

Biomass, productivity and nutrient cycling in alpine *Rhododendron* community of Central Himalaya

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Abstract. The paper describes biomass, productivity and nutrient cycling of the *Rhododendron* scrub (*R. campanulatum* D. Don and *R. barbatum* Wall.), occurring in the timberline areas of the Central Himalaya. The total biomass of vegetation was 40.5 t ha⁻¹ and the net primary production was 10.0 t ha⁻¹ yr⁻¹. The latter is on the higher side of the range, 4.2-10.2 t ha⁻¹ yr⁻¹ reported for the productivity of certain alpine and subalpine communities occurring in the mountains of the temperate region. The production efficiency of leaf (net primary productivity / leaf mass) was markedly higher (3.41 g g⁻¹ foliage mass) than those of the close canopied forests occurring in the Central Himalaya (0.74-3.10 g g⁻¹ foliage mass yr⁻¹).

Present estimates of standing crop of nutrients in vegetation were 173.1 kg ha⁻¹ for N, 13.2 kg ha⁻¹ for P and 94.1 kg ha⁻¹ for K. The net uptake of nutrients was 51.7 kg ha⁻¹ yr⁻¹ for N, 4.8 kg ha⁻¹ yr⁻¹ for P and 31.6 kg ha⁻¹ yr⁻¹ for K. Nutrient use efficiency in terms of NPP per unit of nutrient uptake was 235 for N, 2769 for P and 507 for K, which are greater than those of the close-canopied forests of the region.

Keywords: High altitude, scrub community, nutrient use

Introduction

Increasing the data base for productivity and nutrient cycling of woody vegetation is important for assessing them in future environments which are likely to be different than the present ones due to global warming and CO₂ augmentation of atmosphere. Little is known about the structure and functioning of the Himalayan timberline communities. They grow in an environment dissimilar to that of timberline communities that have been described in detail. The summer is divisible into early dry summer and three wet months, winters are moderate for the latitude and altitude.

Predominance of the broad-leaved evergreen species with single-yr leaf longevity in the entire elevational range (from 300 to 3000 m or more) that supports forest vegetation is a characteristic feature of the Indian Central Himalayan forests (Singh and Singh 1987). *Rhododendron arboreum* Smith, also a broad-leaved single-yr evergreen tree species is most common in the undercanopy of various forest types that occur over a wide elevational range. Only above 3000 m elevation or

more, in timberline areas, other rhododendrons (mainly *R. campanulatum* D. Don and *R. barbatum* Wall.) form tree vegetation of short stature (3-4 m tall). These short stemmed, copiously branched rhododendrons are also broad leaved evergreen. The objectives of this study were : (i) to provide with basic ecosystem characters of the Central Himalayan alpine rhododendron scrub, (ii) to contribute to the understanding of ecosystem properties that change from forests (close canopy forest) to open woody communities of timberline areas and, (iii) to compare this alpine timberline community to those of other mountain areas. To attain the second objective this broadleaf evergreen community has been compared with the close canopy forests of the region having broad-leaved single-yr evergreen species as dominance studied in the past.

Material and Methods

Site description

The study site was located at 3,300 m elevation in the Pindari catchment of Nanda devi Biosphere Reserve (between 79°40'-80°50'E long. and 30°17'-30°41'N lat.) in Central Himalaya. The climate is monsoon type. The summer is divisible into early dry summer (April to mid-June) and late wet summer, commonly referred to as rainy season (mid-June to September). The snow-free period is between May and October, during which rainfall is 2,170 mm (Sundariyal 1992). During the snow-free period the mean monthly temperature ranges from 7°C in October to 13°C in June. From May to August the mean monthly temperature ranges from 12 to 13°C. It has long been recognised that the arctic and alpine limits of growth generally corresponds to the location of the 10°C for the warmest month (Arno 1984).

The area has a high mean relative humidity (70%) and seldom declines below 50% even during the relatively rainless early summer. Soil temperature at 5 cm soil depth is reported to vary from 6° C (October) to 11° C (August). (Sundariyal 1992). Solar radiation on a clear day reaches 2592 J m⁻² day⁻¹.

The bed rock is sillimanite rich kyanite-garnet bearing psammite schists and interbedded with calc-silicate and amphibole bearing calc gneisses (Valdiya and Goel 1983). This community occurs on relatively steeper slopes (> 40°). The gentler slope in the same timber line area are occupied by taller vegetation of deciduous Birch (*Betula utilis* D. Don). Soil is brown earth type with sandy loam texture and pH 5.0-5.45 across the depth.

Vegetation analysis

Species composition of rhododendron community was studied in May 1990 just after snow melt. The trees were analysed by using 10, 10x10 m size quadrats and the shrubs were studied by using 10, 5x5 m quadrats.

Biomass estimation

For biomass estimation 12 sample trees of *R. campanulatum* and 9 *R. barbatum* were felled at groundline (stump height less than 15 cm). Sample trees were selected to represent the range in diameters (10-70 cm, cbh — circumference at breast height i.e. 1.37m from ground level) within the stand.

Aboveground tree parts were separated into bole (stem), branch, twig and foliage. For each section (approximately 1 m) of bole a 4-6 cm disc was cut at both ends for determination of bark thickness and volume measurements. Root system of each sample tree was excavated from 1 m³ earth; separated into stump, lateral and fine root fractions. The 1 m depth included all the roots, except of the largest individuals, in which case a small fraction of roots could not be collected. All the components were weighed green, bagged and transported to the laboratory. After oven drying various tree components at 80°C to constant weight, dry weight : fresh weight ratio were used to convert fresh weight taken in the field into dry weight. Bole bark : bole wood ratios were used to convert bole bark and bole wood fresh weight into dry weight for each section. Biomass equations by tree components were developed to relate oven-dry weight to tree cbh. The form of the allometric function of the equation was :

$$\text{Ln}Y = a + b \text{Ln}X$$

Where, Y = mass of tree component in kilograms, and X is tree cbh in centimeters measured at breast height.

Mean cbh value for a cbh class was used in equation for a particular component and the value obtained was multiplied by the tree density. Finally, the biomass across cbh class was summed up to get estimate for a component. By summing up the values for different components, total biomass for a species was obtained.

Concerning with shrubs, for each species six individuals representing all dgl (diameter at ground line i.e. 10 cm above ground level) classes were harvested and fresh weights of different components viz.; stem (main stem + branch + twig), foliage and root were taken separately. Sub-samples (about 200 g) for different aboveground and belowground components were brought to the laboratory and oven-dried at 80°C to constant weight. The biomass for shrubs was calculated as for the trees.

All herbaceous plants were harvested at monthly intervals from May 1989 to November 1989 using 1 x 1 m, 10 randomly disposed quadrats. Aboveground and belowground fresh weights for different species were weighed in the field. Sub-samples (about 200g) for

aboveground and belowground components were brought to the laboratory and oven-dried to constant weight at 80°C. The fresh: dryweight factor was used to determine the biomass. The biomass totalled across different species furnished the biomass of entire herbaceous vegetation in the forest.

Litter fall

Rates of litterfall were measured at monthly intervals from May 1989 to November 1989 and thereafter in April 1990. The amount of winter litterfall was assessed from the data of November 1989 and April 1990. Lack of logistic facilities prohibited litter collection during winter months when sites were under snow cover. However, leaf shedding does not occur during winters in these rhododendrons (Troup 1921). Litter was collected using randomly located litter traps, made up of wooden slates of 50 cm length, 50 cm width and 15 cm depth with nylon mesh in bottom. Nine traps were emptied and samples were brought to the laboratory and then sorted out into different components viz., leaf, wood, reproductive and miscellaneous (parts other than above, e.g. bark etc.)

Annual turnover rate was calculated by dividing annual litter fall by mean standing crop of litter for that year (Olson 1963).

Net production estimation

Following the establishment of a sample plot of one ha diameter growth at breast height was measured on increment cores from all tree individuals of 10 cm cbh and more (tree individuals smaller than 10cm cbh were rare). Annual increment may show year to year variation, therefore, diameter increments for several years are required (Prescott, Corbin and Parkinson 1989). Diameter increment for five-yr period was divided by five to obtain average annual increment. Dry biomass increments of different tree components were calculated using the biomass equations.

The net changes in biomass accumulation in different tree components yielded net biomass accretion in the tree. Annual leaf litter fall values were added to the foliage biomass accumulation to calculate foliage production. Wood, reproductive parts and miscellaneous litter fall values were summed in biomass accumulation of twigs. Fine root mortality was estimated by monthly cutting of soil cores. Fine root mortality when added to biomass accumulation yielded net production for fine roots.

For shrubs 3 individuals of about the average basal diameter for different species were marked at base (10 cm above the ground level), and increments were measured periodically twice at an interval of one year to estimate increments. The differences between increments for two years were insignificant. Shrub net production was assessed by calculating differences between biomass at time t_1 (obtained as described earlier) and time t_2 (one year interval) by allowing for the increment in diameter of marked individuals. To this value, foliage biomass was added by assuming 100% leaf replacement. To the root biomass accumulation, 1/5 of leaf litter was added (mortality in fine roots) based on

assumptions of Kalela (1954); Orlov (1955, 1968); Ogino (1977). However, this may grossly underestimate root production (Persson 1978, 1985; Santantonio and Hermann 1985).

For herbaceous vegetation, the net production was calculated by summing up all positive increments in biomass by all species across months.

Laboratory analysis

All the vegetation samples used for dry mass determination or chemical analysis were dried to constant mass at 80° C before weighing. Vegetation and litter samples were ground with a Wiley mill to pass through a 0.85 mm mesh stainless steel sieve.

Total N in vegetation and soil was measured with the Kjeldahl digestion method (Peach and Tracey 1956; Misra 1968). Phosphorous concentrations were determined by phosphomolybdic blue colorimetric method (Jackson 1958), and Potassium concentrations by a flame photometry (Jackson 1958).

The average N, P and K concentrations of each biomass component were multiplied by the mass of that component. Nutrient mass values of all species of tree, shrub and herb were summed up to estimate the total mass of N, P and K in biomass and annual net primary production.

The amount of nutrients in each stratum (0-10; 10-20; 20-30 cm) of soil was estimated from bulk density, soil volume and nutrient concentration values. The amount of nutrients estimated in all three strata were summed to obtain total nutrient content down to 30 cm depth.

The retranslocation of N, P, and K was calculated as follows:

$$\text{Nutrient in per unit weight of green foliage} \times \text{Amount of litter fall} = x$$

$$\text{Nutrient in per unit weight of abscised foliage} \times \text{Amount of litter fall} = y$$

$$\% \text{ retranslocation} = \frac{x - y}{x} \times 100$$

This calculation assumes no mass loss or leaching during leaf senescence (Rawat and Singh 1988; Prescott, Corbin and Parkinson 1989; Lugo 1992). Amounts of N, P and K reabsorbed from foliage and twigs annually were subtracted from the amounts in net primary production to estimate the amounts of N, P and K taken up annually by vegetation to produce new biomass. The efficiency of nutrient use of vegetation was estimated by dividing the amount of new biomass by amount of N, P and K taken up in one year. To compute the amount of nutrient transfer to the forest floor, the nutrient concentration of litter fall components were multiplied by the weight of annual litter fall.

Results

Species composition

Two tree species constituted this community, of which *Rhododendron campanulatum* accounted for 92.6 % tree basal area and *R. barbatum* for 7.4%. The total

	Density (Individuals ha ⁻¹)	Total Basal Area (m ² ha ⁻¹)	IVI*	Leaf Area Index (LAI; m ² m ⁻²)
TREES				
<i>R. campanulatum</i> D.Don	1110.0	10.8	277.6	1.2
<i>R. barbatum</i> Wall.	70.0	0.9	22.4	0.1
TOTAL	1180.0	11.7	300.0	1.3
SHRUBS*				
<i>Berberis umbellata</i> Wall. ex G. Don	230.0	4.0	129.1	-
<i>Cotoneaster bacillaris</i> Wall.	250.0	1.5	88.1	-
<i>Rosa sericea</i> Lindl.	180.0	1.0	65.0	-
<i>Lonicera wabbiana</i> Wall ex. DC	30.0	0.1	17.8	-
TOTAL	690.0	6.6	300.0	-

Table 1. Woody species composition of the *Rhododendron* scrub (* Basal area cm² ha⁻¹; ** IVI, Importance Value Index is equal to sum of relative density, relative frequency, and relative total basal area).

basal area $11.6 \text{ m}^2 \text{ ha}^{-1}$ and leaf area index, $1.3 \text{ m}^2 \text{ m}^{-2}$ in the stand (Table 1) were far lower than generally found in the forests of Central Himalaya (30 to $100 \text{ m}^2 \text{ ha}^{-1}$ and 6 to $20 \text{ m}^2 \text{ m}^{-2}$, respectively; Singh and Singh 1992).

Among the shrubs (4 species in total) *Berberis umbellata* (IVI = 129) was most important and *Polygonum paniculatum*, *Ainsliaea aptera*, *Anaphalis-busua* and *Geranium nepalense* were the important herbs (19 species in total).

Biomass

Allometric regression equation and parameters relating cbh to biomass of different components for the tree species are given in Table 2. The total tree biomass was 38.7 t ha^{-1} , of which a substantial portion (33%) was belowground. The shrubs resembled rhododendrons in biomass allocation to belowground and aboveground parts, indicating a similarity in their growth habit. In the aboveground biomass the crown's (branch, twig and leaf) share was about as large as the bole's share (Table 3). The shrub biomass was inconspicuous (0.1 t ha^{-1}) and was exceeded by herb biomass 1.7 t ha^{-1} (Table 4).

Litter fall

More litter fall occurred during rainy summer ($1.7 \text{ t fall ha}^{-1}$; July to September), than either during dry summer (May to June) or winter (October to April). The total

annual litter fall was $3.5 \text{ t ha}^{-1} \text{ yr}^{-1}$, of which the leaf litter was 48.3% (Table 5).

Net production

The tree production (mostly due to *R. campanulatum*) was $7.8 \text{ t ha}^{-1} \text{ yr}^{-1}$. The crown (combined twig and foliage) production was about five times of the bole production. The fine roots accounted for about 23% of the tree production (Table 6). Of the total tree production 35% was belowground and 65% aboveground, almost same proportions as observed for their biomass. The net production of herbs, $2.2 \text{ t ha}^{-1} \text{ yr}^{-1}$ was sizeable (59% aboveground parts) and shrub production was negligible (Table 6). Net production of the entire vegetation of the forest was $10.0 \text{ t ha}^{-1} \text{ yr}^{-1}$, to this the rhododendrons contributed about 78%.

Nutrient storage and nutrient uptake

Among the nutrients, the concentrations in plant tissues were higher for N, followed by K and P (Table 7). The leaf : bole wood nutrient concentration ratios in *R. campanulatum* and *R. barbatum*, were 6.5 and 7.9 for N, 13 for P (for each), and 5.6 and 5.1 for K, respectively.

Nutrient concentration of understory vegetation in general, followed the order : leaves > stem > root for shrubs and aboveground > belowground for herbs. Foli-

Components	Intercept (a)	Slope (b)	r^2
<i>Rhododendron campanulatum</i>			
Bole wood	-0.7392912	0.9158064	0.909
Bole bark	-5.4474565	1.4964137	0.865
Branch	-4.0323895	1.6123475	0.871
Twig	-5.2774090	1.6512267	0.920
Foliage	-3.3708055	1.6943625	0.898
Total aboveground	-1.3881729	1.2646820	0.916
Stump root	-3.8982123	1.6744537	0.912
Lateral root	-5.5925266	1.8029562	0.917
Fine root	-5.4481550	1.3933838	0.786
Total belowground	-3.5998418	1.6836037	0.916
Total	-1.4691188	1.4041426	0.928
<i>R. barbatum</i>			
Bole wood	-1.21091	1.1049773	0.841
Bole bark	-4.1225877	1.2338553	0.910
Branch	-3.0603128	1.4328473	0.934
Twig	-4.3643404	1.5001729	0.914
Foliage	-4.0828232	1.4472511	0.896
Total aboveground	-1.0805116	1.2620488	0.931
Stump root	-2.9308043	1.4822956	0.922
Lateral root	-4.2722535	1.5632668	0.876
Fine root	-4.4806783	1.3428884	0.814
Total belowground	2.5512118	1.4843676	0.935
Total	-0.8911893	1.3254643	0.943

Table 2. Allometric relationships between the biomass of tree components (Y , kg tree⁻¹) and cbh (X , cm) ($\text{Ln } Y = a + b \text{ Ln } X$). Significant at $p < 0.01$.

Species	Bole Wood	Bole Bark	Branch	Twig	Foliage	Total Above-ground	Stump Root	Lateral Root	Fine Root	Total Below-ground	TOTAL
<i>R. campanulatum</i>	13.08 (36.8)	0.90 (2.6)	5.90 (16.7)	1.90 (5.4)	2.10 (5.9)	23.80 (67.4)	8.40 (23.8)	2.50 (7.1)	0.60 (1.7)	11.50 (32.6)	35.30 (100.00)
<i>R. barbatum</i>	1.10 (32.4)	0.10 (2.9)	0.60 (17.6)	0.20 (5.9)	0.20 (5.9)	2.20 (64.7)	0.80 (23.5)	0.30 (8.8)	0.10 (3.0)	1.20 (35.3)	3.40 (100.00)
TOTAL	14.10 (36.4)	1.00 (2.6)	6.50 (16.8)	2.10 (5.5)	2.30 (5.9)	26.00 (67.2)	9.20 (23.8)	2.80 (7.2)	0.70 (1.8)	12.70 (32.8)	38.70 (100.00)

Table 3. Componentwise distribution of tree biomass (t ha⁻¹). Values in parentheses are percentages of total biomass.

Component	Above-ground	Below-ground	Total
Tree layer	26.00 (67.2)	12.70 (32.80)	38.70 (100.0)
Shrub layer	0.06 (66.7)	0.03 (33.30)	0.09 (100.0)
Herb layer	0.90 (52.9)	0.80 (47.10)	1.70 (100.0)
TOTAL	26.96 (66.60)	13.53 (33.40)	40.49 (100.0)

Table 4. Stand biomass (t ha⁻¹). Values in parentheses are the percent of the total biomass.

Components	Winter	Dry Summer	Rainy Summer	Total
Leaf litter	0.472	0.189	1.008	1.669
Wood litter	0.290	0.340	0.608	1.238
Reproductive litter	0.208	0.560	0.080	0.344
Miscellaneous litter	0.139	0.430	0.026	0.208
Total litter	1.109	0.628	1.722	3.459

Table 5. Seasonal litter fall pattern (t ha⁻¹ yr⁻¹).

Component	Net Production
Tree	
Bole wood	0.68 (6.8)
Bole bark	0.08 (0.8)
Branch	0.49 (4.9)
Twig	1.98 (19.7)
Foliage	1.85 (18.4)
Stump root	0.73 (7.2)
Lateral root	0.23 (2.3)
Fine root	1.77 (17.6)
Total tree	7.81 (77.7)
Shrub	
Stem	0.01 (0.1)
Foliage	0.02 (0.2)
Root	0.01 (0.1)
Total shrub	0.04 (0.4)
Herb	
Aboveground	1.30 (12.9)
Belowground	0.90 (9.0)
Total herb	2.20 (21.9)
Total vegetation	10.04 (100.0)

Table 6. Net production (t ha⁻¹ yr⁻¹). Values in parentheses are the percentages of the total net production in different components.

Components	N	P	K
Trees			
<i>R. campanulatum</i>			
Bole wood	0.25±0.023	0.01±0.001	0.18±0.010
Bole bark	0.46±0.036	0.05±0.003	0.27±0.020
Branch	0.39±0.027	0.03±0.002	0.23±0.021
Twig	0.71±0.053	0.05±0.003	0.30±0.030
Foliage	1.62±0.169	0.13±0.015	0.78±0.040
Stump root	0.32±0.032	0.03±0.001	0.15±0.012
Lateral root	0.36±0.040	0.03±0.002	0.14±0.010
Fine root	0.46±0.040	0.04±0.003	0.20±0.021
<i>R. barbatum</i>			
Bole wood	0.21±0.021	0.01±0.001	0.13±0.015
Bole bark	0.45±0.044	0.04±0.004	0.31±0.021
Branch	0.34±0.025	0.03±0.002	0.18±0.010
Twig	0.67±0.046	0.05±0.002	0.32±0.021
Foliage	1.65±0.136	0.13±0.012	0.66±0.021
Stump root	0.29±0.030	0.02±0.001	0.16±0.015
Lateral root	0.32±0.026	0.03±0.002	0.15±0.012
Fine root	0.46±0.032	0.04±0.004	0.31±0.021
Shrubs			
<i>Berberis umbellata</i>			
Stem	0.56±0.042	0.05±0.003	0.49±0.038
Foliage	1.61±0.149	0.02±0.001	0.92±0.086
Root	0.53±0.041	0.05±0.003	0.33±0.027
<i>Rosa sericea</i>			
Stem	0.58±0.049	0.05±0.004	0.37±0.030
Foliage	1.41±0.121	0.14±0.010	0.58±0.046
Root	0.55±0.041	0.04±0.003	0.28±0.019
Inter species			
Stem	1.00±0.093	0.10±0.001	0.56±0.036
Foliage	1.35±0.097	0.12±0.011	0.58±0.040
Root	0.81±0.073	0.06±0.003	0.33±0.027
Herbs			
Aboveground	0.91±0.067	0.09±0.008	0.62±0.047
Belowground	0.67±0.044	0.08±0.006	0.32±0.028
Soil across 0-30 cm depth			
0-10	0.49±0.04	0.021±0.002	0.15±0.02
10-20	0.41±0.03	0.009±0.001	0.12±0.01
20-30	0.34±0.03	0.006±0.001	0.10±0.01

Table 7. Nutrient concentration (% ± 1 SE) in different components of the trees, shrubs, herbs and soil.

Components	N	P	K
Trees			
Bole wood	34.86 (21.9)	1.41 (12.1)	24.87 (29.0)
Bole bark	4.74 (3.0)	0.51 (4.4)	2.92 (3.3)
Branch	24.83 (15.6)	1.93 (16.5)	14.53 (17.0)
Twig	15.50 (9.5)	1.07 (9.1)	6.48 (7.6)
Foliage	37.14 (23.4)	2.97 (25.4)	17.59 (20.5)
Stump root	29.17 (18.3)	2.68 (22.9)	13.87 (16.2)
Lateral root	9.75 (6.1)	0.82 (7.0)	3.87 (4.5)
Fine root	3.43 (2.2)	0.30 (2.6)	1.59 (1.9)
Total tree	159.07 (100)	11.69 (100)	85.62 (100)
Shrubs			
Stem	0.28 (52.8)	0.026 (63.4)	0.24 (63.1)
Foliage	0.11 (20.8)	0.002 (4.9)	0.06 (15.8)
Root	0.14 (26.4)	0.013 (31.7)	0.08 (21.1)
Total shrub	0.53 (100)	0.041 (100)	0.38 (100)
Herbs			
Aboveground	8.21 (60.8)	0.81 (56.3)	5.58 (68.8)
Belowground	5.29 (39.2)	0.63 (43.7)	2.53 (31.2)
Total herb	13.50 (100)	1.44 (100)	8.11 (100)
Total Vegetation	173.10	13.17	94.11
Soil (0-30 cm depth)	6190.00	166.10	1841.70
Litter mass	62.20	7.10	22.40

Table 8. Standing state of nutrients (kg ha⁻¹) in vegetation, soil and litter. Values in parentheses are the percentages.

Nutrient	% reabsorption	Amount of reabsorption (kg ha ⁻¹ yr ⁻¹)
N	43.81	7.95
P	38.25	0.60
K	55.15	3.99

Table 9. Reabsorption of nutrients from leaves during senescence.

Components	N	P	K
Trees			
Bole wood	1.7	0.07	1.2
Bole bark	0.3	0.03	0.2
Branch	1.9	0.15	1.1
Twig	11.5 (7.8)	0.79 (0.61)	4.6 (3.4)
Foliage	18.1 (10.2)	1.57 (0.97)	7.2 (3.5)
Stump root	2.3	0.21	1.1
Lateral root	0.8	0.07	0.3
Fine root	8.2	0.71	4.6
Total tree	44.8 (33.2)	3.60 (2.82)	20.3 (15.4)
Shrubs			
Stem	0.1	0.01	0.07
Foliage	0.3	0.01	0.12
Root	0.1	0.01	0.04
Total shrub	0.5	0.03	0.23
Herbs			
Above ground	12.2	1.2	8.3
Below ground	5.8	0.7	2.8
Total herb	18.0	1.9	11.1
Total Vegetation	63.3 (51.7)	5.5 (4.75)	31.6 (26.7)

Table 10. Nutrient uptake ($\text{kg ha}^{-1} \text{ yr}^{-1}$) by different layers of vegetation and their components. Values in parentheses are the nutrient uptakes after adjustment for reabsorption.

Component	N	P	K
Leaf	0.91±0.032	0.08±0.003	0.35±0.023
Wood	0.50±0.021	0.04±0.002	0.24±0.015
Reproductive parts	0.75±0.030	0.05±0.003	0.28±0.020
Miscellaneous	0.76±0.047	0.02±0.001	0.08±0.003

Table 11. Concentration ($\% \pm 1 \text{ SE}$) of nutrients in tree litter fall.

Component	N	P	K
Trees			
Leaf	15.19 (59.5)	1.33 (65.5)	5.84 (58.6)
Wood	6.18 (24.2)	0.49 (24.1)	2.97 (29.9)
Reproductive parts	2.58 (10.1)	0.17 (8.4)	0.96 (9.6)
Miscellaneous	1.58 (6.2)	0.04 (2.0)	0.17 (1.7)
Total tree	25.53 (100)	2.03 (100)	9.94 (100)
Shrubs			
Aboveground	0.10	0.007	0.05
Belowground	0.01	0.001	0.01
Total shrub	0.11	0.008	0.06
Herbs			
Aboveground	11.83	1.17	8.06
Belowground	6.03	0.72	2.88
Total herb	17.86	1.89	10.94
Total vegetation	51.41	4.62	25.33

Table 12. Amount of nutrients (kg ha⁻¹ yr⁻¹) in litter fall of different components of the vegetation.

age nutrient concentrations in shrubs were generally lower than the nutrient concentration in tree foliage (Table 7).

Most of the nutrient storage was in soil (up to 30 cm depth). For example, of the total N storage in ecosystem (6425 kg ha⁻¹), 96% was in soil, 3% in biomass and 1% in forest floor litter mass (Table 8).

The proportional reabsorption of nutrients from green tree foliage during senescence was about 44% for N, 38% for P and 55% for K (Table 9).

The net nutrient uptake in rhododendrons was 51.7 N, 4.7 P and 26.7 kg K ha⁻¹ yr⁻¹ (Table 10). The concentration of nutrients in litter is given in Table 11. Values of nutrient return through litter fall (sum of aboveground and belowground litter fall) to soil were close to the net uptake values (Table 12), indicating little nutrient accumulation in tree biomass, especially keeping in view the fact that some nutrient loss would have occurred through leaching by rain and snow. Nutrient return via aboveground litter fall was at least three times as great as via belowground litter fall for different nutrients (Table 12).

In the rhododendrons the nutrient turnover time was in the range of 3.26 yr to 4.20 yr which were similar to those for the forest floor.

Discussion

Biomass and net production

The most obvious general pattern in plant morphology is a decrease in stature with increase in altitude (Friend and Woodward 1990). Comparison with the forest types that occur towards higher elevations in Central Himalaya indicates that the biomass declines sharply from 308 t ha⁻¹ in Maple (*Acer cappadocicum* Gled.) at about 2800 m to 177 t ha⁻¹ in Birch (*Betula utilis*) at 3150 m elevation to 40 t ha⁻¹ in the rhododendron scrub of the present study.

Reduction in fraction of production that is accumulated in biomass appears to be one of the major factors that cause stunted vegetation in timberline areas. Severe abrasion caused by high wind speed and winter desicca-

tion of trees unable to mature fully because of low rates of production of lignin, cuticle, etc. (Wardle 1971) may limit biomass accumulation in timberline areas of alpine belt. In natural forests the differences in biomass accumulation ratio result mainly due to varied condition of the size and rate of wood increment, as affected both by environmental conditions and the age of trees. The biomass accumulation ratios for the woody plants of present study (5) is markedly lower than those (12-46) reported for several Central Himalayan forests occurring between 300 and below 3150 m elevation (Singh and Singh 1987; Garkoti 1992). Biomass accumulation ratios in some forests with relatively smaller trees is reported to range from 13-21 in the Great Smoky Mountain and Hubbard Brook areas and within the range 2.5-11 reported for heath balds in the Great Smoky Mountains (Whittaker et al. 1974).

In a severely cold climates only those woody species survive whose growth form permit them to occupy the warmest close-to-the-ground microenvironment. In the close-to-the-ground microenvironment the leaf boundary layer (the unstirred air around leaf) is less vulnerable to disturbance by wind, consequently, woody plants with stunted growth habit are able to substantially elevate leaf temperatures above atmospheric temperatures in sunlight (Givnish 1987). Compared to close canopied forests of the lower elevations (Singh and Singh 1992) in the timberline rhododendrons more biomass is allocated to crowns (28% compared to < 20%) and belowground parts (33% compared to < 28%). In severe alpine climate the low temperatures would limit the availability of nutrients and water. The alpine plants seem to develop proportionately larger root system to mine nutrients and to have access to water frozen soils (Chapin, Shaver and Kedrowski 1986). This explains the greater allocation to the belowground biomass in rhododendron. In *R. campanulatum* more root growth to support shoot growth is required as individuals become larger (Garkoti 1992). Evidently the carbon cost of nutrient acquisition (because of more root growth) would increase as plants become larger. The enhanced carbon cost of root production for sustaining shoot growth would limit productivity by restricting the leaf mass. The LAI in the present study was 1.3, compared to 2.81 in the Central Himalayan Birch (*Betula utilis*) at 3150 m, and more than 6 in several forest types occurring between 2300 and 2800 m in the region (Adhikari 1992; Garkoti 1992; Rawat and Singh 1988).

The present rhododendron community is more productive (aboveground tree net production = 5.1 t ha⁻¹ yr⁻¹) than the *Tsuga mertensiana* Carr. forest (aboveground net production = 4.2 t ha⁻¹ yr⁻¹) of the subalpine zone of the Pacific North-west, U.S.A. (Gholz 1982). The total productivity (10 t ha⁻¹ yr⁻¹) was very close to that reported for the subalpine, *Abies lasiocarpa* (Hook.) Nutt. forest (10.2 t ha⁻¹ yr⁻¹) for Santa Catalina mountain by Whittaker and Niering (1975). Similar productivities are reported for the mid elevation Hubbard Brook forest (10.4 t ha⁻¹ yr⁻¹; Whittaker et al. 1974), the Gray Beech forest (9.1 t ha⁻¹ yr⁻¹) and the Upper Cove forest (11.0 t ha⁻¹ yr⁻¹, Whittaker 1966).

Relatively moderate winters and humidities similar to maritime climates (Sakai and Malla 1981) of the region appear to raise productivity to a higher level than those

of the subalpine and alpine communities of temperate latitudes. The moderate nature of climate is also reflected in the presence of broadleaf species in which leaves are replaced annually.

Considering the low altitude forests of the region a 1:3 ratio approaches between the productivity of the highest elevation rhododendron community and the most productive lower elevation communities of the region. This seems to be a fairly constant feature, as ratios almost same as this are reported from elevational gradients of some other areas (Whittaker 1966; Gholz 1982).

Compared to the Central Himalayan forests of lower elevations the stem wood production relative to leaf production in the present rhododendron community is lower. A decreasing trend for stem wood production relative to leaf production toward higher elevations is observed when a number of Central Himalayan forests varying in elevation are compared. Such a shift seems to occur in response to a more rigorous environment. It seems that in unfavourable climates the stem dimensions are short partly because more leaf production is required to support a given unit of stem production.

The above ground herbaceous production in the present site (1.3 t ha⁻¹ yr⁻¹) is 13% of the total community production, which is greater than that reported for the close-canopied forests of Central Himalayan forests (< 8%; calculated from Rana, Singh and Singh 1989).

The net production elaborated per unit leaf weight is called net assimilation rate or production efficiency (Johnson and Risser 1974) or leaf efficiency (Satoo 1968), calculated as NPP : foliage biomass ratio was 3.41 g g⁻¹ foliage mass yr⁻¹ in the rhododendron community. It was higher than the values (0.74-3.10 g g⁻¹ foliage mass yr⁻¹) reported for the forests of the region (Singh and Singh 1992). This may be partly because foliar standing crop in the rhododendron trees was comparatively much smaller, consequently leaves would be well exposed to light.

Nutrient storage and nutrient cycling

The ratios between the highest (in leaf) and lowest (in bole wood) tissue nutrient concentrations in the present study (5.1-13.0) were similar to those reported for several close canopied forests of Central Himalaya (Singh, Khanna and Singh 1985). Thus, lower leaf to wood nutrient concentration relative to temperate zone trees (10.3-20.3, see Singh, Khanna and Singh 1985) can be considered a characteristic feature of the trees of entire elevational range in Central Himalaya. Higher nutrient accumulation in wood is considered a nutrient conservation strategy (see Singh, Khanna and Singh, 1985), as nutrients stored in wood cycle slowly, therefore, are less vulnerable to leakage from the ecosystem than the rapidly cycling foliage nutrients.

Present estimates of standing crop of N and P of above ground vegetation are lower than the values (156.58-304.77 N and 19.14-36.81 kg P ha⁻¹ yr⁻¹) reported for certain subalpine pine (*Pinus contorta* Loudon), spruce (*Picea glauca* (Moench) Voss) and fir (*Abies lasiocarpa*) forests of Southern Alberta (Prescott, Corbin and Parkinson 1988). However, the nutrient uptake values of the present forest were higher than those of the above forests.

The foliar nutrient concentrations in *R. campanulatum* was higher than in the rhododendrons of lower elevations of the region (see Singh and Singh 1992), despite the expected decrease in nutrient availability due to altitudinal decline in soil temperature. It seems the low temperatures at high altitudes reduce the plant growth rates more than the N supply. Rhododendrons of the region including *R. campanulatum* showed greater proportional retranslocations of foliage nutrient mass from senescing leaves than the other evergreen broadleaf species, indicating greater nutrient use efficiency. Among the rhododendrons, the retranslocation tends to increase with increase in elevation (e.g., retranslocation of N being 21% in *R. arboreum* as reported by Singh, Rawat and Singh (1992) at 2650 m elevation and 44% in this study for *R. campanulatum*). The higher retranslocation of nutrients from senescing leaves in the high altitude rhododendrons of the present study would give greater independence of soil nutrients during leaf production in early summer where temperatures are often limiting.

Since nitrogen may be limiting to productivity in many environments, productivity calculated per unit leaf nitrogen is of interest in comparing different species. Compared to the low elevation rhododendrons of Central Himalaya the rhododendrons of the present study was more efficient species, realizing a value (210 g g⁻¹ N) clearly greater than them (35.0-163.3 g g⁻¹ as reported by Singh and Singh 1992).

The nutrient use efficiency is best expressed as the amount of net primary production per unit of net nutrient uptake (Lugo 1992). In this respect the efficiency was 235 N, 2769 P and 507 K for the present study, which are greater than those reported for the various evergreen broadleaf forests of the Central Himalaya (Singh and Singh 1992).

Conclusion

The present Central Himalayan timberline community seems to experience a relatively favourable environment (moderate winters and high relative humidities), compared to the timberline communities occurring in mountains of temperate latitudes. This is reflected in the presence of evergreen broad-leaved species which replace almost entire crown annually and the net primary productivity value higher than in similar communities reported elsewhere. Compared to forests with the closed-canopies that occur immediately below the elevation of present timberline site the productivity is only 50% lower, though biomass and LAI show several-fold reductions. A marked reduction in biomass accumulation ratio and a greater allocation to roots result in a conspicuously smaller aboveground biomass in this rhododendron community. A smaller decline in NPP in the timberline community is made possible due to increased efficiencies of foliage (NPP/ foliage mass) and nutrient-use by trees.

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Appendix 1: Composition of herb layer.

Species	Density herbs m ⁻²	Biomass g m ⁻²	IVI
<i>Polygonum paniculatum</i> Bl.	9.6	14.53	27.06
<i>Ainsliaea aptera</i> DC.	14.0	11.01	25.23
<i>Anaphalis busua</i> (Ham.) Hand. Ma53	14.4	12.82	23.58
<i>Geranium nepalense</i> Sw.	8.0	11.61	23.07
<i>Potentilla fulgans</i> Wall. ex Hook	18.8	4.32	21.35
<i>Ranunculus diffusus</i> DC.	9.2	8.18	21.10
<i>Carex nubigena</i> D.Don	22.8	4.10	19.14
<i>Galium aprine</i> Linn.	14.4	2.74	16.23
<i>Smilacina pallida</i> Royle	10.8	6.16	15.78
<i>Parochetus communis</i> Buch. Ham.ex D.Don	16.0	1.92	14.80
<i>Primula edgeworthii</i> (Hook. f.)Pax	10.9	2.83	14.41
<i>Adiantum venustum</i> D. Don	14.0	1.82	13.74
<i>Clinopodium umbrosum</i> (M. Bieb.) Koch	11.6	0.87	11.55
<i>Viola canescens</i> Wall.	11.6	0.81	11.49
<i>Anemone rupicola</i> Buch. Ham.	8.0	1.33	10.38
<i>Gagea lutea</i> Schultz. f.	6.8	1.19	9.65
<i>Anemone rivularis</i> Buch. Ham.	5.2	3.22	8.59
<i>Mondo intermedium</i> (D. Don) Bailey	1.0	0.43	7.36
<i>Swertia cordata</i> (G.Don) Clarke	5.2	0.16	5.19
Total	212.3	90.05	