

Gradational forest change along the climatically dry valley slopes of Bhutan in the midst of humid eastern Himalaya

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Abstract

Altitudinal forest and climate changes from warm, dry valley bottom (1250 m a.s.l.) to cool, humid ridge top (3550 m a.s.l.) along the typical dry valley slopes of the Bhutan Himalaya were studied. Annual mean temperature decreased upslope with a lapse rate of $0.62\text{ }^{\circ}\text{C}\cdot 100\text{ m}^{-1}$ from $18.2\text{ }^{\circ}\text{C}$ at the valley bottom to $4.3\text{ }^{\circ}\text{C}$ at the ridge top. On the contrary volumetric soil moisture content increased from 14.7 to 75.0%. This inverse relationship is the major determinant factor for the distribution of different forest types along the altitudinal gradient. Based on the quantitative vegetation data from 15 plots arranged ca. 200 m in altitude interval (1520–3370 m a.s.l.), a total of 83 tree species belonging to 35 families were recorded. Three major formation types of lower and upper coniferous forests, and a mid-altitude evergreen and deciduous broad-leaved forest were contrasted. Including two transitional types, five forest zones were categorized based on cluster analysis, and each zone can be characterized by the dominants and their phytogeographical traits, viz. (1) west Himalayan warm, dry pine (1520–1760 m a.s.l.), (2) wide ranging east-west Himalayan mixed broad-leaved (1860–2540 m a.s.l.), (3) humid east Himalayan evergreen broad-leaved (2640–2820 m a.s.l.), (4) cool, humid east Himalayan conifer (2950–3210 m a.s.l.), and (5) wide ranging cold, humid conifer (3305–3370 m a.s.l.). Structurally, total basal area (biomass) increased from $15.2\text{ m}^2\text{ ha}^{-1}$ in the pine forest (1520 m) to $101.7\text{ m}^2\text{ ha}^{-1}$, in the conifer forest (3370 m a.s.l.). Similarly, soil organic carbon increased from 2.7 to 11.3% and nitrogen from 0.2 to 1.9% indicating dry, poor nutrient fragile ecosystem at the dry valley bottom. We concluded that low soil moisture content ($<20\%$) limits downslope extension of broad-leaved species below 1650 m a.s.l. while coldest month's mean temperature of $-1\text{ }^{\circ}\text{C}$ restricted the upslope extension of evergreen broad-leaved species above 3000 m a.s.l. Along the dry valley slopes, the transition from dry pine forest in the valley bottom, to a mixture of dry west Himalayan evergreen and deciduous east Himalayan broad-leaved, and to humid evergreen oak–laurel forests feature a unique pattern of forest type distribution.

Introduction

Ecologically, the Himalayas comprise of an outer zone of monsoon forest, an inner zone of coniferous forest and the Tibetan zone of arid steppe along the series of ranges ca. 3000 km in

length with a varying width from 80 to 300 km (Troll 1972; Singh and Singh 1987). The unique characteristics of the Himalayan ranges are the existence of typical dry valleys even in the midst of humid eastern Himalaya, first shown on the 1957 vegetation map of the Himalaya portrayed

in a three-dimensional arrangement of vegetation (Schweinfurth 1957, 1968, 1992). These typical dry valleys are distributed from Kabul in the west to Chang Jiang in the east running perpendicular to the prevailing mountain ranges, cutting through north to south including Bhutan located in the humid eastern Himalaya (Figure 1A). In the Bhutan Himalaya, the dry valleys are developed in the inner valleys from west to east. The strong valley wind that ascends every afternoon together with high temperature during the day increases evapotranspiration at the valley bottom leading to specific local dryness. These dry valleys are prominent in the middle reaches of big rivers extended from south to north dissecting the mid-mountains between southern mid-Himalaya and northern greater Himalaya (Ohsawa 1987a; Eguchi 1997). The vegetation distribution pattern along the dry valley slopes revealed that the slopes and ridges are wetter than the valley bottom due to subsidence over valleys in the slope wind circulation. Wangduephodrang town located in the dry valley bottom of Punatsangchu where the present study was carried out is known for strong valley wind, which can be symbolized with fluttering of prayer flags in every afternoon.

Even though the altitudinal climax vegetation zonation in the Nepal Himalayas were studied by several scientists (Kawakita 1956; Numata 1966; Troll 1967; Stainton 1972; Ohsawa 1983), yet only limited studies were carried out in the Bhutan Himalayas. A few scientists proposed Bhutan's vegetation classification into zonal or topography controlled diversification (Grierson and Long 1983–2000; Negi 1983; Sargent 1985; Sargent et al. 1985; Ohsawa 1987a). Floristically, the vegetation of the Bhutan Himalaya can be divided into six major forest zones, viz. (1) tropical zone between 100–1000 m a.s.l. along the southern foothill is dominated by *Shorea robusta*, *Tetrameles nudiflora*, *Pterospermum acerifolium*, *Phoebe hainesiensis*, *Acacia catechu*, *Bombax ceiba*, etc., (2) sub-tropical zone between 1000–2000 m a.s.l. is dominated by *Schima wallichii*, *Castanopsis tribuloides*, *Exbucklandia populnea*, *Duabanga sonneratioides*, and *Betula alnoides* while in the inner dry valley of this zone is dominated by *Pinus roxburghii* with its upper limit at ca. 2000 m a.s.l. and associated communities of *Quercus lanata*, *Q. semecarpifolia* and ericaceous *Rhododendron arboreum* and *Lyonia ovalifolia*, (3) warm-temper-

ate zone between 2000 and 2500 m a.s.l. is dominated by oak–laurel species of *Q. glauca*, *Q. oxyodon*, *Q. lamellosa*, *C. hystrix*, *Persea clarkeana*, *Cinnamomum impressinervium*, *Litsea elongata*, and *Phoebe cathia*, while in the inner dry valley of this zone is characterized by dominance of *P. wallichiana* and associated communities of *Q. semecarpifolia*, *Populus ciliata* and *P. rotundifolia*, (4) cool temperate zone between 2500 and 3000 m a.s.l. is mainly dominated by conifer species of *Picea spinulosa*, *Tsuga dumosa*, and *Abies densa* and associated understory communities of deciduous broad-leaved *Betula utilis*, *Gamblea ciliata*, and *Acer campbellii*, and evergreen *Q. semecarpifolia*, (5) sub-alpine zone between 3000 and 4000 m a.s.l. is dominated by wide ranging cold conifer species of *A. densa*, *T. dumosa*, and *Juniperus recurva*, and (6) alpine zone above 4000 m a.s.l. is the limit of tree growth and the alpine zone starts but sometimes scattered scrubs of dwarf junipers and rhododendrons occurred as high as 4932 m a.s.l. (Ohsawa 1987a).

However, no detail quantitative study on vegetation and ambient climatic factors along the steep slopes of typical dry valleys in the Bhutan Himalaya was undertaken. Coincidentally, dry valley ecosystems are developed along the dry valley bottom where the major towns of Bhutan are also located.

Materials and methods

Study site

The present study was carried out in one of the least studied areas of the typical dry valley along Punatsangchu (river), west central Bhutan (Figure 1). The dry valley extends ca. 50 km from Kamechu (720 m a.s.l.) at the lower valley, to Bajo (1250 m a.s.l.) in the central, to Punakha (1350 m a.s.l.) at the upper valley (Figure 1B). Specifically, the study area was located along the dry valley slopes facing to the east of Punatsangchu between Bajo (1250 m a.s.l., 27°30' N, 89°52' E) at the valley bottom to Lunchozeykha (3550 m a.s.l., 27°28' N, 89°45' E) on the ridge top (Figure 1). The topographical pattern of vegetation along the study area was mainly related to the environmental gradient from valley bottom, to slope, and to ridge top.

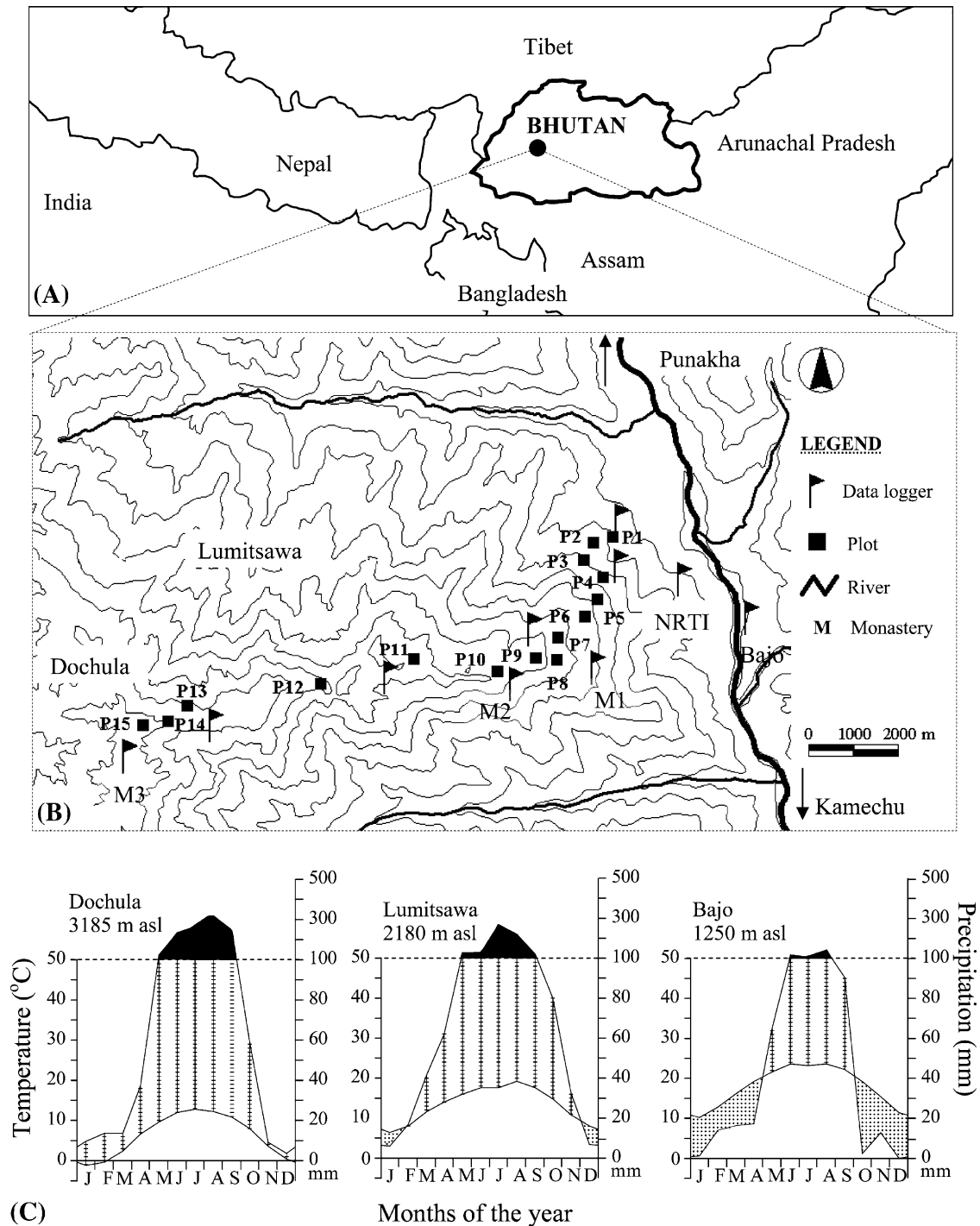


Figure 1. Map of the study area; (A) Location of Bhutan along the Himalayan range, (B) location of sampling plot (P1–P15) and data loggers along the altitudinal gradients between 1250–3550 m a.s.l., and (C) Walter's climate diagram at three locations (Bajo (1250 m) at the valley bottom, Lumitsawa (2180 m) in the evergreen broad-leaved forest, and Dochula (3185 m) at the ridge top). NRTI=Natural Resources Training Institute at Lobesa in the pine forest. ↑↓ indicates direction of dry valley extension.

There are three monasteries located along the slopes of the study area, viz. Pangsho (M1, at 2320 m a.s.l.), Lamzeykha (M2, at 2650 m a.s.l.), and Lunchozeykha (M3, at 3550 m a.s.l.) while settlements are confined to the wide valley bottom on both sides of Punatsangchu and utilizing the nearby forests for cattle grazing, firewood and timber harvesting, and collection of non-timber forest products (Figure 1B).

Floristically, contrasting vegetation distribution patterns are observed along the dry valley slopes of the study area. The valley bottom is dominated by dry habitat shrubs such as *Rhus paniculata*, *Pyllanthus emblica*, *Jatropha curcas*, *Woodfordia fruticosa*, and *Jasminum officinale* (Ohsawa 1987a) and, tree species of *P. roxburghii*. Ascending the slope is mesic type of evergreen broad-leaved species of *Q. lanata*, *Q. glauca*, *C. tribuloides*, *C. hystrix*, and a deciduous oak species of *Q. griffithii*. Near the ridge top, humid coniferous species of *T. dumosa*, *A. densa*, and *J. recurva* are common indicating closed humid conifer physiognomy.

The present study focused on the relationship of environmental factors on the forest distribution. Specifically the objectives of the study are (1) to clarify major environmental factors of climate and soil nutrient change along the altitude, (2) to describe physiognomic pattern of forest distribution and classify major forest zones, and (3) to clarify the functional attributes of forest ecosystem and environmental factors in terms of biomass, litter and soil nutrients along the steep altitudinal, and environmental gradients. This will contribute to better management and conservation of vegetation

and human life in a peculiar dry valley of the Bhutan Himalaya.

Environmental data collection: meteorology and soil moisture

The meteorological instrument used in measuring air temperature and relative air humidity was HOBO Onset data logger enclosed in the solar radiation shield (Onset Computer Co. MA, USA) and mounted on a pole about 1.3 m high above the ground. Data recordings were set at 1-h interval measurements and were downloaded after every 6 months using BoxCar Pro for Windows, Version 4.3 provided by Onset Computer Co. After each downloading, batteries were replaced and reset the logger for further measurements. Totally 10 data loggers were installed along the altitudinal gradients between Bajo (1250 m a.s.l.) to Lunchozeykha (3550 m a.s.l.) since October 1999–September 2004 (average of 5 years) and are still continuing recording (Figure 1B). For details such as location and altitude, refer Table 1.

Precipitation data was gathered from four different locations (1250, 1450, 2180, and 3185 m) along the altitudinal gradients of the study site. We used tipping bucket type rain gauge with data loggers (OTA KEIKI SEISAKUSHO CO. Tokyo) having measurement resolution of 0.5 mm set at hourly interval recording since October 1999–September 2004 (average of 5 years).

Data recorded were analyzed using thermal and humidity indices by the following methods:

Table 1. Climatic conditions along the altitudinal gradients of the study area.

Location	Altitude	AMT	CMT	WMT	WI	SMC	RH	PPT	PER
Lunchozeykha ridge top (conifer forest)	3550	4.3	-2.5	10.9	21.2	75.0	95.2		
Dochula ridge top (conifer forest)	3185	6.6	-1.0	12.7	36.8	68.7	93.5	1575.5	0.2
Above Lamzeykha (broad-leaved forest)	2820	7.9	1.4	13.3	43.3	39.7	92.8		
Near Lamzeykha monastery (broad-leaved)	2650	9.4	2.0	14.8	58.3	31.3	90.0		
Beside Pangsho monastery (broad-leaved)	2320	11.4	4.1	17.2	77.5	25.3	88.4		
Lumitsawa (broad-leaved forest)	2180	12.8	5.9	18.9	97.6	25.8	87.5	1032.6	0.7
Below Pansho (pine-broad-leaved)	2000	13.9	6.3	19.8	106.6	24.0	84.9		
Firing ground (forest edge)	1520	17.1	9.3	22.0	145.8	16.9	79.1		
Natural Resources Training Institute, Lobesa	1450	17.7	9.9	23.2	154.6	14.7	75.5	882.6	1.2
Bajo valley bottom (Research centre)	1250	18.5	11.1	24.1	159.9		75.0	572.0	1.9

(AMT=annual mean temperature, CMT=coldest months mean temperature, WMT=warmest months mean temperature, SMC=soil moisture content, RH=relative air humidity, PPT=mean annual precipitation, PER=potential evapotranspiration ratio). Warmth Index (WI) is calculated as the sum of monthly mean temperature exceeding 5 °C (Kira 1976).

- Climate diagram was drawn by Walter and Lieth's method (Walter et al. 1961–1967; Lieth et al. 1999);
- PER was calculated by Holdridge's (1967) method;

$$\text{PER} = (\text{ABT} * 58.93) / \text{PPT}$$

where, ABT = annual biotemperature (°C) and PPT = precipitation (mm).

Soil moisture content was measured by Hydrosense (CD 620 + CS 620) (CAMPBELL SCIENTIFIC INC., Logan, Utah) bearing 12 and 20 cm probes during every field survey occasions. Since measurements using 12 and 20 cm probes gave similar results, the soil moisture value was expressed as the mean value of three measurements for each probe (total six measurements in each plot). Soil hardness was measured by Yamanaka's soil hardness tester (Kiya Seisakusho, Ltd. Tokyo) and instantaneous soil and air temperature were measured by digital thermometer (DELTA_{SK-200} MC, Sato Keiryoki MFG. Co., Ltd. Tokyo)

Plot lay-out and tree inventory

Fifteen sampling plots were established along the altitudinal gradients from Bajo (1250 m a.s.l.) to Lunchozeykha (3550 m a.s.l.). For plot details such as altitude, aspect, slope, and plot size refer Appendix 1. The plot size varies from 400 to 800 m² because of the difficulty at several locations to set up larger plots due to abrupt topography such as steep cliffs and deep valleys, etc. The size of each plot was the possible maximal size at each altitude along the survey route. All tree individuals occurring within the quadrat attaining a height greater than 1.3 m ($H \geq 1.3$ m) were identified, measured and recorded for tree height (H , m) and diameter at breast height (DBH, cm at 1.3 m above ground). Fieldwork was carried out from late August to early September 2001, August to early September 2002, and late August to early September 2003.

Nomenclature of plants followed after Flora of Bhutan (Grierson and Long 1983–2000), Flowers of the Himalaya (Polunin and Stainton 1984), and

Flowers of the Himalaya: A supplement (Stainton 1988).

Data analyses

Species basal area (BA, cm²) was calculated from DBH data of tree individuals and calculated the relative proportion of each species' basal area in percent (Relative Basal Area, RBA%). The RBA of each species was used as abundance measure of species in a community. The dominant species of the altitudinal plots were determined based on the dominance analysis (Ohsawa 1984; Kikvidze and Ohsawa 2002) and the species diversity was calculated using Shannon–Wiener index (H').

The vegetation data was then analyzed quantitatively to obtain general statistics of forest tree data using the computer software FOREST program developed by Laboratory of Ecology, Chiba University. The processed data was analyzed by PC-ORD version 4 (McCune and Mefford 1999) and cluster analysis was performed using distance measure of Sorensen (Bray–Curtis method). Relationship between vegetation and environmental variables were determined by Canonical Correspondence Analysis.

Soil and litter sampling

Litter and soil samples were collected from four small quadrats (0.5 m by 0.5 m) in each vegetation plot along the altitudinal gradient. The samples were separated into litter, fermentation-humus, and soil surface layer. The samples were measured for the fresh weights (FW) and oven dry weights (ODW) at 85 °C for 48 h. Dried samples were then analyzed at the Soils and Plant Analytical Laboratory (SPAL), Semtokha, Bhutan. Soil pH was measured in suspensions of the soil in distilled water and 1 M KCl (1:2:3) using a PHM 83 automatic pH meter. Total nitrogen (N) is extracted and converted into ammonium form by micro-Kjeldahl digestion with H₂HSO₄ and a Se-based catalyst. Ammonium-N and nitrate-N are extracted by shaking with 0.01 M CaCl₂ for 2 h. Organic carbon was measured by the Walkley–Black method of low temperature oxidation with acidified K₂Cr₂O₇ and titration of the excess dichromate.

Results

Altitudinal climate and soil moisture change

Temperature and humidity conditions were inversely related along the altitudinal gradient. The annual mean temperature decreased linearly up slope with an annual mean lapse rate of $0.62\text{ }^{\circ}\text{C}\cdot 100\text{ m}^{-1}$ from $18.2\text{ }^{\circ}\text{C}$ (maximum monthly mean temperature of $23.6\text{ }^{\circ}\text{C}$ in July, and a minimum of $10.2\text{ }^{\circ}\text{C}$ in January) at the valley bottom (1250 m) to $4.3\text{ }^{\circ}\text{C}$ (maximum monthly mean temperature of $10.9\text{ }^{\circ}\text{C}$ in August, and a minimum of $-2.5\text{ }^{\circ}\text{C}$ in February) at the ridge top (3550 m) (Table 1).

The seasonal lapse rate and mean relative air humidity revealed significant pattern along the altitude (Figure 2A). The summer month of August had the minimum lapse rate of $0.5\text{ }^{\circ}\text{C}\cdot 100\text{ m}^{-1}$ coinciding with the most humid month, and the highest lapse rate of $0.7\text{ }^{\circ}\text{C}\cdot 100\text{ m}^{-1}$ was observed in February and March of the driest months (Figure 2A). Temperature inversion occurred at ca. 2000 m (between 1960 and 2180 m) where the monthly mean temperature of 2180 m was higher than 1960 m during mid November and January indicating mild winter months along the dry valley slope (Figure 2B). The coldest month's mean temperature of $-1\text{ }^{\circ}\text{C}$ which control the upper limit of evergreen broad-leaved trees coincided at ca. 3000 m a.s.l. in the upper conifer forest and still evergreen broad-leaved species were found as understory of canopy conifers.

On the contrary to annual mean temperature, mean annual precipitation (1999–2004) increased

along the altitude from 572.0 mm at Bajo (1250 m) to 882.6 mm at NRTI (1450 m) through 1032.6 mm at Lumitsawa (2180 m) and finally to 1575.5 mm at Dochula (3185 m) (Table 1). June to September had the highest precipitation days corresponding to the monsoon months and received over 80% of the total precipitation. The seasonal patterns of precipitation were illustrated by Walter's climate diagram (cf. Figure 1C) and were closely correlated to the seasonal pattern of soil moisture content. The valley bottom remained under water stress in the months of October to April where mean temperature curve exceeded the precipitation curve (cf. Figure 1C). On the contrary at the ridge top, the precipitation curve exceeded the temperature curve and remained under humid condition for whole year round. Similarly, soil moisture content changed from 5.0% at the valley bottom (1520 m) to 46.8% at the ridge top (3370 m) in April and from 28.7% to 74.2% in August. Accordingly, Holdridge's PER ranged from 1.9 of very dry forest at the valley bottom (1250 m) to 1.2 of dry forest at NRTI (1450 m) through 0.7 of moist forest at Lumitsawa (2180 m) and finally to 0.2 of wet forest at Dochula (3185 m) (Table 1).

Floristic composition and forest zones along the dry valley slopes

A total of 83 tree species comprising of 35 families were recorded from 15 sampling plots (Table 1, Appendix 1). Three major life-forms of trees forming

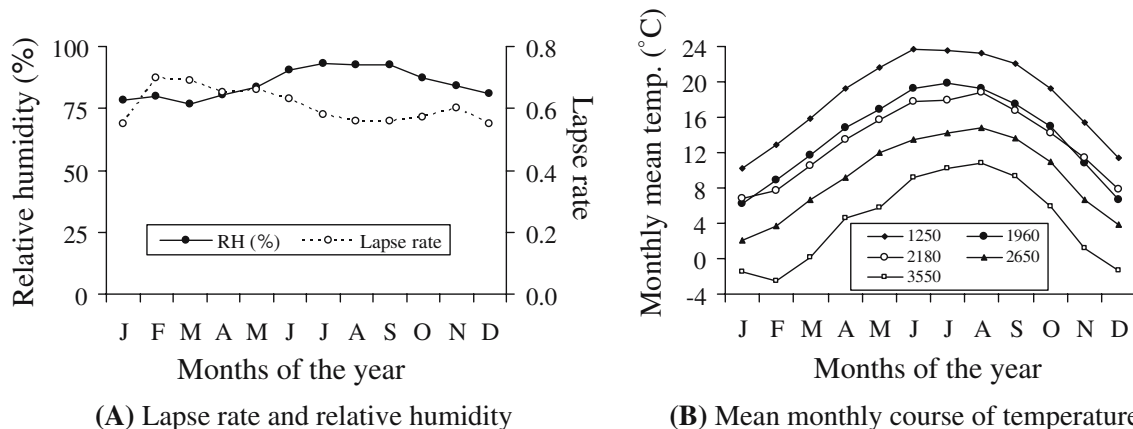


Figure 2. Climatic background of the study area; (A) change of monthly mean lapse rate and annual mean air relative humidity along the altitude, (B) monthly course of mean temperature indicating temperature inversion ca. 2000 m a.s.l. (between 1960 and 2180 m a.s.l.).

physiognomic patterns of three altitudinal formation belts of lower conifers, mid-evergreen and deciduous mixed broad-leaved, and an upper conifer were contrasted along the altitudinal gradient (Figure 3).

These three major life-form belts were classified into five altitudinal forest zones by cluster dendrogram arbitrarily at 65.0% similarity threshold (Figure 4B). Five forest zones defined by dominants can be characterized by Holdridge's biotemperature and humidity provinces and phytogeographical traits of the species, i.e., Zone 1, warm-dry west Himalayan type of *P. roxburghii* forest (P1, 1520 m to P3, 1760 m), Zone 2, wide ranging east-west Himalayan type of *Q. lanata*-*Q. griffithii*-*R. arboreum* mixed broad-leaved forest (P4, 1860 m to P9, 2540 m), Zone 3, humid east Himalayan evergreen broad-leaved forest of *Q. semecarpifolia*-*Q. glauca*-*Q. oxyodon* (P10, 2640 m to P11, 2820 m), Zone 4, cool humid east Himalayan conifer type of *T. dumosa*-*A. densa* (P12, 2950 m to P13, 3210 m), and Zone 5, wide ranging cold humid conifer forest of *A. densa*-*J. recurva* (P14, 3305 m to P15, 3370 m) (Figure 4B, C).

Forest zone 1 was dominated by west Himalayan element of *P. roxburghii* irrespective of topography at the lower, warm, dry valley bottom. The gradual change in associated understory species from xeric

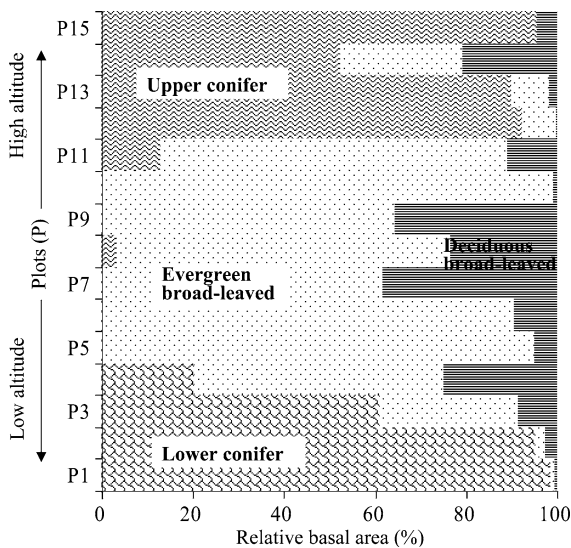


Figure 3. Altitudinal distribution pattern of three major life-forms from lower conifer, to mid-deciduous and evergreen broad-leaved, and to upper conifer forests. Both lower and upper altitudes are dominated by conifers. RBA = relative basal area, P = sampling plot.

type (*Ziziphus*, *Berberis*, *Phyllanthus* 2 spp., *Toricellia*, and *Indigofera*) in P1 (1520 m) to mesic type of evergreen broad-leaved species (*Quercus*, *Schima*, *Rhododendron*, *Myrsine*, *Rapanea*, and *Symplocos*) and deciduous broad-leaved species (*Quercus*, *Lyonia*, *Benthamidia*, *Rhus*, *Prunus*, *Carpinus*, *Viburnum*, and *Rubus*) in P3 (1760 m), along the altitude indicated the change in moisture condition (Appendix 1). In P4 (1860 m), *P. roxburghii* was confined to ridge tops only and the slopes are dominated by dry evergreen broad-leaved species of *Q. lanata* and *R. arboreum* and deciduous broad-leaved species of *Q. griffithii* and *L. ovalifolia* (from P5, 2000 m to P9, 2540 m) (Zone 2). These dominants were replaced by evergreen broad-leaved species of *Q. semecarpifolia*, *Q. glauca* and *Q. oxyodon* (from P10, 2640 m to P11, 2820 m) (Zone 3). During the course of change in canopy dominant, the associated understory species of *Eurya* and *Symplocos* also became dominant in P9 (2540 m a.s.l.). Forest zone 3 of moist/wet evergreen broad-leaved forests (P10, 2640 m to P11, 2820 m) are the transitional zone from moist mixed broad-leaved forests of P9 (2540 m) to upper humid conifer forest of *T. dumosa* and *A. densa* (Zone 4). Juniper forest formed the tree line at 3500 m, rather low altitude partly because of clearing by the yak and cattle herders for grazing, firewood collection, and probably short span of altitudinal range to the ridge top.

Species distribution along the altitudinal gradient

The altitudinal distribution of tree species were expressed in terms of basal area along the soil moisture gradient (Figure 5).

P. roxburghii, a west Himalayan element dominated in the lower plots (from P1, 1520 m to P4, 1860 m) with a peak distribution of $24.6 \text{ m}^2 \text{ ha}^{-1}$ in P3 (1760 m) within the low soil moisture content of 16.9–21.9%. The accumulated basal area of *P. roxburghii* was relatively low compared to the accumulated basal area of evergreen broad-leaved species and upper conifer species (Figure 5, Appendix 1). *Q. lanata* showed its peak basal area distribution of $44.6 \text{ m}^2 \text{ ha}^{-1}$ in P6 (2020 m) while *Q. griffithii* had its peak distribution of $15 \text{ m}^2 \text{ ha}^{-1}$ in P9 (2540 m) at a higher altitude and comparatively lower basal area. These two species occurred within the soil moisture content of 21.9–31.7% (Figure 5,

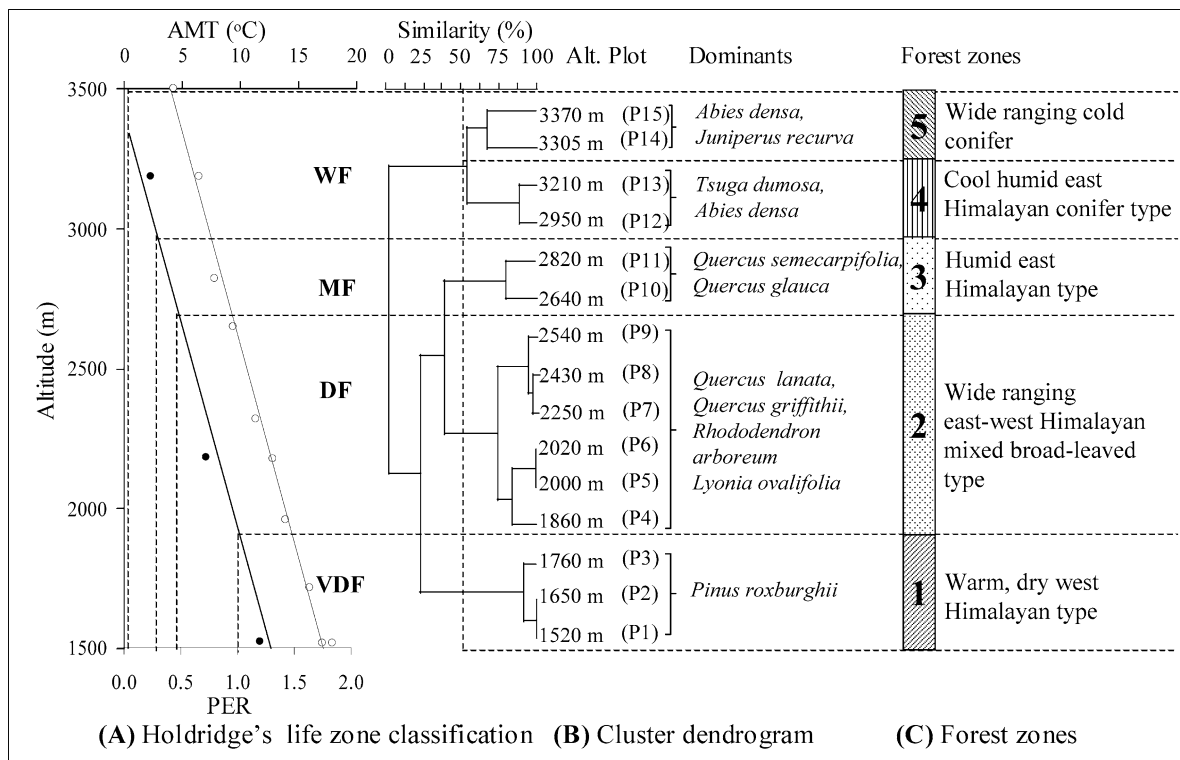


Figure 4. Climatic conditions, similarity dendrogram, plot details and forest zones along the study site; (A) Holdridge's life zone classification system (● PER, ○ AMT, AMT = annual mean temperature, PER = potential evapotranspiration ratio, VDF = very dry forest, DF = dry forest, MF = moist forest and WF = wet forest. Numbers 1–5 refers to forest zones along the altitudinal gradient, (B) Cluster dendrogram depicting forest zones with dominant species and (C) forest zones along the altitudinal gradients.

Table 1). Upper limits for *Q. lanata* and *Q. griffithii* were nearly at the same altitude in P9 (2540 m) while *R. arboreum* ascended up to P13 (3210 m). Interestingly, *R. arboreum* revealed two basal area distribution peaks (bimodal distribution) with a larger one in P5 (2000 m) and a lesser one in P13 (3210 m) by *R. arboreum* subsp. *campbelliae* usually found above 3000–3600 m (Figure 5).

The two humid evergreen oak species of *Q. oxyodon* and *Q. glauca* (both subgen. *Cyclobalanopsis*) occurred under relatively high soil moisture content of 31.3–39.7% (Figure 5). While *Q. glauca* had wider altitudinal range of ca. 800 m starting from P5 (2000 m) and reached its upper limit in P11 (2820 m) with its peak distribution of basal area in P10 (2640 m), *Q. oxyodon* was found to appear in a short altitudinal range of ca. 200 m from P10 (2640 m) to P11 (2820 m) (Figure 5). The accumulated basal area of above two species were rather low compared to other broad-leaved species (Figure 5, Appendix 1). *Q. semecarpifolia* (subgen.

Quercus), a west Himalayan element or alpine oak in Chinese, also co-existed with the humid oaks (P10, 2640 m to P11, 2820 m) and dominated the forest with a high total basal area of 46.7 and 44.4 m² ha⁻¹ (Figure 5, Appendix 1). *T. dumosa* began to appear from P11 (2820 m) and reached its upper limit in P14 (3305 m) with a peak basal area distribution of 134.1 m² ha⁻¹ in P12 (2950 m). *A. densa* and *J. recurva* showed their peak basal area distribution in P15 (3370 m) corresponding to the upper limit of *T. dumosa* under high soil moisture content of 45.3–68.0% and attained relatively high total basal area of nearly 3-fold of the lower conifer (*P. roxburghii*) (Figure 5, Appendix 1).

Species richness and diversity along the altitudinal gradients

The number of species by each life-form illustrated that conifer forest had the least while evergreen broad-leaved and deciduous broad-leaved forest

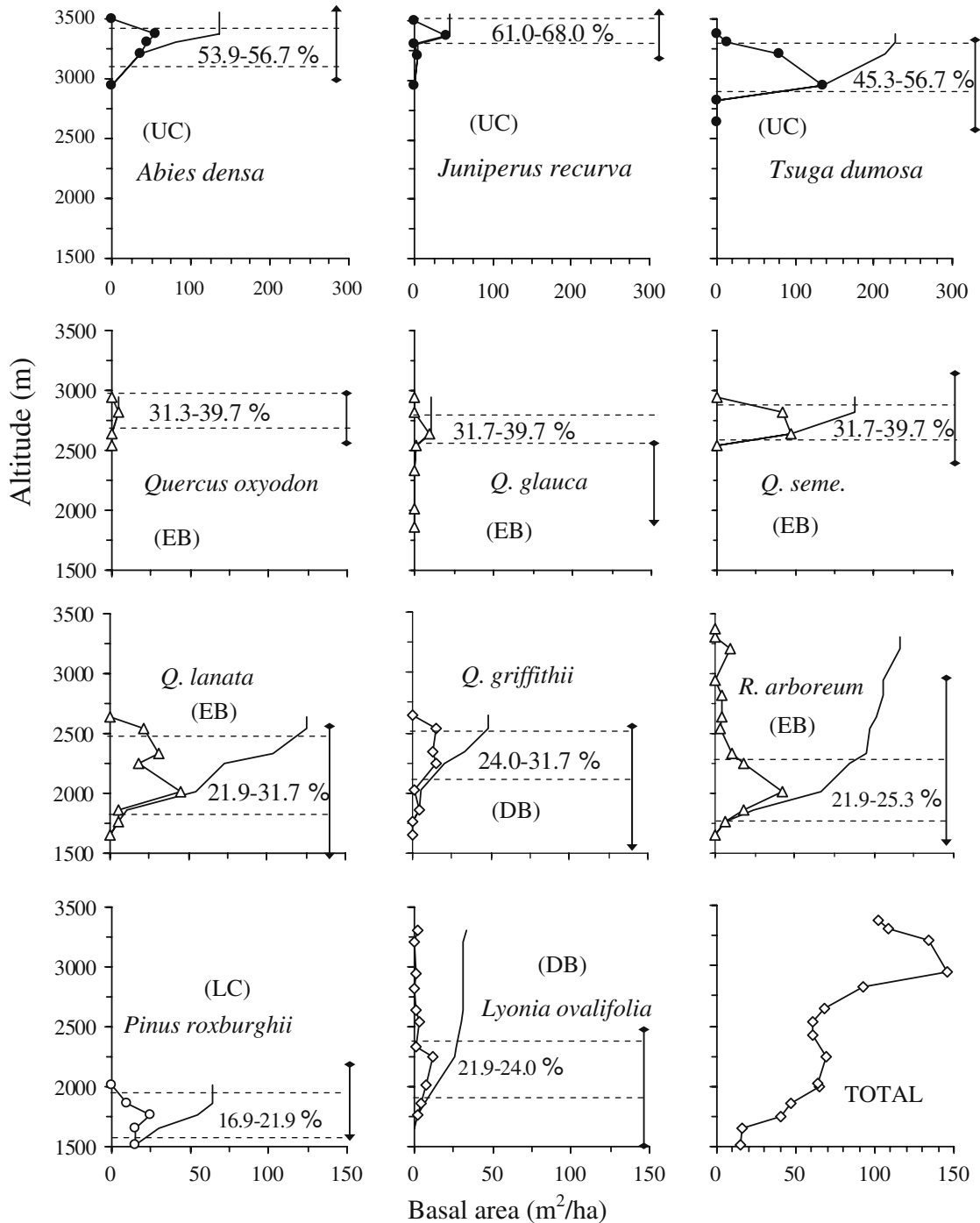


Figure 5. Basal area distribution of dominant tree species (line with dots) and line without dots indicates accumulated basal area; UC=upper conifer, EB=evergreen broad-leaved and DB=deciduous broad-leaved. LC=lower conifer. Horizontal broken lines indicated range of species distribution defined by ca. 75% basal area thresholds of peak values for each species along the altitudinal gradient. Vertical solid lines with arrowhead indicated normal distributional range of species. SMC=soil moisture content in between broken lines.

had higher number of species (Figure 6A). A total of 83 tree species in the present study area comprised of 37 evergreen broad-leaved, 40 deciduous broad-leaved and 6 coniferous species (Appendix 1). Evergreen broad-leaved species showed a peak value of 13 species in P9 (2540 m)

Similarly, deciduous broad-leaved species showed a maximum number of 12 species in P3

(1760 m) and nine species in P4 (1860 m) and were mostly understory shrubs (Figure 6A). Conifer species were found both in the lower and upper altitudes. Only one conifer species was found in the lower altitude plots (P1, 1520 m to P4, 1860 m), while five conifer species were recorded in the upper altitude plots (P12, 2950 m to P15, 3370 m) (Figure 6A, Appendix 1). Total number of species

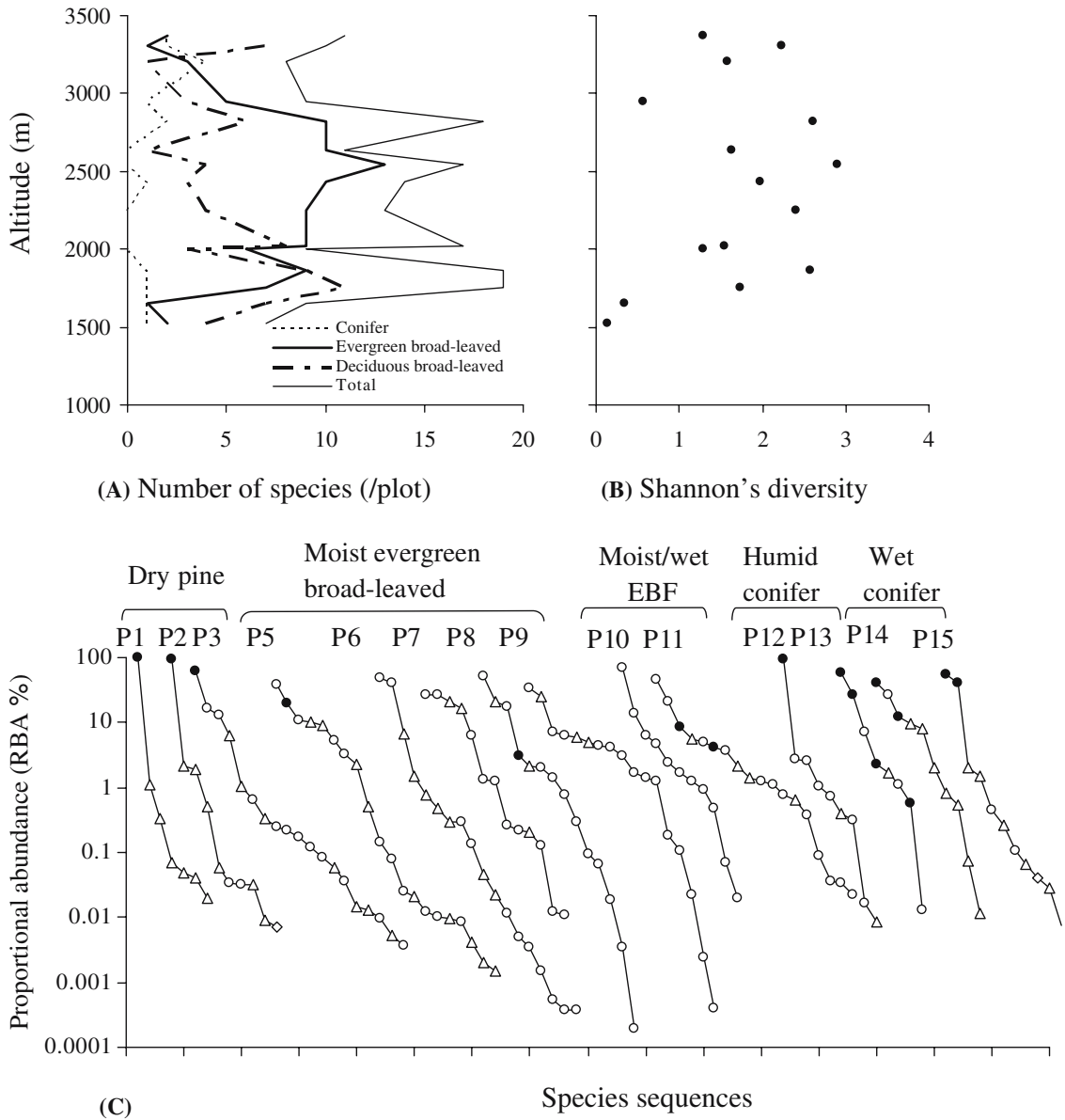


Figure 6. Diversity relations in the series, (A) species richness by each life form and the total number of species, (B) Shannon's diversity (H'), and (C) dominance-diversity curves (closed circle = conifers, open circle = evergreen broad-leaved and open triangle = deciduous broad-leaved species) of different forest zones along the altitudinal gradients.

per plot was fluctuated and revealed hump-shaped pattern along the altitudinal gradient. Lower species richness of seven species in P1 (1520 m) and eight species in P13 (3210 m) were recorded from both lower and upper conifer forest while species richness of 20 species in P3 (1760 m), 20 species in P4 (1860 m), and 18 species in P11 (2820 m) were recorded in the transitional forest and in the mixed broad-leaved forest where different life-forms co-existed (Figure 6A, B). Accordingly, Shannon's diversity index (H') exhibited similar trend from 0.1 (P1, 1520 m) to 2.9 (P9, 2540 m) and to 1.3 (P15, 3370 m) indicating higher diversity at the mid-altitude evergreen broad-leaved forest and relatively low diversity at the two extreme conifer forests (Figure 6B).

The species dominance–diversity curves revealed the dominance structure of each plot along the altitudinal gradient (Figure 6C). Conifer

forests both in the lower and upper plots were represented by geometric type of distribution where the top one or two dominants (*P. roxburghii* at the lower conifer, and *T. dumosa*, *A. densa*, and *J. recurva* at the upper conifer) became conspicuous and were followed by exponential decrease in abundance. On the other hand evergreen broad-leaved forests in between revealed gentle curves showing a log-normal type of distribution where several co-dominant species shared the mid-abundance (*Q. lanata*, *Q. griffithii*, *R. arboreum*, *S. ramossisima*, and *L. ovalifolia*) (Figure 6C).

Forest structural features along the altitudinal gradients

Structural features along the altitudinal gradients are illustrated by maximum height (Figure 7A),

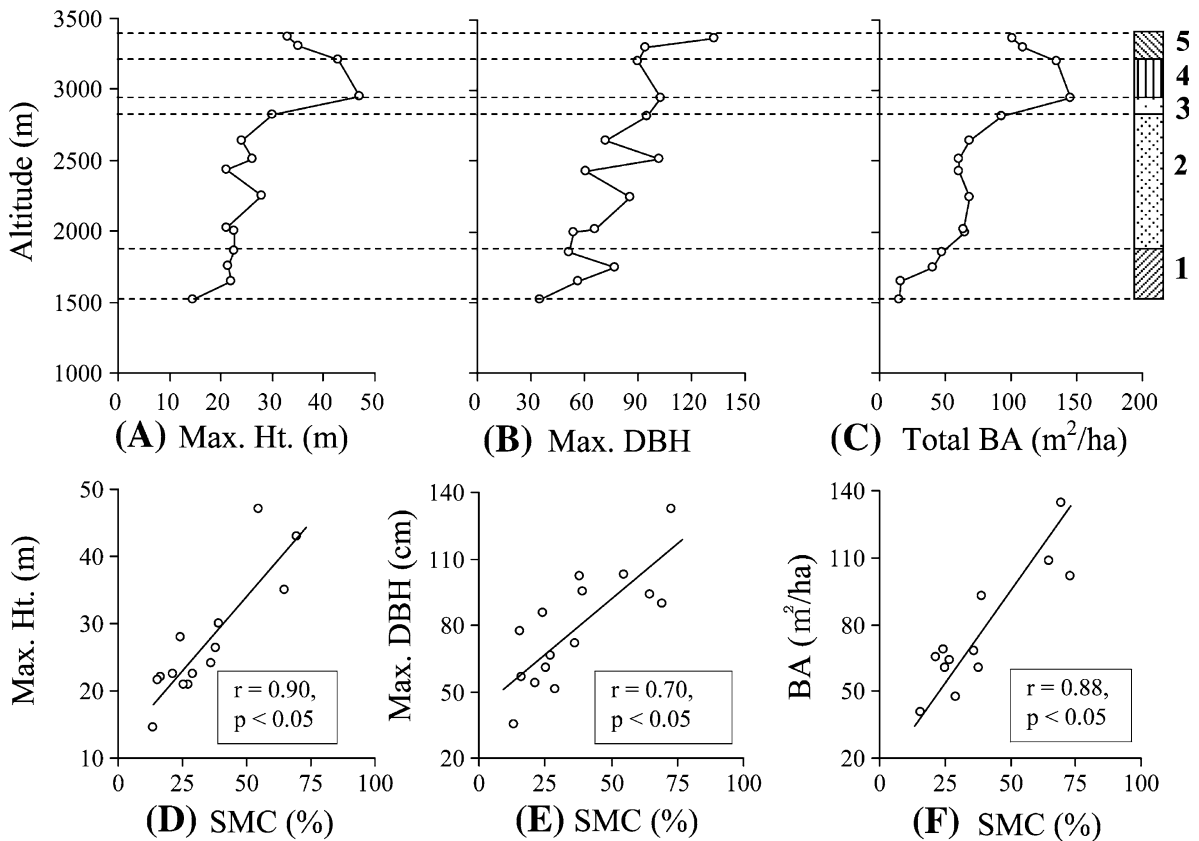


Figure 7. Forest structural traits in each plot along the altitudinal gradients; (A) maximum height, (B) maximum diameter at breast height, (C) total basal area, and (D–F) their correlation with soil moisture content (SMC%), (D) maximum height and soil moisture content, (E) maximum diameter at breast height and soil moisture content, and (F) total basal area and soil moisture content along the altitudinal gradient. The bar (1–5) refers to forest zones in Figure 4.

maximum diameter at breast height (Figure 7B), and total basal area (Figure 7C) of the tree. The maximum height and maximum diameter at breast height of a tree in each plot increased with increasing altitude from 14.6 m and 35.5 cm of *P. roxburghii* in P1 (1520 m) through 28.0 m and 85.5 cm of *Q. lanata* in P7 (2250 m) to 47.0 m and 103.0 cm of *T. dumosa* in P12 (2950 m). However, maximum height decreased to 33.0 m though diameter kept increasing to 132.5 cm of *A. densa* in P15 (3370 m)

(Figure 7A, B, Appendix 1). Increase in tree height was linearly correlated with increasing soil moisture content along the increasing altitude (Figure 7D).

Maximum diameter at breast height was positively correlated with soil moisture content and revealed significant but a little weaker comparing to tree height (Figure 7E). A total basal area also increased along the altitude from 15.2 m² ha⁻¹ in P1 (1520 m) through 68.7 m² ha⁻¹ in P7 (2250 m), to 101.7 m² ha⁻¹ in P15 (3370 m).

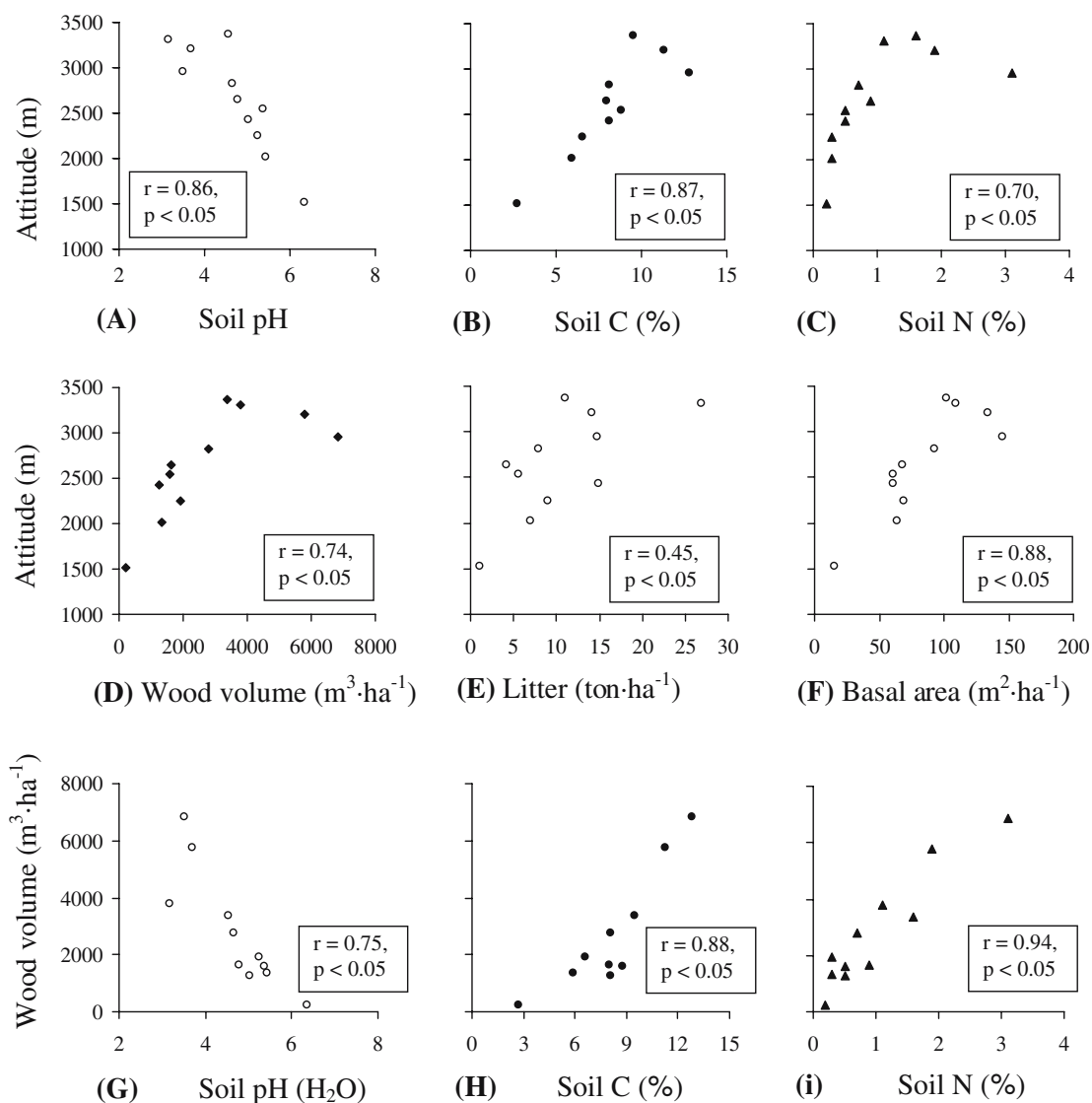


Figure 8. Altitudinal soil nutrient properties and biomass change, (A) soil pH, (B) soil C, (C) soil nitrogen, (D) wood volume, (E) litter accumulation, and (F) basal area distribution along the altitudinal gradients of the study area, and (G–I) correlation of wood volume (biomass) and soil properties, (G) biomass vs. soil pH, (H) biomass vs. soil C, and (I) biomass vs. soil N.

Similarly a tight correlation was found between the total basal area and soil moisture content along the increasing altitude of the study area (Figure 7C, F).

Forest wood volume equivalent and soil properties

Soil reaction showed slightly acidic of pH 6.2 at the lower, warm, dry pine zone in P1 (1520 m) to strongly acidic of pH 3.7 at the upper, cold, humid conifer zone in P13 (3210 m) (Figure 8A).

Soil organic carbon (C%) and nitrogen (N%) increased with increasing altitude from 2.7%, 0.2% in P1 (1520 m) to 11.3%, 1.6%, respectively in P13 (3210 m) (Figure 8B, C). Similarly, the biomass of the forest indicated by total wood volume equivalent, litter accumulation (oven dry weight), and total basal area, were increased from 220.5 m³ ha⁻¹, 1.1 ton ha⁻¹, 15.2 m² ha⁻¹ in P1 (1520 m) to 5777.3 m³ ha⁻¹, 14.2 ton ha⁻¹, 134.4 m² ha⁻¹ in P15 (3210 m) (Figure 8D–F). Soil pH was found negatively correlated with wood biomass equivalent (Figure 8G). Forest biomass indicated by wood volume showed positive correlation with soil organic carbon and nitrogen and were directly correlated with increasing altitude since biomass increased with altitude (Figure 8H, I).

Discussion

Temperature and vegetation distribution along the altitudinal gradient

Altitude encompass both temperature and humidity gradient that are decisive in vegetation distribution particularly in a steep terrain like in the Himalayas. The annual mean temperature lapse rate for the past 5 years (1999–2004) along Lunchozeykha series of dry valley slope was fairly higher at 0.62 °C·100 m⁻¹ compared to 0.54 of the humid slopes of Bhutan Himalaya (Eguchi 1987; Agro-met, MoA 1994–2001), 0.55 on Mt. Kinabalu (4101 m a.s.l., 6°5' N, 160°33' E) in the tropical region (Kitayama 1992), and 0.54 on Mt. Emei (3099 m a.s.l., 29°34.5' N, 103°21.5' E) in the transition zone between tropical and temperate forest (Tang and Ohsawa 1997). The relatively high lapse rate along the typical dry valley slopes indicated specific local dryness particularly at the valley bottom. The temperature inversion at ca. 2000 m a.s.l. coincided with the upper limit of *P. roxburghii* and the start of the mixed broad-leaved forest probably induced by the change in soil moisture regime, relative humidity and temperature (cf. Figure 2B).

The coldest month's mean temperature of -1 °C indicating upper limit of evergreen

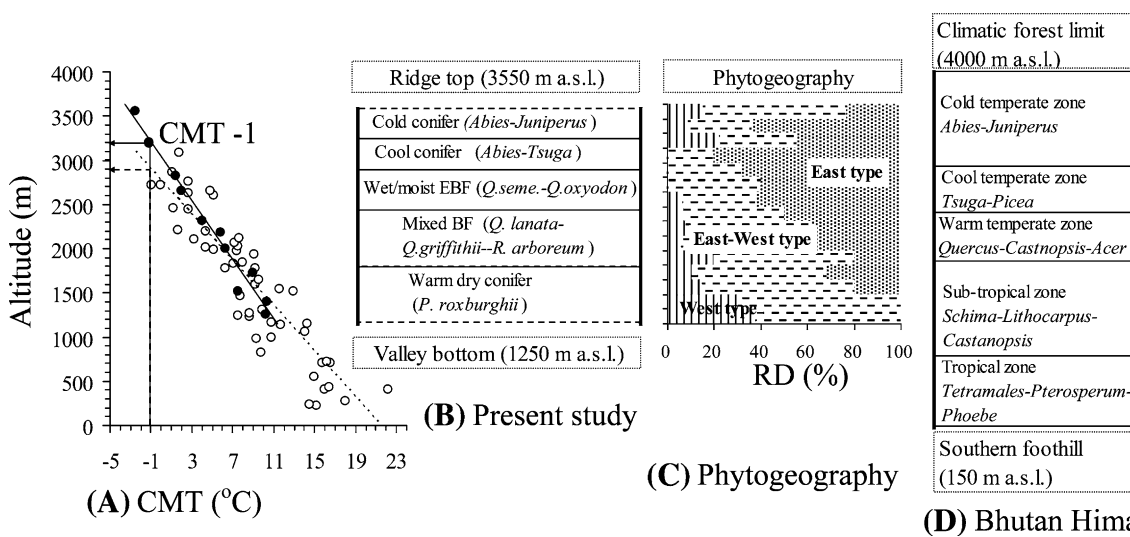


Figure 9. Climatic and floristic comparison between the dry valley slopes and the whole Bhutan Himalaya, (A) coldest months mean temperature, closed circle for dry valley series and open circle for the whole Bhutan Himalaya, (B) forest zones along the dry valley slopes, (C) phytogeography, and (D) forest zones of the Bhutan Himalaya.

broad-leaved forest in South and East Asian mountains (Ohsawa 1990) coincided at 3200 m a.s.l. along the dry valley slopes while at 2900 m a.s.l. along the humid slopes of the Bhutan Himalaya. An altitudinal difference of ca. 300 m may partly be related to the effect of temperature inversion at 2000 m a.s.l. by influencing mild winter temperature at higher altitude favoring upper extension of evergreen broad-leaved species as has been clarified in the

present study (Figure 9A). Above 2950 m, the relative basal area was predominated by huge, emergent conifers (*T. dumosa* and/or *A. densa*) among the evergreen broad-leaved sub-canopy (*Q. semecarpifolia*, *Litsea* sp. and *Ilex* spp.), thus the physiognomy of the forest itself exhibited coniferous appearance in the case of the Himalaya, though the closed sub-canopy were still dominated by evergreen broad-leaved trees.

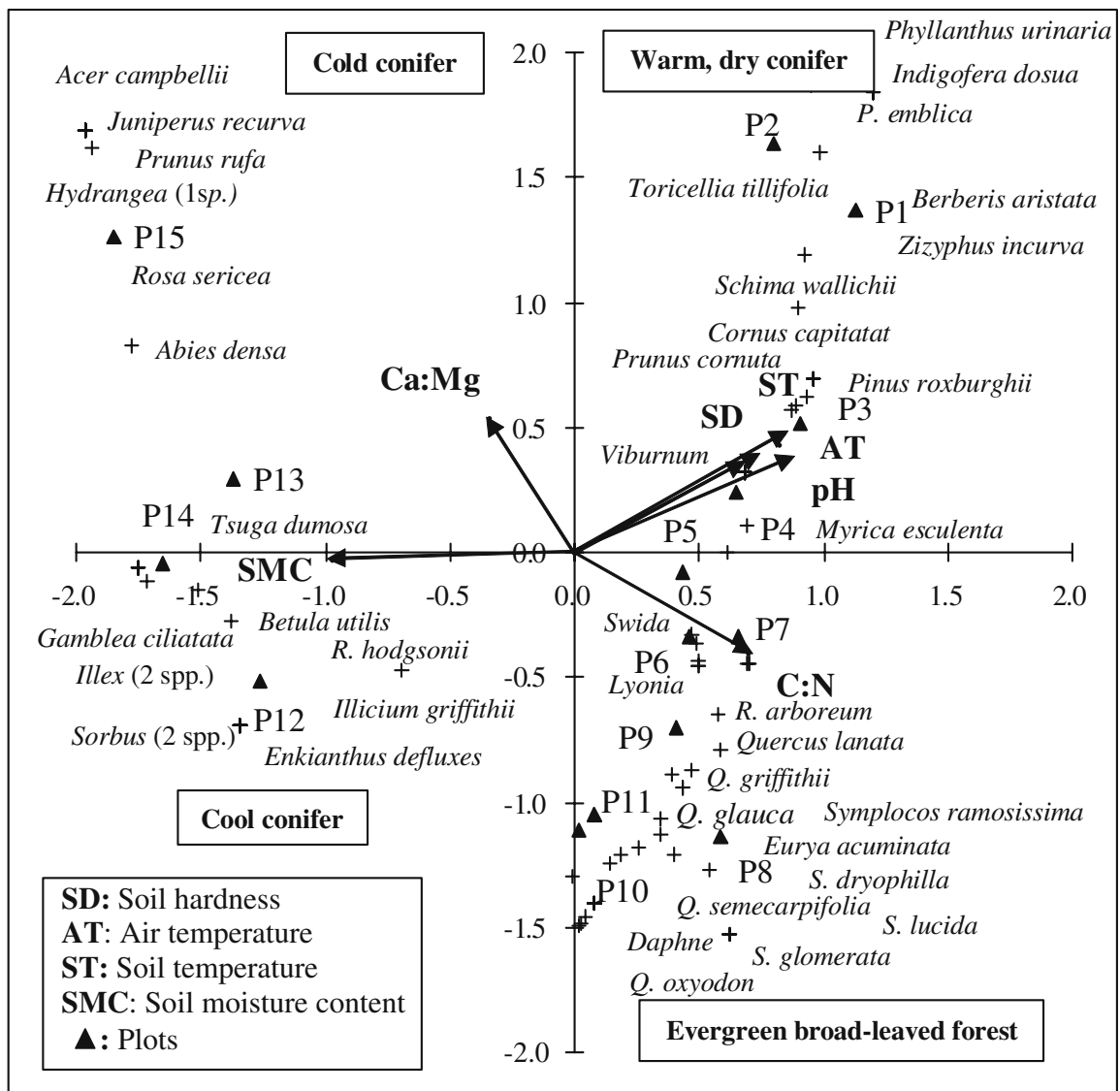


Figure 10. Biplot of 83 tree species and 7 environmental variables from CCA analysis combining vegetation information and environmental variables of soil hardness (SD), Soil (ST) and air temperature (AT), soil moisture content (SMC), soil pH, and soil C/N along the altitudinal gradients (1250–3350 m a.s.l.).

Table 2. Correlations for the seven environmental variables as a result of CCA analysis.

Variable	Correlations		
	Axis 1	Axis 2	Axis 3
Air temperature (AT)	0.82	0.41	-0.24
Soil temperature (ST)	0.84	0.45	-0.19
Soil hardness (SD)	0.73	0.37	0.17
Soil pH (pH)	0.86	0.36	0.22
Soil Ca:Mg	-0.34	0.51	0.04
Soil moisture content (SMC)	-0.96	-0.03	0.21
Soil C:N ratio	0.70	-0.39	0.28
Eigenvalue	0.94	0.75	0.42
% variance explained	21.90	17.30	9.80
Cumulative % explained	21.90	39.20	48.90
Pearson correlation (Spp.-Env)	0.99	0.96	0.86

Species preference, community structure and environmental variables

Canonical correspondence analysis (CCA) was used to determine the relationship between vegetation and environmental factors along the altitudinal gradient (Figure 10, Table 2).

The biplot showed clear pattern of species distribution with various groupings of species emerging. Species of the dry and/or open habitat (*Phyllanthus*, *Toricellia*, *Berberis*, *Glochidion*, *Pinus*, and *Rubus*) were shown to the right side of axis 1 while species of humid, mesic habitat (*Abies*, *Juniperus*, *Tsuga*, *Acer*, and *Gamblea*) were shown to the left side of axis 1. The evergreen broad-leaved species (*Quercus*, *Symplocos*, *Eurya*, *Myrsine*, *Myrica*, and *Ilex*) occurred to the lower right side of axis 2. The length of each arrow showed the magnitude of environmental factor's effect on the vegetation distribution.

Soil moisture had the longest arrow length indicating high effectiveness on the vegetation distribution followed by soil and air temperature (Figure 10, Table 2). Soil hardness and Ca/Mg ratio had the shortest arrow length thus signifying low effect on the vegetation distribution along the altitudinal gradient.

The above groupings of dry and mesic habitat species were closely related to the environmental factors. The species of dry habitat appeared in high pH, compacted soil, and under high air and soil temperature. The evergreen broad-leaved species tend to perform better under high C/N ratio and was least affected by other factors indicating low

turnover and/or high productivity of litters due to dominance of evergreen broad-leaved species (mainly Fagaceae, Symplocaceae, Theaceae and Ericaceae). On the other hand humid, mesic species mainly upper conifers (*Abies*, *Tsuga*, and *Juniperus*) and deciduous trees (*Gamblea*, *Sorbus*, *Acer*, and *Betula*) appeared under high soil moisture content and low Ca/Mg ratio (Figure 10, Table 2). The position of each environmental arrow with respect to each axis indicated its correlation with that factor. Soil water content was highly correlated to the left side of the first axis and confirmed by the strong correlation of -0.96 (Table 2).

Soil moisture can explain the trend of forest structural traits such as height, and diameter. Maximum height of tree in a closed canopy in general indicated approximately the biomass accumulation. Kimmins (1987) used soil and moisture conditions to evaluate site index using vegetation height, and found that soil and moisture variables were able to account for 81% of the variability in vegetation height (site index). Ohsawa (1995) showed the difference in altitudinal changes of tree height between tropical and temperate humid mountains. In tropical mountains tree height decreased along the increasing altitude whereas in the temperate mountains tree height did not show appreciable change except at around the forest limit. On the contrary, the tree height increased with altitude along the climatically dry valley slope indicating soil moisture as the limiting factor for tree height (cf. Figure 7A, D). In tropical and temperate humid mountains, temperature sum showed significant relationship with tree height however along the dry valley slopes moisture was found to be the determinant factor. This contrasting structural trait of tree height features one of the unique characteristics of the climatically dry valley vegetation.

The concave patterns of tree height, basal area, and biomass have been reported in Nepal Himalaya (Yoda 1968; Ohsawa 1983) and Kumaun Himalaya (Singh et al. 1994). Similarly the present study observed high basal area at ca. 3000 m in the *Tsuga-Abies* forest and low basal area at 1520 m in the *P. roxburghii* forest coinciding with the dry valley ecosystem. Hence, clarifying the low basal area of pine forest as a result of low soil moisture content in the typical dry valley with occasional human use that contributed to the concave pattern of basal area distribution in the Himalayas.

Comparing forest zones with other parts of the Himalayas

The altitudinal forest zones of the dry valley slopes were compared with those from much wider, humid slopes of the Bhutan Himalaya and phytogeography of the species from west to east Himalayas (Stainton 1972; Polunin and Stainton 1984; Ohsawa 1987a, 1992; Grierson and Long 1983–2000) (Figure 9).

The comparisons of dry valley forest zones with other parts of Himalayas are interesting because even in the midst of humid eastern Himalaya, there are occurrences of dry west Himalayan elements. The most prominent example is *P. roxburghii*, a west Himalayan element appeared along the climatically dry valleys in the midst of humid eastern Himalaya and usually made a mono-dominant canopy (Stainton 1972). The pure stands of *P. roxburghii* forest zones (1520–2000 m) in the present study corresponded to the subtropical zone of *Castanopsis hystrix*, *C. tribuloides*, *Schima wallichii* and *Exbucklandia populnea* of the humid slopes of the Bhutan Himalaya (Figure 9B, D). This forest zone also coincided with the *P. roxburghii*–*P. excelsa* forest zones of the west Nepal Himalaya (Stainton 1972). *Q. lanata* and *Q. incana* were often mixed into understorey of seral pine forest and became successor of the pioneer/seral pine forests in the east and south facing slopes of the humid eastern Himalaya (Stainton 1972; Ohsawa et al. 1986; Ohsawa 1987b, 1991a). Whereas in the dry extreme of this series only *P. roxburghii* can grow persistently in a site where the volumetric soil moisture content ranged between 16.9 and 21.9% and no successor along the successional time course because of low habitat potential (e.g. limited by the amount of soil moisture and nitrogen) as discussed by Ohsawa (1987b). Thus, clarifying that *P. roxburghii* zone in the Bhutan Himalaya represented the outpost of dry west Himalayan type of vegetation and featured special characteristics of the climatically dry valley (Figure 9B, C).

The altitudes of 2000 m in the western Nepal Himalaya (Stainton 1972) and of 1850 m in Murree, Northern Pakistan (Ohsawa 1991b) are the observed direct transition altitudes from *P. roxburghii* to *P. excelsa* (syn. *P. wallichiana*) which extended further up to 3000 m a.s.l.. On

the contrary, in the present study, the transition of *P. roxburghii* was directly to a mixed broad-leaved forest of *Q. lanata* (West Himalayan element) and *Q. griffithii* (deciduous East Himalayan element) (Figure 9B). The broad-leaved species of *Q. lanata* and *Q. griffithii* replaced *P. roxburghii* canopy at 2000 m under increased higher soil moisture level (21.9–31.7%) (cf. Figure 5). Thus, in the present series these three species having similar potential altitudinal distribution range (equi-thermal species) segregated into different altitudes choosing respective, favorable moisture conditions exhibited along altitudes. The dominant species of a mixture of East Himalayan deciduous and West Himalayan evergreen broad-leaved trees are found to be unique feature of the climatically dry valley of Bhutan. Not many studies are conducted on forest having deciduous oak (*Q. griffithii*) as dominants in other parts of the Himalayan region.

Conclusion

Forest zonation along the altitudinal and environmental gradients are the basic ecological information for better conservation and management of mountain forest ecosystems in the Himalayas. In the present study, we clarified that air temperature and soil moisture content are inversely correlated, and are the major environmental factors for the forest tree distribution and the structural changes of the forest along the altitudinal gradient in the dry valley slopes of the Bhutan Himalaya. Low soil moisture content restricted the broad-leaved trees below 1650 m a.s.l. and thus light demanding pine can dominate in the lower valley bottom. On the other hand, coldest month's mean temperature of -1°C limits the upslope extension of evergreen broad-leaved species above 3000 m a.s.l. favoring the upper conifers to dominate. Accordingly the mid-altitudes in between were co-dominated by both western evergreen (*Q. lanata*) and eastern deciduous (*Q. griffithii*) broad-leaved species under the transient soil moisture and temperature conditions. The diverse transitional forests of both west and east Himalayan elements were sandwiched between west Himalayan type of *P. roxburghii* forest and east Himalayan type of *Abies-Tsuga* forests.

Appendix A1. Plot details and floristic composition of the study plots (1520–3370 m.a.s.l.). Species are arranged by life-form groups (coniferous, evergreen broad-leaved trees and shrubs, deciduous broad-leaved trees and shrubs). TBA refers to total basal area.

Plot number	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	Total
Altitude (m)	1520	1650	1760	1860	2000	2020	2250	2430	2540	2640	2820	2950	3210	3305	3370	
Aspects (Degree)	S94E	E	S95E	E	N51E	N51E	N50E	N50E	N50E	N50E	E	N88E	SS200	N88E	SSE156	
Inclination (degree)	29°	11°	17°	35°	15°	28°	23°	28°	17°	25°	15°	15°	32°	13°	22.6°	
Plot size (m ²)	600	800	800	400	200	800	600	600	800	400	600	400	400	400	400	
Total Ba/ha (m ² /ha)	15.2	15.7	40.3	47.1	65.3	63.8	68.7	60.4	60.4	68.2	92.6	145.6	134.4	108.8	101.7	1088.3
Max ht. (m)	14.6	22.0	21.5	22.6	22.5	21.0	28.0	21.0	26.3	24.0	30.0	47.0	43.0	35.0	33.0	
Max. DBH (cm)	35.5	56.5	77	51	54	66	85.5	61	102	72	95	103	90	94	132.5	
Species no./plot	7	10	20	20	9	18	13	14	17	11	18	9	8	10	11	83
No. of dominants/plot	1	1	2	4	2	4	3	3	4	1	3	2	2	3	2	
Diversity (H')	0.1	0.3	1.7	2.6	1.3	1.5	2.4	2.0	2.9	1.6	2.6	0.6	1.6	2.2	1.3	
Evenness (H)	0.0	0.1	0.5	0.6	0.4	0.4	0.7	0.5	0.7	0.5	0.6	0.2	0.7	0.5	0.4	
Relative Basal Area (%)	RBA	RBA	RBA	RBA	RBA	RBA	RBA	RBA	RBA	RBA	RBA	RBA	RBA	RBA	RBA	TBA
CONIFEROUS TREES																
<i>Pinus roxburgii</i>	98.4	95.3	61.0	20.2	0.0	0.0	0.0	3.1	0.0	0.0	12.7	92.1	89.9	52.4	95.5	486.8
<i>Pinus wallichiana</i>								3.1								64.1
<i>Taxus baccata</i>											8.6		0.6			1.9
<i>Tsuga dumosa</i>											4.1					8.7
<i>Abies densa</i>												92.1	59.8	12.1		231.4
<i>Juniperus recurva</i>													27.1	40.2	55.0	136.1
Sub-total													2.5		40.5	44.6
EVERGREEN BROAD-LEAVED TREES																
<i>Glochidion velutinum</i>	0.0															0.0
<i>Rhododendron arboreum</i>																162.1
<i>Quercus lanata</i>																125.2
<i>Schinus molle</i>																0.1
<i>Myrsine semiserrata</i>																4.9
<i>Rapanea capitellata</i>																0.0
<i>Symplocos lucida</i>																0.0
<i>Castanopsis hystrix</i>																2.4
<i>Acer oblongum</i>																0.0
<i>Quercus thomsoniana</i>																0.0
<i>Quercus glauca</i>					0.5	0.1	6.3	0.0	1.2	13.7	0.8					10.5
<i>Myrica esculenta</i>																4.4
<i>Symplocos sumunita</i>							0.2	1.4								1.0
<i>Symplocos dryophila</i>								2.0	1.6							2.2
<i>Symplocos glomerata</i>								0.1	0.2	0.1	0.1					0.2
<i>Symplocos ramosissima</i>								0.0	6.2	1.2	4.9					9.2

Appendix A1. Continued

Plot number	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	Total
Altitude (m)	1520	1650	1760	1860	2000	2020	2250	2430	2540	2640	2820	2950	3210	3305	3370	
<i>Michelia doltsopa</i>									4.1							2.5
<i>Ilex dipyrrena</i>									0.0	2.4	0.4					2.0
<i>Quercus semecarpifolia</i>										68.6	44.8					88.2
<i>Quercus oxydon</i>										0.5	3.6					4.2
<i>Rhododendron hodgsonii</i>											1.3		1.1		0.1	2.8
<i>Litsea albenscens</i>											0.0					0.0
<i>Rhododendron falconeri</i>												2.8				0.0
<i>Rhododendron barbatum</i>												2.6	0.0	26.8		4.0
Sub-total	0.0	0.0	30.1	52.4	94.8	90.4	60.4	71.9	56.8	94.3	76.3	5.4	8.4	26.8	0.1	458.9
EVERGREEN BROAD-LEAVED SHRUBS																
<i>Berberis aristata</i>	1.1	2.1	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0						0.7
<i>Viburnum cylindricum</i>		0.0	0.6	5.3	0.3	0.3	0.1	0.3			1.1					4.4
<i>Coriaria nepalensis</i>				2.3												1.1
<i>Daphne bhola</i>					0.0	0.0	0.1		0.0	0.1					0.0	0.1
<i>Gaultheria fragrantissima</i>					0.0											0.0
<i>Ardrisia microphylla</i>						0.0										0.0
<i>Eurya acuminata</i>							1.3	1.4	7.3	4.7	0.0					9.5
<i>Campylotropis spiciosa</i>							0.0					1.0				0.0
<i>Ilex hookeri</i>												0.7				1.5
<i>Ilex macrophylla</i>												0.3				1.0
<i>Illicium griffithii</i>																0.5
Sub-total	1.1	2.1	0.9	7.8	0.3	0.3	1.5	1.8	7.3	4.8	1.1	2.1	0.0	0.0	0.0	18.8
DECIDUOUS BROAD-LEAVED TREES																
<i>Lyonia ovalifolia</i>			6.3	8.9	4.9	6.7	16.6	2.1	5.0	0.9	5.7	0.4		2.0		38.5
<i>Benthamidia capitata</i>			1.0	0.5												0.7
<i>Quercus griffithii</i>			0.0	10.2	1.5	21.3	21.0	24.8								48.1
<i>Rhus chinensis</i>			0.3	0.0	0.0											0.1
<i>Prunus cornuta</i>			0.2													0.1
<i>Carpinus viminea</i>			0.0		0.8											0.5
<i>Prunus rufa</i>			0.0	0.0											0.0	0.0
<i>Corylus faginea</i>			0.0													0.0
<i>Sorbus sp.</i>					0.3		0.2									0.2
<i>Swida oblonga</i>									5.9							0.1
<i>Betula alnoides</i>											2.2					13.9
<i>Gamblea ciliata</i>											1.4		1.7	9.5		0.6
<i>Magnolia campbellii</i>											0.7					0.0

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