh and Singh, 1992) and for temperate forests (40–84 %; Rodin and Bazilevick, 1967). However, wood litter represented 3–7 %, which is much lower than the value reported for various forests around the world (10–36 %; Bray and Gorham, 1964; Killingbeck and Wali, 1978; Singh and Singh, 1992) but close to values reported for Tarai poplar plantations (2–5 %; Lodhiyal et al., 1995).

Our estimates of leaf litter turnover (2·0–3·4 t ha⁻¹ year⁻¹) are towards the higher end of the range (1·3–4·2 t ha⁻¹ year⁻¹) reported for poplar (*Populus tremuloides* and *Populus tristis*; Crow, 1974; van Cleave and Noonan, 1975; Zavitkovski, 1981), but the present estimates are lower than those reported for *Eucalyptus regnans* and many deciduous forests (5·7–7·8 t ha⁻¹ year⁻¹; Ashton, 1975; Singh and Mishra, 1978; Singh, 1989; Lodhiyal et al., 1995a), dry deciduous forests (8–10 t ha⁻¹ year⁻¹; Jenny et al., 1949), bamboo/mixed broad leaf forests of eastern Himalaya (9·6 t ha⁻¹ year⁻¹; Toky and Ramakrishnan, 1983a), moist tropical forest (10·5 t ha⁻¹ year⁻¹; Golley et al., 1975) and tropical forests (8–12 t ha⁻¹ year⁻¹; Procter et al., 1983).

TABLE 9. *Total net primary productivity (NPP) of Shisham forests compared with other forests and plantations around the world*

Vegetation	Location	NPP (t ha^{-1} year^{-1})	References
Camelia japonica	Japan	29·4	Kan *et al.* (1965)
Cryptomeria japonica	Japan	10·9	Tadaki *et al.* (1965)
Pine forest	USA	11·0	Whittaker (1966)
Tropical rain forest	Thailand	28·6	Kira *et al.* (1967)
Conifer forests	USSR	7·0–10·0	Rodin and Bazilevick (1967)
Tropical rain forest	Java	24·3	Warner (1970)
Tropical moist forest	–	11·4	Golley *et al.* (1975)
Dry deciduous forest	India	14·6–15·7	Singh (1979)
Sal old growth forest	India	16·0–18·9	Singh and Singh (1979)
Tropical rain forest	Malaysia	19·2	Bullock (1981)
Shisham plantation (24 years old)	India	7·2	Sharma *et al.* (1988)
Rianj dominated forest	India	15·5	Rana *et al.* (1989)
Chir-pine forest	India	17·3	Rana *et al.* (1989)
Eucalyptus plantation (8 years old)	India	23·4	Bargali *et al.* (1992)
Low density poplar plantation (8 years old)	India	24·5	Lodhiyal *et al.* (1995)
High density poplar plantation (4 years old)	India	32·4	Lodhiyal and Lodhiyal (1997)
Gmelina arborea forest	India	10·0	Pacholi (1997)
Cassia siamea forest	India	18·8	Pacholi (1997)
Dalbergia sissoo forest	Bihar(India)	22·3	Pacholi (1997)
Tarai Shisham forests	Uttaranchal (India)	12·6–20·3	Present study

TABLE 10. *Biomass accumulation ratio (BAR, biomass/ total NPP of tree) in different tree components of Tarai Shisham forests*

	Age of forests (years)		
Component	5	10	15
Bole wood	2·96	4·17	4·11
Bole bark	0·60	0·79	0·74
Branch	0·43	0·60	0·62
Twig	0·20	0·29	0·31
Leaf	0·35	0·37	0·31
Reproductive parts	0·04	0·07	0·09
Stump root	0·62	0·75	0·69
Lateral roots	0·23	0·34	0·35
Fine roots	0·08	0·12	0·13
Total	5·51	7·50	7·35

Net primary productivity

Total NPP (t ha^{-1} year^{-1}) of Shisham forests at different ages is given in Table 8. NPP in the tree layer ranged from 9·1 (5-year-old stand) to 16·7 t ha^{-1} year^{-1} (15-year-old stand). Above-ground parts account for 78 (15-year-old stand) to 81 % (5-year-old stand) and below-ground parts for 19 (10-year-old stand) to 22 % (15-year-old stand) (Table 8). The net primary productivity of the shrub layer was 0·7 (5-year-old stand) to 1·3 t ha^{-1} year^{-1} (15-year-old stand). Of this, foliage and roots accounted for 14–17 % and 25–31 %, respectively (Table 8). The productivity of the herb layer was 2·4 (15-year-old stand) to 2·8 t ha^{-1} year^{-1} (5-year-old stand). Above-ground parts accounted for 76 (15-year-old stand) to 79 % (5-year-old stand) and below-

ground parts for 21 (5-year-old stand) to 24 % (15-year-old stand) (Table 8).

The total NPP in vegetation ranged from 12·6 (5-year-old stand) to 20·3 t ha^{-1} year^{-1} (15-year-old stand), of which the tree layer accounted for 72 (5-year-old stand) to 82 % (15-year-old stand), the shrub layer for 5 (5-year-old stand) to 7 % (10-year-old stand) and the herb layer for 12 (15-year-old stand) to 22 % (5-year-old stand) (Table 8).

The NPP: foliar standing crop (FSC) ratio ranged from 2·6 (10-year-old stand) to 3·3 (15-year-old stand). The production efficiency of *Dalbergia sissoo* leaves is similar to that (2·5 kg kg^{-1} FSC) reported for a eucalypt plantation (Bargali *et al.*, 1992) and a *Pinus roxburghii* forest (Singh and Singh, 1992), but is higher than that reported for poplar plantations (Lodhiyal *et al.*, 1995) in an adjacent area of central Himalaya. The greater efficiency of Shisham forests seems to be largely due to their longer growing period; it could also be due to higher photosynthetic efficiency (Singh and Singh, 1992). The production of herbaceous vegetation was greater than that of shrubs, and decreased significantly ($P < 0.01$) with the age of the forest (see Table 8). Similar observations of herbaceous production have been reported for exotic poplar plantations in the region (Lodhiyal *et al.*, 1995). Comparisons with other forests and plantations around the world show that the NPP of the present Shisham forests (13–20 t ha^{-1} year^{-1}) is slightly lower than that reported for an 8-year-old fast-growing exotic eucalypt plantation (23·4 t ha^{-1} year^{-1}; Bargali *et al.*, 1992), and for a 100+-year-old natural Sal (*Shorea robusta*) forest in an adjacent area (22 t ha^{-1} year^{-1}; Singh and Singh, 1987); however, it was much lower than the value of 32·4 t ha^{-1} year^{-1} reported for a 4-year-old high density poplar plantation (Lodhiyal
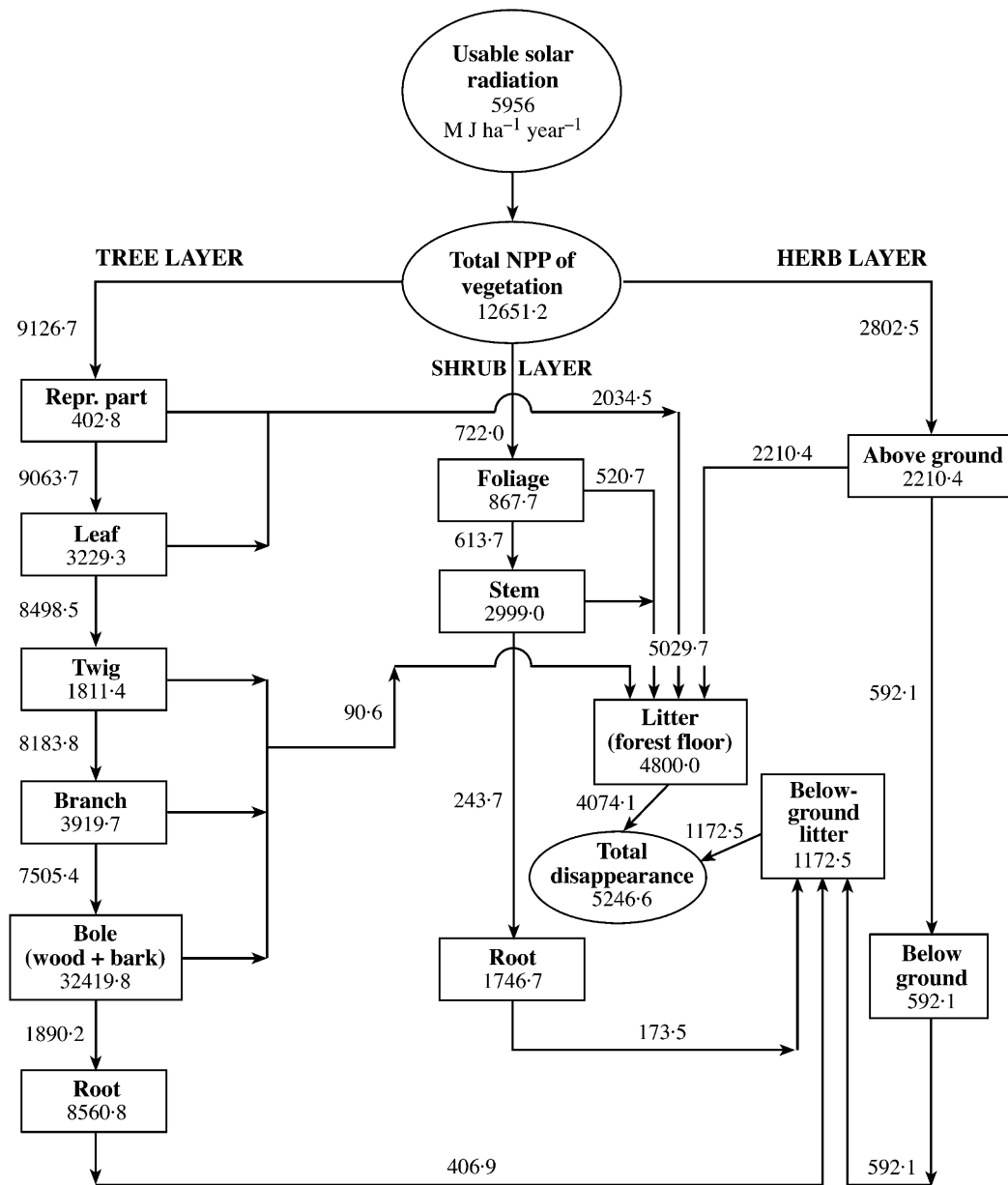
FIG. 2. Compartment model for dry matter distribution in 5-year-old Shisham (*Dalbergia sissoo* Roxb) forest. Rectangles represent compartments for standing crop of dry matter, arrows represent net flux rate. The three ovals represent total annual amounts of usable solar radiation (M J ha^{-1} year^{-1}), total net production (kg ha^{-1} year^{-1}) and total disappearance (kg ha^{-1} year^{-1}). Compartment values are in kg ha^{-1} and turnover rate in kg ha^{-1} year^{-1}.

and Lodhiyal, 1997) (Table 9). NPP values in the study forests are higher than the 12–15 t ha^{-1} year^{-1} reported for many mature stable temperate forests of favourable environments, and fall within the normal range of NPP (10–20 t ha^{-1} year^{-1}) of world forests growing in favourable climates (Whittaker, 1975).

In this context, productivity of Shisham can be increased substantially by planting trees at a higher density with the help of better silvicultural management input (Lodhiyal, 2000). Comparison with other deciduous forests in India suggests that fine root production in the present study is perhaps an underestimation. A value of fine root production

of 0·5 (5-year-old stand) to 1·0 t ha^{-1} year^{-1} (15-year-old stand) gives ratios of fine root production to above-ground production of 13 (10-year-old stand) to 15 (5-year-old stand), compared with ratios of 5 and 11 reported for *Shorea robusta* and *Populus deltoides*, respectively (Singh and Singh, 1992; Lodhiyal *et al.*, 1995). According to Nadelhoffer and Raich (1992), the ratio of fine root to above-ground production is influenced by the soil status; these authors argued that there is still uncertainty with regards to understanding of soil systems. Moreover, little fine root production in our study indicates the higher fertility of sites and is similar to values reported for fast-growing
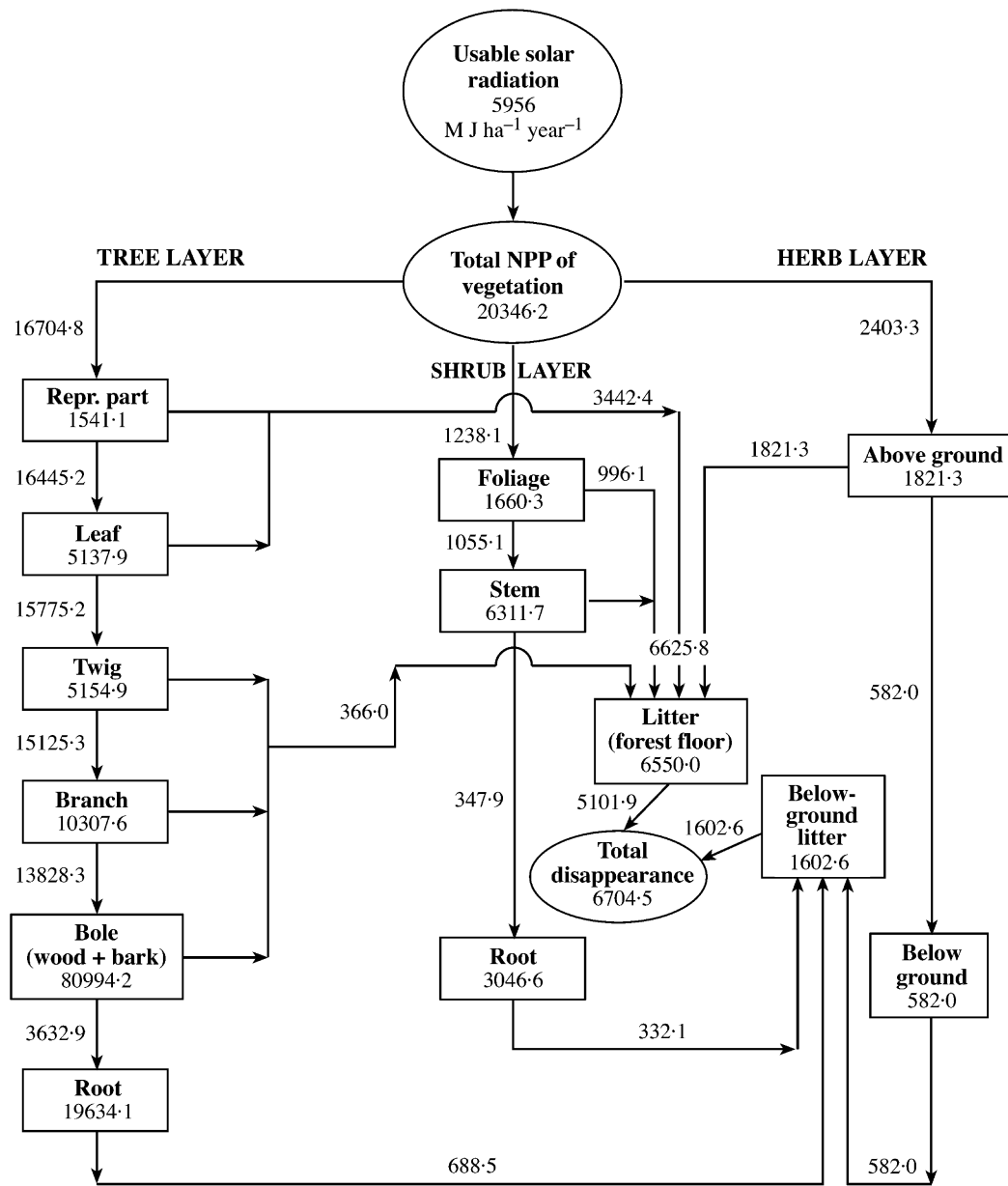
FIG. 3. Compartment models for dry matter distribution in 15-year-old Shisham (*Dalbergia sissoo* Roxb.) forest. Rectangles represent compartments for standing crop of dry matter, arrows represent net flux rate. The three ovals represent total annual amounts of usable solar radiation (M J ha^{-1} year^{-1}), total net production (kg ha^{-1} year^{-1}) and total disappearance (kg ha^{-1} year^{-1}). Compartment values are in kg ha^{-1} and turnover rate in kg ha^{-1} year^{-1}.

exotic plantations in adjacent areas (Singh, 1989; Lodhiyal *et al.*, 1995).

Biomass accumulation ratio

The biomass accumulation ratio (BAR; biomass/NPP) is an expression of the quantity of biomass retained per unit of net production. BAR has been used to characterize the production conditions in communities (Whittaker, 1966; Whittaker and Woodwell, 1969; Lodhiyal and Lodhiyal, 1997). BAR is a measure of accumulation of primarily persistent material, a characteristic largely dependent on the age of the dominant species and environmental harshness. BAR ranges between 5·5 and 7·5 for *Dalbergia sissoo* forests (Table 10); this is higher than the values of 0·9–5·9 reported for eucalypt plantations (Bargali *et al.*, 1992), and falls within the range of 4·9–7·7 reported for *Populus deltoides* plantations (Lodhiyal *et al.*, 1995). The high BAR

suggests that Shisham forests produce more dry matter than eucalypt plantations, and a similar amount to poplar plantations growing in an adjacent area of central Himalaya.

Dry matter transfer

A compartment model of dry matter flow in 5- and 15-year-old forests is given in Figs 2 and 3. The mean annual incident solar insolation is 5956 M J ha^{-1} year^{-1}. Of this, about 2978 M J ha^{-1} year^{-1} (50 % of the total) is considered photosynthetically active.

The biomass of the vegetation is 58.7×10^3 kg ha^{-1} in the 5-year-old stand and 136.1×10^3 kg ha^{-1} in the 15-year-old stand. Trees account for 86 %, shrubs 9 % and herbs 5 % of the total dry matter (biomass) of vegetation in the 5-year-old forest; these figures are 90 %, 8 % and 2 %, respectively, in the 15-year-old forest. In the tree layer, the above-ground ratio of photosynthetic : non-photosynthetic tissue ranged from 0.52 (15-year-old stand) to 0.08 (5-year-old stand), and the root : shoot ratio ranged from 0.19 (15-year-old stand) to 0.20 (5-year-old stand). These ratios are similar to those of natural forests (Chaturvedi and Singh, 1987*b*; Rawat and Singh, 1988) and eucalypt plantations (Bargali *et al.*, 1992), and are quite similar to those of poplar plantations (Lodhiyal *et al.*, 1995).

Net primary production is 12 651 kg ha^{-1} year^{-1} in the 5-year-old stand and 20 346 kg ha^{-1} year^{-1} in the 15-year-old stand. Tree, shrub and herb layers accounted for 72 %, 6 % and 22 % of NPP in the 5-year-old stand, and 82 %, 6 % and 12 % in the 15-year-old stand, respectively.

In the tree layer, the highest fraction of net production is by bole wood (51 %) followed by bole bark (10 %) in the 5-year-old stand, and bole wood (52 %) followed by bole bark (9 %) in the 15-year-old stand. Leaves accounted for about 6 % in the 5-year-old stand and 4 % in the 15-year-old stand.

The apportioning of net production in shrubs follows the order: stem (52 %) > roots (33 %) > foliage (15 %) in the 5-year-old stand, and stem (57 %) > roots (28 %) > foliage (15 %) in the 15-year-old stand. However, the order: foliage > stem > roots was reported for the shrub layer in pine (Chaturvedi and Singh, 1987*b*) and oak forests (Rawat and Singh, 1988) and in poplar plantations (Lodhiyal *et al.*, 1995).

In the herb layer, the proportion of NPP by above-ground components (76 % in 15-year and 79 % in 5-year-old stands) is much higher than that in central Himalayan forests (62–64 %; Chaturvedi and Singh, 1987*b*; Rawat and Singh, 1988), but is similar to that of poplar plantations (80 %; Lodhiyal *et al.*, 1995). The maximum production of photosynthetically active parts of the different vegetational layers was in the order: herbs > shrubs > trees.

The restitution of biomass through litter formation is 5030 (5-year-old stand) to 6626 kg ha^{-1} year^{-1} (15-year-old stand). Of the total litter fall from the tree layer, leaf litter constitutes about 74 % in the 5-year-old stand and 67 % in the 15-year-old stand. The present values are similar to those of natural forests (67–77 %; Chaturvedi and Singh, 1987*a*; Rawat and Singh, 1988) and are higher than those of a eucalypt plantation (55 %; Bargali *et al.*, 1992) but lower than those of a poplar plantations (94–96 %; Lodhiyal *et al.*, 1995).

In terms of dry matter, biomass restitution is 23 (15-year-old stand) to 25 % (5-year-old stand) of the total annual production of trees and 18 (5-year-old stand) to 19 % (15-year-old stand) of the total vegetation. Our estimates are lower than those for poplar (Lodhiyal *et al.*, 1995) and eucalypt plantations (Bargali *et al.*, 1992) and natural forests of oak (Rawat and Singh, 1988) and pine (Chaturvedi and Singh, 1987*a*).

The mean standing crop of litter on the forest floor ranged from 4800 (5-year-old stand) to 6550 kg ha^{-1} (15-year-old stand), which is 5.3 (15-year-old stand) to 9.5 % (5-year-old stand) of the tree biomass and 4.9 (15-year-old stand) to 8.6 % (5-year-old stand) of the total vegetation.

Decomposition of litter at the soil surface, as indicated by turnover rate, is 4074 (5-year-old stand) to 5102 kg ha^{-1} year^{-1} (15-year-old stand) of the total litter input. This amounts to 77.0 (15-year-old stand) to 81.0 % (5-year-old stand) of the total litter input. Compared with this, in the present 5- and 15-year-old forests, the annual weight loss in leaf litter as determined by litter bags was 93 (15-year-old stand) to 94 % (5-year-old stand) (Lodhiyal, 2000). At the end of the annual cycle, 956 (5-year-old stand) to 1524 kg ha^{-1} year^{-1} (15-year-old stand) litter remains under composed, and is carried over to the next year. According to Lodhiyal *et al.* (1995), little mortality of main roots occurs in actively growing trees and shrubs, but considerable mortality occurs in fine roots. Orlov (1968) and Ogino (1977) found that mortality of fine roots is equivalent to one-fifth of leaf litter; we made the same assumption here. However, our present estimates of fine root production may be a gross underestimation (Fogel, 1983; Vogt *et al.*, 1986). Since herbaceous vegetation at all three sites is annual, root mortality was assumed to be 100 %. The root mortality of trees, shrubs and herbs amounts to 407, 174 and 592 kg ha^{-1} year^{-1}, respectively, in the 5-year-old forest, and 689, 332 and 582 kg ha^{-1} year^{-1} in the 15- year-old Shisham forest.

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