THE BOTANICAL REVIEW

VOL. 53 JANUARY–MARCH, 1987 NO. 1

Forest Vegetation of the Himalaya

J. S. SINGH[1] AND S. P. SINGH[2]

[1]Department of Botany
Banaras Hindu University
Varanasi 221005, India
[2]Department of Botany
Kumaun University
Naini Tal 263002, India

Copies of this issue [53(1)] may be purchased from the Scientific Publications Department, The New York Botanical Garden, Bronx, NY 10458-5126 USA. Please inquire as to prices.

The Botanical Review 53: 80–192, Jan.–Mar., 1987

© 1987 The New York Botanical Garden

I. Abstract

This review deals with the forest vegetation of the Himalaya with emphasis on: paleoecological, phytogeographical, and phytosociological aspects of vegetation; structural and functional features of forest ecosystem; and relationship between man and forests.

The Himalayan mountains are the youngest, and among the most unstable. The rainfall pattern is determined by the summer monsoon which deposits a considerable amount of rain (often above 2500 mm annually) on the outer ranges. The amount of annual rainfall decreases from east to west, but the contribution of the winter season to the total precipitation increases. Mountains of these dimensions separate the monsoon climate of south Asia from the cold and dry climate of central Asia. In general, a rise of 270 m in elevation corresponds to a fall of 1°C in the mean annual temperature up to 1500 m, above which the fall is relatively rapid.

Large scale surface removals and cyclic climatic changes influenced the course of vegetational changes through geological time. The Himalayan ranges, which started developing in the beginning of the Cenozoic, earlier supported tropical wet evergreen forests throughout the entire area (presently confined to the eastern part). The Miocene orogeny caused drastic changes in the vegetation, so much so that the existing flora was almost entirely replaced by the modern flora. Almost all the dominant forest species of the Pleistocene continue to maintain their dominant status to the present. Presently the Himalayan ranges encompass Austro-Polynesian, Malayo-Burman, Sino-Tibetan, Euro-Mediterranean, and African elements. While the Euro-Mediterranean affinities are well represented in the western Himalayan region (west of 77°E long.), the Chinese and Malesian affinities are evident in the eastern region (east of 84°E long.). However, the proportion of endemic taxa is substantial in the entire region.

A representation of formation types in relation to climatic factors, viz., rainfall and temperature, indicates that boundaries between the types are not sharp. Formation types often integrate continuously, showing broad overlaps. Climate does not entirely determine the formation type, and the influence of soil, fire, etc., is also substantial. The ombrophilous broad leaf forests located in the submontane belt (< 1000 m) of the eastern region are comparable to the typical tropical rain forests. On the other extreme, communities above 3000 m elevation are similar to sub-alpine and alpine types. From favorable to less favorable environments, as observed with decreasing moisture from east to west, or with decreasing temperature from low to high elevations, the forests become increasingly open, short-statured and simpler, with little vertical stratification. Ordination of forest stands distributed within 300–2500 m elevations of the central Himalaya, by and large indicates a continuity of communities, with scattered centers

of species importance values in the ordination field. Within the above elevational transect, sal (*Shorea robusta*) and oak (*Quercus* spp.) forests may be designated as the climax communities, respectively, of warmer and cooler climates. The flora of a part of the central Himalayan region is categorized as therohemigeophytic and that of a part of the western Himalayan region as geochamaephytic.

An analysis of population structure over large areas in the central Himalaya, based on density-diameter distribution of trees, suggests that old-growth forests are being replaced by even-aged successional forests, dominated by a few species, such as *Pinus roxburghii.* Paucity of seedlings of climax species, namely *Shorea robusta* and *Quercus* spp. over large areas is evident.

The Himalayan catchments are subsurface-flow systems and, therefore, are particularly susceptible to landslips and landslides. Loss of water and soil in terms of overflow is insignificant.

Studies on recovery processes of forest ecosystems damaged due to shifting cultivation or landslides indicate that the ecosystems can recover quite rapidly, at least in elevations below 2500 m. For example, on a damaged forest site, seedlings of climax species (*Quercus leucotrichophora*) appeared only 21 years after the landslide.

In the central Himalaya, the biomass of a majority of forests (163–787 t ha^{-1}) falls within the range (200–600 t ha^{-1}) given for many mature forests of the world, and the net primary productivity (found in the range of 11.0–27.4 t ha^{-1} yr^{-1}) is comparable with the range of 20–30 t ha^{-1} yr^{-1} given for highly productive communities of favorable environments. In most of the forests of this region, the litter fall values (2.1–3.8 t C ha^{-1} yr^{-1}) are higher than the mean reported for warm temperate forests (2.7 t C ha^{-1} yr^{-1}). Of the total litter, the tree leaves account for 54–82% in the Himalayan forests.

The rate of decomposition of leaves in some broadleaf species of submontane belt (0.253–0.274% day^{-1}) are comparable with those reported for some tropical rain forest species. Because of the paucity of microorganisms and microarthropods in the forest litter and soil, high initial C:N ratio and high initial lignin content in leaves, the rate of leaf litter decomposition in *Pinus roxburghii* is markedly slower than in other species of the central Himalaya. The fungal species composition of the leaf litter of *Pinus roxburghii* is also distinct from those of other species.

A greater proportion of nutrients is accumulated in the biomass component of the Himalayan forests than in the temperate forests. Although litter fall is the major route through which nutrients return from biomass to the soil pool, a substantial proportion of the total return is in the form of throughfall and stemflow. Among the dominant species of the central

Himalaya, retranslocation of nutrients from the senescing leaves was markedly greater in *Pinus roxburghii* than in *Quercus* spp. and *Shorea robusta.* Consequently, the C:N ratio of leaf litter is markedly higher in *Pinus roxburghii* than in the other species. Immobilization of nutrients by the decomposers of the litter with high C:N ratio is one of the principal strategies through which *Pinus roxburghii* invades other forests and holds the site against possible reinvasion by oaks.

Observations on the seasonality of various ecosystem functions suggest that Himalayan ecosystems are geared to take maximum advantages of the monsoon period (rainy season).

Most of the human population depends on shifting-agriculture in the eastern region and on settled agriculture in the central and western regions. Either of these is essentially a forest-dependent cultivation. Each unit of agronomic energy produced in the settled agriculture entails about seven units of energy from forests. Consequently, forests with reasonable crown cover account for insignificant percentage of the land. Tea plantations and felling of trees for timber, paper pulp, etc., are some of the major commercial activities which adversely affected the Himalayan forests.

Résumé

Cette revue concerne la végétation forestière de l'Himalaya. Elle précise l'information concernant la paléoécologie, la phytogéographie, la phytosociologie, le structure et le fonctionnement des écosystèmes et le rapport entre l'homme et la forêt.

Les montagnes de l'Himalaya sont les plus jeunes et parmi les plus instables. La pluviométrie dépend surtout de la mousson d'été et les chaînes extérieures sont bien arrosées (>2500 mm par an). Les précipitations annuelles décroissent de l'Est vers l'Ouest tandis que la composante hivernale augmente. Ces montagnes séparent les climats de mousson de l'Asie du Sud des climats froids et secs de l'Asie Centrale.

L'érosion du sol sur une grand étendue et des changemenets cycliques du climat ont déterminé des changements dans le couvert végétal tout au long des temps géologiques. Les chaînes Himalayennes qui ont commencés leur soulèvement au commencement du coenozoïque étaient entièrement couvertes d'une forêt ombrophile tropicale. (Ce type se trouve encore de nos jours dans la partie orientale de l'Himalaya.) L'orogénie miocène provoqua de tels changements dans la végétation que la flore de cette époque a été entièrement remplacée par la flore moderne. Les espèces forestières dominantes du pleistocène gardent leur importance dans les forêts actuelles.

Des éléments floraux Austro-Polynésiens, Malais-Birmans, Sino-Ti-

betains, Euro-Méditerranéens et Africains sont actuellement présents sur les montagnes himalayennes. Tandis que les affinités Euro-Mediterranéennes sont bien représentées dans l'Himalaya occidental (à l'Ouest du 77° Est), les affinités Chinoises et Malaises sont évidentes dans la partie orientale (à l'Est de 84°E). Cependant la proportion des éléments endémiques est importante dans toute la région.

La relation entre les types de formations et les facteurs climatiques (pluviosité, température) indique que les limites entre les types sont approximatives. D'ailleurs, le climat lui même ne détermine pas exclusivement les types et les effets du sol, du feu, etc., peuvent être importantes. Les forêts feuillues ombrophiles localisées dans l'étage sous-montagnard (< 1000 m) de la région orientale sont comparables aux forêts ombrophiles tropicales typiques. A l'opposé les communautés qui se trouvent au-dessus de 3000 m d'altitude sont comparables aux types subalpins et alpins. En allant des conditions favorables vers le moins favorables soit par exemple d'Est en Ouest le long de l'axe de diminution des précipitations soit en suivant les gradient altitudinal de baisse des températures les forêts deviennent de plus en plus ouvertes, basses et structurellement simples avec peu de stratification verticale. L'ordination des peuplements forestières situés entre 300–2500 m dans l'Himalaya central indique une continuité des communautés avec des centres de valeurs d'importance des espèces dispersés dans le champ d'ordination. Dans ce transect altitudinal, les forêts à sal (*Shorea robusta*) et à chêne (*Quercus* spp.) peuvent être désignés comme des communautés climax pour les climats chaud et froid respectivement.

Le spectre biologique basé sur les formes biologiques de Raunkiaer est du type Théro-Hémi-Géophytique dans l'Himalaya central tandis que celui de l'Himalaya occidental est du type Géo-Chamaephytique.

L'analyse de la structure du peuplement couvrant une superficie assez importante dans l'Himalaya central basé sur la répartition des arbres par densité-diamètre suggère que les anciennes forêts sont en train d'être remplacées par des forêts équiennes de succession, dominées par un petit nombre d'espèces, tel que *Pinus roxburghii.* La mauvaise régénération des espèces climax, à savoir le sal (*Shorea robusta*) et le chêne (*Quercus*) sur une aire assez vaste est un fait bien établi.

Les bassins versants de l'Himalaya sont du type à l'écoulement hypodermique et sont donc sensibles aux glissements de terrain. La perte d'eau et de sol en terme d'épanchement est peu important.

L'étude de la reconstitution des écosystèmes forestiers dégradés par les cultures itinérantes ou par les glissements de terrain montre que les écosystèmes endommagés peuvent se reconstituer assez rapidement au moins en dessous de 2500 m.

Par exemple, sur un site forestière dégradée, les plantules de l'espèce climax (*Quercus leucotrichophora*) sont réapparues seulement 21 ans après le glissement du terrain.

Dans l'Himalaya central, la biomasse de la majorité des forêts (163–783 t ha^{-1}) tombe dans la classe de la plupart des forêts du monde (200–600 t ha^{-1}) et la productivité nette primaire (11.0–27.4 t ha^{-1} an^{-1}) est comparable à celle des meilleures forêts (20–30 t ha^{-1} an^{-1}) soumises à des conditions favorables. Les valeurs de la chute de litière des forêts de cette région (2.1–3.8 t C ha^{-1} an^{-1}) sont plus élevées que la moyenne de celles des forêts tempérées chaudes (2.7 t C ha^{-1} an^{-1}). La contribution des feuilles d'arbre à la litière totale est entre 54 et 82 pourcent dans les forêts Himalayennes.

Le taux de décomposition des feuilles chez certains feuillus de l'étage sous-montagnard (0.253–0.274% par jour) est comparable à celui de certaines espèces de la forêt ombrophile. C'est à cause d'une pauvreté de la litière forestière et du sol en microorganismes et des microarthropodes, du rapport initial élevé C:N et du pourcentage initial élevé en lignine des feuilles, que le taux de décomposition des aiguilles de *Pinus roxburghii* est significativement plus lent que chez les autres espèces de l'Himalaya central. D'ailleurs la composition de la flore fongique de la litière des aiguilles de *Pinus roxburghii* est bien différente de celles des autres espèces.

Une plus grande proportion d'éléments biogéochimiques est accumulée dans la composante biomasse des forêts Himalayennes par rapport aux forêts tempérés.

Bien que la chute du litière constitue la voie principale par laquelle les éléments de la biomass retournent au sol, une fraction assez importante est restituée sous formes de pluviolessivats et d'écoulements sur le tronc.

Parmi les espèces dominantes d l'Himalaya central, la redistribution des éléments des feuilles senescentes est plus important chez *Pinus roxburghii* que chez *Shorea* ou *Quercus*. Par conséquent, le rapport C:N de la litière de feuille est plus élevé chez le pin que chez les autres espèces. L'immobilisation des éléments par les décomposeurs de la litière à rapport C:N élevé est une des stratégies principales par laquelle *Pinus roxburghii* envahit les autres forêts et évite la reconquête par les autres espèces.

L'étude saisonnière des divers fonctionnements de l'écosystème met en évidence des liens étroits avec la régime des pluies de mousson.

La majorité de la population humaine pratique la culture itinérante dans la région orientale et l'agriculture sédentaire dans les parties central et occidentale. Ces deux types d'agriculture sont très liés à la forêt. Chaque unité d'énergie agronomique produite en agriculture sédentaire demande sept unités d'énergie des forêts. Par conséquent, les forêts peu ouvertes à canopées assez fermées n'occupent plus qu'un pourcentage négligeable de

ces régions. Les plantations de thé et l'exploitation forestière (bois d'oeuvre, pâte à papier, etc.) sont parmi les activités qui ont contribué à degrader les forêts de l'Himalaya.

II. Introduction

The Himalayan ranges extend in an almost unbroken line for about 3000 km from west to east, and occupy more than ten degrees of North latitude (27–38°N). The altitude varies considerably, from about 300 m to more than 5000 m, and the climatic conditions are very diverse.

The temporal and spatial variations in physical conditions have resulted in markedly diversified phytogeographic stocks, characterized by a high degree of endemism. The species combined and recombined in time, to constitute varied forest communities, which range from species-rich broadleaf forests with trees assuming the characters generally attributed to those of humid tropical forests, to the woody scrubs often called alpine scrubs, beyond which large expanses of grasslands ensheath the mountain surfaces. According to one estimate, the ecological stages in the Himalaya correspond to latitude displacement of over 5000 km (Anonymous, 1977).

Fascinated by these diversities, European naturalists initiated expeditions to the Himalaya as early as the end of the eighteenth century, and information regarding the Himalayan plants started accumulating. Gen. Thomas Hardwick, who visited Garhwal (central Himalaya) in 1796, was perhaps the first naturalist to collect plants from the Himalaya; Hamilton was the pioneer plant explorer to visit Nepal (1802–1803); Govan was the first to collect plants from Punjab; Victor Jacquemont was the first to examine the plants of Kashmir (1831); and Sir Joseph Hooker and Thomas Thompson made the beginning botanical explorations in the eastern Himalaya (Gupta, 1981). By the mid-nineteenth century, not only was the flora of some parts known, but accounts elucidating the vegetation and climate had also been published; noteworthy were the contributions of Hooker (1852) and Thompson (1852). The establishment of organized forestry towards the later half of the nineteenth century gave impetus to the studies on forests and silviculture. This eventually led to the publication of the monumental work of Troup (1921) on the silviculture of Indian trees. Around that period some notable contributions were made to the understanding of successional patterns of forest communities of the central Himalaya (Dudgeon & Kenoyer, 1925; Kenoyer, 1921). H. G. Champion was the first to describe and classify the forests of a large portion of the Himalaya (Champion, 1936). Subsequently, interest was generated in the paleoecological aspects of the Himalayan vegetation. Establishment of universities and the emergence of ecological centers (particularly of Kumaun University in the central region, and the North-eastern Hill

University in the eastern region) around 1975 resulted in rapid accumulation of knowledge pertaining to the ecology of the Himalayan forests. Forest communities were analyzed on the basis of quantitative data on species composition, as well as on the structural and functional features of trees.

We focus, in this review, primarily on the analysis of forest vegetation (including paleoecological, phytogeographical, and phytosociological aspects), and on the structural and functional features of the forest ecosystems (including the recovery processes, seasonal periodicities of functional processes, productivity, and nutrient cycling); and explore the relationship between man and the forests.

III. Environmental Background

The Himalaya is a young mountain range, having been uplifted about 60–70 million years ago. The central axis of the Himalaya comprises crystalline rocks—gneisses and metamorphosed sediments, ranging from Pre-cambrian to as late as Miocene in age. A mass of sedimentary rocks, namely Tethys sediments, occurring north of the crystalline axis, contains well-preserved fauna and flora (Cambrian–Eocene). These sedimentary rocks were deposited in shallow marine basins. To the south of the crystalline axis occur mixed zones of sedimentary and metamorphic rocks which are highly folded and faulted. The north contact of the sediments with the central crystalline, is a well-marked tectonic feature—the Main Central Thrust—along which the crystallines are thought to have partially moved over the sedimentary zone. Similarly, the southern boundary of this zone is marked by another major tectonic feature, known as the Main Boundary Fault. Details of geology are given by Patriat and Achache (1984), Raina et al. (1980), Roy Chowdhury (1973), Valdiya (1970), and Wadia (1936, 1937, 1963).

Tucker (1983) has described the Himalayan landforms. Along the southern edge of the Himalaya, the mountains rise abruptly from the alluvial plains. The Siwaliks, the first mountains (10–50 km wide) stand 500–1200 m. Behind them lie numerous transverse valleys. Beyond these valleys is the outer Himalaya, where northwest to southeast ranges rise sharply to 2500 m and above. The Himalayan river gorges provide only occasional, difficult access routes to the inner mountains. Beyond the outer ranges, lie another series of valleys then, finally, their headwaters in the glaciers and permanent snows of the greater Himalaya, where many peaks rise beyond 5000 m.

Between the deep alluvial Gangetic plains and the Siwaliks, a thin belt of "bhabar" towards the hills and of "tarai" towards the plains are recognizable. The bhabar is a belt (15–250 km wide) of talus gravel slopes deposited by the Himalayan rivers over the millenia. For much of the year the streams subside beneath the bhabar, emerging again to carry finer alluvial silts more slowly into the tarai, the plain of high water table. The rivers emerge again in the tarai, which was marshy until agriculture began in a big way in the 1950's.

These youngest and loftiest of mountains are also the most susceptible to landslips and erosion, owing to the presence of residual stresses and the highly compressed and tectonized rocks. Extremely varied rock formations are shattered into intricate and unstable striations, and therefore the threat of landslips and earthquakes is constant.

Mountains of these dimensions have resulted in the dividing of the monsoon climate of South Asia from the cold dry climate of Central Asia. From mid-June to September the monsoon storms generally deposit 700–4500 mm of rain on the slopes of the outer Himalaya. The southern slopes receive more of it than the northern slopes. The heavy monsoon clouds do not penetrate beyond the great Himalaya, north of which is one of the planet's greatest rain shadow regions, the Tibetan plateau. As shown in Figure 1 the pattern of rainfall varies from east to west. The proportion of winter rain is comparatively much higher in the westernmost region (up to 46% of annual rainfall) than in the rest of the Himalaya (less than 20%). Because of this, the climate of Kashmir resembles that of the Mediterranean region. With the exception of this region, about two-thirds to three-fourths of the annual rainfall is received during the rainy season (later summer), which commences earlier (May) in the eastern region than in the central and the western regions (June). The dry period is shorter in the eastern part, since in this region the monsoon recedes later (in October) than in other regions (mid-September). The summer is thus divisible into an earlier dry and warm period, usually referred to as the summer season, and a wet and warm period, referred to as the rainy season. The annual rainfall declines from east to west. For example, between 1500 and 2000 m elevations it may be more than 4000 mm in the eastern region, about 2000 mm in the central region and less than 1000 mm in the western region.

In general, a rise of 270 m in altitude corresponds to a fall of 1°C in the mean temperature up to about 1500 m, above which the fall is more rapid. Details of climate are given in Hill (1976), Kaushik (1962), Rao (1980), and others.

Dhir (1967), Ghildyal (1980), Mukerji and Das (1940, 1941), Murthy and Pandey (1980), Raychaudhri et al. (1963), and others have studied the Himalayan soils. The major soil groups in the region are Palehumults (brown hill soils), Hapludalfs (submontane soils), Cryoborolls (mountain meadow soil), Lithic Entisols (skeletal soil), Paleustalfs, Rhodustalfs, and Haplustalfs (red loamy soils) (Murthy & Pandey, 1980). Members of or-

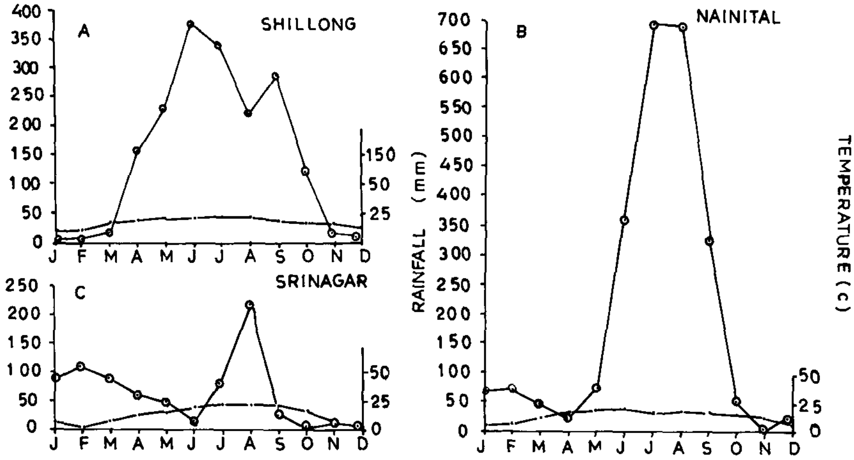

Fig. 1. Ombrothermic diagram for three representative localities: A. Shillong, eastern Himalaya (developed from data in Boojh & Ramakrishnan, 1981); B. Naini Tal, Central Himalaya (after J. S. Singh & Singh, 1984b); C. Srinagar, western Himalaya (developed from data in Zutshi & Vass, 1978).

thents, fluvents, and orchrepts are also found. Brown hill soils have developed from the Tertiary sedimentaries comprising sandstone, shale, and micaceous grey sandstone between 600 and 700 m elevation with an average annual rainfall of 800 to 2000 mm. The texture varies from loam to silty clay loam. The pH varies generally from 6 to 7.6. Percentages of organic carbon and nitrogen in the soil range from 0.7 to 4.0% and 0.02 to 0.46%, respectively (Singh & Singh, 1984a).

Submontane soils have developed under conditions of high rainfall and complex geological and geomorphological formations. Generally, the soils are acidic with a pH of 5. The percentages of organic matter and nitrogen vary from 1.5 to 3.0% and 0.1 to 0.3%, respectively. The mountain meadow soils are shallow to moderately deep and immature. They suffer from moisture deficiency resulting from prolonged drought, wind erosion, and snow action. The skeletal soils are very shallow and badly affected by wind erosion. Paleustalfs, Rhodustalfs, and Haplustalfs occur in association with one another in the upper slopes where the soils are freely drained.

IV. Phytogeography and Paleo-history

A. PHYTOGEOGRAPHY

Phytogeography of the Himalayan region generated much interest right from the beginning of this century or even before, when floristic studies were initiated. A number of publications (e.g., Blasco, 1970, 1971a, 1971b, 1977; Burkill, 1924; Chatterjee, 1939; Croizat, 1968; Dobremez, 1972, 1973, 1977; Gupta, 1972; Hora, 1950; Kanai, 1963, 1966; Legris & Meher-Homji, 1968; Mani, 1974; Meher-Homji, 1970, 1972, 1974; Meher-Homji & Misra, 1973; Meusel, 1971; Puri, 1960a; Razi, 1955; Schweinfurth, 1957, 1968; Spate, 1967; Stainton, 1977; Tripathi & Chandra, 1972; Vishnu-Mittre, 1972) dealt with such aspects as botanical regions, affinities of taxa, discontinuous distribution of Himalayan taxa in the Indian subcontinent, and distribution of taxa within the Himalayan region. It is evident that the Himalayan ranges encompass various elements: Austro-Polynesian, Malayo-Burman, Sino-Tibetan, Euro-Mediterranean, and African. The Himalaya has acted as a bridge in many cases, facilitating the flux of various taxa, but also as a barrier, promoting endemism. For example, about 29% of the endemic taxa of the Indian dicotyledonous flora occurs in these mountains. According to Jain and Sastry (1980), about 4000 species, which account for about half of the higher plant species documented from the Himalaya, are endemic. The important families which make up most of the endemic flora of the Himalaya are Brassicaceae (87 endemic species), Caryophyllaceae (57 species), Rubiaceae (170 species), Asteraceae (102 species), Asclepiadaceae (73 species), Acanthaceae (188 species), and Euphorbiaceae (119 species) (Chatterjee, 1939).

1. Botanical Regions

Earlier workers (Clarke, 1898; Hooker, 1906) recognized two botanical regions, viz., the western and the eastern Himalaya. Later workers (Chatterjee, 1939; Razi, 1955) identified four regions. The third region, common to these later classifications, was the central Himalaya. The fourth region was Assam in Chatterjee's (1939) and north-east India in Razi's (1955) classification. The latter region includes plains as well as mountains. For the sake of simplicity, we recognize three major botanical regions, viz., the western, the central, and the eastern Himalaya including the mountains of north-eastern India and Assam. Roughly, the mountain ranges west of 77°E long. fall within the western region (Kashmir, Punjab, and Himachal Pradesh), between 77° and 84°E long. in the central region (mountains of Uttar Pradesh and western Nepal) and beyond 84° E long. in the eastern region (Fig. 2).

The eastern Himalayan region supports luxuriant evergreen broadleaf forests in the lower ranges, often referred to as tropical rain forests. Compared to the western region, conifers have a low expression, and the conifer forests are generally mixed with broadleaf species. Because the impact of the Pleistocene glaciation was limited in this region, environmental conditions were relatively stable in the geological past, compared to those of the western region. Consequently, speciation was more developed; for example, the number of species of *Rhododendron* and *Quercus* in this

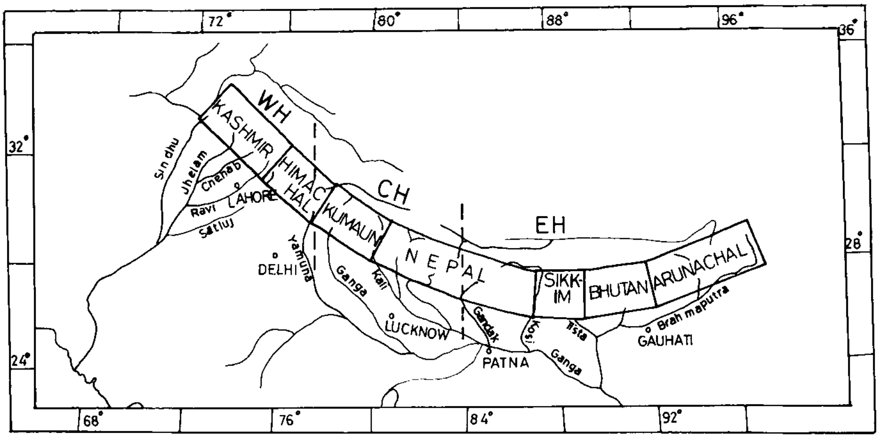

Fig. 2. Geographic subdivisions of the Himalaya following Valdiya and Bhatia (1980). The dotted lines separate western (WH), central (CH), and eastern (EH) Himalayan sectors.

region is several-fold greater than either in the central or in the western region.

Tree ferns are mostly confined to the eastern region. Epiphytes, in abundance in the eastern region, become less abundant in the central region and rare in the western region. Of particular interest is the distribution pattern of 17 cupuliferous trees (10 *Quercus* species, 4 *Castanopsis* species, and 3 *Lithocarpus* species). With the exception of two *Quercus* species, viz., *Q. ilex* and *Q. floribunda* (rather doubtful, Stainton, 1977), all are eastern or central Himalayan (Dobremez, 1977). Of the remaining eight oaks, *Q. leucotrichophora, Q. lanuginosa,* and *Q. semecarpifolia* appear to be central Himalayan, while *Q. serrata, Q. glauca, Q. griffithii, Q. lamellosa,* and *Q. lineata* var. *oxydon* are eastern Himalayan.

2. *Floristic Affinities*

The western Himalayan region shows pronounced Euro-Mediterranean affinities, and the eastern Himalayan region shows Chinese and Malesian affinities. As expected, the central Himalayan region contains a mixture of these two regions. The list of taxa that have migrated into the Himalayan region from different phytogeographical regions of the world is long. For example, in the Abor hills, located in the valley of the Dihang and Brahmaputra rivers (eastern Himalaya) alone, 529 species represent southern Chinese affinities and 261 eastern Malesian affinities (Burkill, 1924).

Some of the Mediterranean elements of the western Himalayan region are found in drier areas, where the monsoon influence is negligible, e.g., *Quercus ilex, Celtis australis,* and species of *Olea, Acer, Aesculus, Alnus, Fraxinus, Cupressus, Juniperus, Populus, Prunus,* and *Pinus.* Some of these taxa reach up to California and Eurasia. In general, Mediterranean elements do not extend eastward beyond 85°E long. *Terminalia bellerica, Bombax ceiba, Toona ciliata, Syzygium cumini, Lagerstroemia* sect. *Sibia,* and *Shorea robusta* are some of the western Himalayan species (occurring in the submontane to low montane belt) which have been designated as Malesian-Deccanian-pre-Himalayan (Meusel, 1971). These are tropical humid elements. The tropical semi-arid elements, found in the submontane belts of the western Himalaya, such as *Acacia nilotica, Dalbergia sissoo, Grewia oppositifolia,* and *Woodfordia* sp., are African-Deccanian elements. In the drier areas of the western Himalaya the Irano-Turanian elements occur quite frequently.

Engelhardtia spicata, Boehmeria platyphylla, Cassia tora, and species of *Tetrameles, Dipterocarpus, Cinnamomum, Garcinia, Machilus, Phoebe, Litsea, Adina, Schleichera, Artocarpus, Dillenia,* and *Ficus* are some of the Malayan elements found in the eastern Himalayan region. Species of *Rhododendron, Schima, Tsuga,* and *Quercus* (such as *Q. serrata, Q. glauca*), of this region are considered Sino-Japanese. *Zizyphus mauritiana* is the Indo-African representative in the region.

Elevation-wise, Sino-Japanese elements are particularly numerous at middle altitudes, and Deccan elements preponderate up to 2000 m in the Himalayan region.

3. Discontinuous Distribution of Some Trees

Some of the major tree species found in the Himalayan region exhibit the following distribution patterns within the rest of the Indian continent.

(i) More or less continuous distribution through the continent—e.g., *Terminalia tomentosa, T. arjuna, Acacia* spp., *Adina cordifolia, Syzygium cumini, Albizia* spp. These species occur in all regions with the exception of deserts.

(ii) Discontinuous distribution over large parts of the continent—e.g., *Ougeinia oojeinensis, Bombax ceiba, Careya arborea, Anogeissus latifolia* [species lists of (i) and (ii) categories refer to submontane and low montane belts of the entire Himalayan region].

(iii) Discontinuous distribution in Assam (part of eastern Himalaya), Burma, western Ghats and eastern Ghats (hilly tracts along the sea coast)—e.g., *Mesua ferrea, Xylia xylocarpa, Michelia champaca, Lagerstroemia flos-reginae.* These are essentially eastern Himalayan species.

(iv) Discontinuous distribution in eastern Himalaya and other parts of eastern India—e.g., *Podocarpus neriifolia.*

(v) Discontinuous distribution in Assam, Burma, eastern Ghats, western Ghats, Andaman, and Sri Lanka—e.g., *Chickrassia tabularis,* species of *Calophyllum, Artocarpus,* and *Dipterocarpus.*

(vi) Discontinuous distribution in the parts of western Himalaya, eastern India, central India, western and eastern Ghats, and Sri Lanka—e.g., *Toona ciliata, Carallia brachiata, Dillenia pentagyna,* and *Grewia tiliaifolia.*

(vii) Mainly western and central Himalayan taxa with approximately continuous distribution in the eastern Himalaya—this category includes deciduous species, e.g., *Betula alnoides, Ulmus wallichiana, Acer campbellii, A. oblongum, Juglans regia,* and *Dalbergia sissoo.* Some of these are Mediterranean and North American elements. *Bischofia javanica* is unique in the sense that it not only extends up to Burma towards the east, but also descends to the western Ghats in peninsular India.

The present-day physical discontinuity between the Himalayan mountains and the southern Indian mountains (there is about 2000 km between the Nilgiri and Palni hills and the Himalaya), yet the occurrence in common of certain woody and herbaceous taxa above 1500 m elevation, has generated considerable interest among botanists. Several theories, emphasizing the changes in climate during the geological past, have been advanced. The most notable are: (i) that Himalayan glaciation in the Pleistocene, by lowering the temperature, caused a southward migration of Himalayan plants (and animals) and subsequently, with an increase in temperature, the plants moved up the peninsular hills (Burkill, 1924; Medlicot & Blandford, 1879); and (ii) the Satpura hypothesis, which suggests higher altitudes for the Satpura and Vindhyan hills (1500–1800 m) during the Pleistocene, thus connecting eastern Himalayan ranges in the east and the western Ghats in the west, with occurrence of annual rainfall above 2500 mm with high humidity, thus favoring the extension of tropical ombrophilous forests over all these hill ranges down to Sri Lanka (Hora, 1949, 1950). Geological investigations contradict the Satpura theory (Auden, 1949; Dey, 1949), and the glaciation theory therefore appears to be the more plausible.

Geological evidence indicates that in the Himalayan ranges during the Pleistocene, the glaciers were located between 1678 and 1830 m, as against 3350 and 6100 m at the present (Kar, 1972). The Pleistocene glaciation involved the entire Himalayan ranges, but the impact was less in the eastern part (Kar, 1972). However, controversy still exists. For example, Blasco (1970, 1971a, 1971b, 1977) has commented upon the inadequacy of the glaciation theory. Many of the common taxa in the mountains of two separate regions show Asian affinities, and it is argued that the Himalaya does not contribute towards the presence of Asian plants on the south Indian mountains. Meher-Homji (1972), replying to the points raised by Blasco (1970, 1971a, 1971b), argues that despite the above facts, it cannot be ruled out that several Himalayan taxa were pushed southward due to glaciation. He (Meher-Homji, 1972) points out that the presence of different species of the same genus in the Himalayan mountains, south Indian hills, and Sri Lankan hills—e.g., *Rhododendron arboreum* in the Himalaya, *R. nilagiricum* in south India, *R. zeylanicum* in Sri Lanka, and *Berberis* (=*Mahonia*) *nepalensis* in the Himalaya, and *M. leschenaultii* in south India—indicates that the migration had taken place sufficiently earlier (during the Pleistocene) to give enough time to members of these genera to evolve independently. This situation cannot be explained on the basis of the hypothesis, as suggested by Blasco (1970, 1971a, 1971b), that they migrated in recent times through seeds. Meher-Homji (1972) further argues that the presence of *Hemitragus hylocrius,* a close relation of *H. jemlahicus* of the Himalayan region (Charles, 1957, considers them as races) in the Nilgiris, Anamalai, and some hills further south can be explained only on the basis of glaciation theory.

To conclude, it can be suggested that the glaciation did cause southward movement of the Himalayan taxa, but this does not explain the occurrence of all taxa common to Himalayan and south Indian mountains. For explanation of the distribution of certain taxa, factors other than glaciation might have to be considered.

Discontinuous distribution of taxa in relation to the Himalayan ranges and adjacent areas, such as western China, has also been noted. Of particular interest is the observation of Stainton (1977) on the discontinuous distribution of 40 species along a west-to-east transect. This transect included the following areas from west to east: Pakistan Himalaya (Gilgit, Chitral, Swat), Kashmir (including Ladakh and Jammu), Himachal Pradesh, Uttar Pradesh, West Nepal (from Kumaun border to 83°E long.), central Nepal (between 83°E and 86°30′E long.), east Nepal (between 86°30′ E long. and the Sikkim border), Sikkim (including the Darjeeling district), Bhutan, south-east Tibet (from the Bhutan border to China), and western China. In this transect, areas from Pakistan to Uttar Pradesh were regarded as western Himalaya (recall that we consider Uttar Pradesh Himalaya as part of the central Himalaya), Nepal formed the central Himalaya, and the rest of the areas the eastern Himalaya. The major pattern which emerges is that many species, which at first sight seem to be typically western Himalayan, are in fact also recorded further eastwards, such as south-east Tibet and China, although they appear to be absent from the central region and from some parts of the eastern region (Stainton, 1977). Examples are *Quercus floribunda*—present from westernmost Nepal to central Nepal, absent from east Nepal, Sikkim, Bhutan, south-east Tibet, but present in China; *Incarvillea arguta*—present from Himachal Pradesh to central Nepal, absent from east Nepal to Bhutan, but present in south-east Tibet and China; *Viburnum cotonifolium*—present in Pakistan to central Nepal, absent from east Nepal, Sikkim, but present in Bhutan, China, and south-east Tibet; *Myrsine africana*—present from Pakistan to central Nepal, absent from further eastern parts but present in China. Distribution of most of these species appears to be related to climatic humidity, soil moisture, and geological factors. The absence of *Incarvillea arguta,* for example, from east Nepal, Sikkim, and Bhutan is due to the wetness of the region. This species is characteristic of the dry Tibetan borderlands. Any one failing to notice its distribution in south-east Tibet will reach the conclusion that it is a western Himalayan species. On the other hand, *Olea cuspidata,* a species recognized as western Himalayan, reappears in China after a long break from central Nepal to south-east Tibet. Here elevational or geological factors, rather than a moisture factor, appear to be the cause of the discontinuous distribution, for south-east Tibet is drier than many western Himalayan areas where the species is found. The lower elevations to which the species is adapted are not available in Tibet, hence its absence.

Stainton (1977) suggests that if more floristic records were to be made (at present, possibly less than 50% of the species of the Himalayan region are documented), more cases of discontinuous distribution will come to light, and many species hitherto thought to be exclusively western Himalayan may prove also to be in the drier areas of the eastern Himalaya.

B. PALEO-HISTORY OF FOREST VEGETATION AND FLORISTICS

The knowledge of the development of vegetation in the Himalaya through geological times is fragmentary and inadequate. Vishnu-Mittre (1984), while commenting on the problems in documenting the geological history of vegetation pointed out that the confusion might be attributed to insecure identification, utter disregard of sedimentation/preservation phenomena, and ignorance of the ecological and distributional perspectives of the taxa identified. Meher-Homji and Misra (1973) have reviewed the paleoecology of the Indian subcontinent. Recently, Vishnu-Mittre (1984), on the basis of an in-depth literature survey (see Awasthi, 1974, 1982; Lakhanpal, 1970; Prakash, 1965, 1972, 1975, 1979; Singh, 1982; Vishnu-Mittre, 1965, 1966, 1974, 1979, 1984; Vishnu-Mittre et al., 1984) has synthesized the existing information with particular reference to the western Himalaya (including the central Himalaya). Most of the studies cover the period from the lower Miocene to the Recent and, that too, in isolated pockets.

1. *Brief Chronology*

On the southern slopes of the Himalaya there were tropical forests during the lower Miocene. However, the fruits and dicotyledonous leaves of the constituent species have not yet been determined. Palms, whose taxonomic identities are not yet well established, were also members of these forests. Later on, during the upper Pliocene, it is suggested that possibly a palm savanna (consisting of *Palmoxylon wadiai* and *P. jamuense,* with grasses, particularly the *Poacites*) vegetation was established on surfaces, such as conglomerates of boulders in the Siwaliks (Vishnu-Mittre, 1984). These were possibly the seral stages on immature hill surfaces.

Vishnu-Mittre (1984) suggests that during the mid-Miocene there existed an "incipient latitudinal zonation" of vegetation in the Himalaya, then 2200–2400 m high. There occurred wet tropical forests on the lower slopes, wet temperate forests on the higher slopes, with wet subtropical in between. The Palearctic genera occurred in the top two zones as they do today in the eastern Himalayan part. At that time the tropical wet evergreen forests of the western Himalaya consisted overwhelmingly of Malayan and southeastern elements (e.g., *Dipterocarpus, Cynometra, Anisoptera, Gluta, Diospyros, Elaeocarpus, Sterculia, Bursera*), while the temperate forests consisted of a number of Palearctic genera (e.g., *Pinus, Abies, Picea, Alnus, Betula, Magnolia*). The tropical wet evergreen vegetation of the eastern Himalaya had somewhat different species (Awasthi, 1974; Mohan, 1933). Some of the present-day common tree taxa with which older taxa had affinities were *Calophyllum, Dipterocarpus, Shorea, Kayea,* and *Gluta,* etc. It may be pointed out that only the eastern Himalayan region still contains a wet evergreen type of tropical forest. None of the modern species, however, were present during the Miocene.

The Miocene orogeny and perhaps planetary dynamics, led to marked climatic changes involving the pluvial cycles, i.e., the repetition of cold (and dry) and warm (and mesic) phases during the Pliocene. These cycles brought about drastic changes in physiognomy and in vegetation, which included the disappearance of some forest types (e.g., tropical wet evergreen *Dipterocarpus–Anisoptera* forests from the western Himalaya), arrival of species from extra-Himalayan regions, relative increase or decrease in the area occupied by different biomes such as forest and steppe, etc. It is, however, difficult either to interpret the sequences of such changes precisely, or to suggest at what rate and at which time the vegetational changes occurred (see Vishnu-Mittre, 1984).

By the end of the Pliocene, the tropical African elements, such as *Zizyphus mauritiana* had reached the lower slopes of the western Himalaya. In subtropical and temperate belts of Kashmir, a continuous flux between the forests of *Quercus–Carya, Larix–Quercus, Engelhardtia, Quercus–Alnus,* and *Pinus roxburghii* on the one hand, and steppe (Poaceae with or without *Cheno–Amaranthus* and *Artemisia*) on the other, occurred from 3.5 to 2.47 million years B.P. The steppe attained preponderance during the cooling-phase and the forests during the warming-phase. *Cedrus deo-*

dara, a Mediterranean species, immigrated during the Pliocene. During the Pliocene (3.5–2.47 million years B.P.) in the Kashmir valley, subsequent to the decline of *Cedrus–Quercus* forests, *Pinus wallichiana* arrived and expanded. *Pinus wallichiana* declined subsequently to be replaced by *Picea–Cedrus–Quercus* forests.

The subalpine and alpine conditions developed in the Himalaya after the final uplift. At that time, *Q. semecarpifolia* and *Betula utilis* were the chief subalpine and alpine forest-forming species. During the last glaciation (about 0.7 million years ago), the steppes encompassed most of the areas in higher elevations (above 3000 m), but the subsequent warm-phase led to the expansion of junipers in dry areas and of *Q. semecarpifolia* and *Betula utilis* in relatively mesic areas. Similar alternations were found between steppe and *Ephedra* communities in arid parts.

During the Pliocene–early Pleistocene as many as 25 species in subtropical and temperate zones were found which occur today in the Sino-Japanese region. *Abies spectabilis, Betula utilis, Quercus semecarpifolia, Q. glauca, Cinnamomum tamala, Juglans regia, Machilus duthiei, Pinus wallichiana, Ulmus wallichiana, Acer oblongum, Alnus nepalensis, Cupressus torulosa, Litsea elongata,* and *Mallotus philippensis* are examples of trees.

More recently, between about 8000 and 4500 years ago, a warm-phase, which resulted in massive snow-melting and concomitant increase in the sea-level around the Kerala coast (Vishnu-Mittre, 1984), coincided with the invasion of chir pine (*Pinus roxburghii*) forests by oaks (*Quercus* spp.) in the central Himalaya. At this time, in fact, oaks predominated in the entire subtropical and temperate belts of the western Himalaya. In some regions, such as the Kashmir valley (within about the last 500 years) and Himachal Pradesh (during 1400–500 years ago), oaks disappeared or were pushed to sheltered areas within the conifer regimes. The present flora of Kashmir valley is devoid of either oaks or *P. roxburghii* (Puri et al., 1983). In Kashmir, at higher elevations (2000–3000 m), *Pinus wallichiana* (the blue pine) was the main pine species, while in Himachal Pradesh and Kumaun, in the lower elevations, the pine was mainly *P. roxburghii.*

It is interesting that the oaks predominated and invaded the pine forests during the warm-phase of the climate, because at present the oak forests are located at higher elevations (hence cooler environment) than the chir pine (*P. roxburghii*) forest

Thus, the tropical wet evergreen forests, which now are confined to the eastern part existed throughout the east-to-west arch in the geological past. Almost the entire flora existing during the Miocene was replaced subsequently by the modern flora. However, quite a few modern Himalayan species emerged from their precursors in the Miocene tropical flora. Thereafter, the changes were mostly limited to variations in the area of species and their relative importance in different communities. Almost all the dominant forest species of the Pleistocene continue to maintain their dominant status, however, their areas may have changed.

2. *Processes Related to the Vegetational Changes*

Drastic modifications of the mountain surfaces by erosion and deposition destroyed the original vegetation in areas of varying sizes and led to ecological succession until another spell of destruction occurred. Thus, late successional communities were repeatedly destroyed and replaced by early successional ones, and a mosaic of such communities was always there on the face of the mountains.

Depending upon the magnitude of the destruction in a given area at a given time, the proportion of early- and late-successional communities would have varied. Subsequent to a destruction, during the period of quasi-stability, the late successional species would expand again from the vestiges left in sheltered sites. These processes may well explain the reported wide fluctuations in the areas occupied by the early successional chir pine (*Pinus roxburghii*) and the climax banj oak (*Quercus leucotrichophora*) in Kumaun Himalaya during the past 8000 to 4500 years ago (Vishnu-Mittre et al., 1984).

The Himalayan ranges started developing in the beginning of the Cenozoic (during the Eocene), when angiosperms had already established their global dominance. The uplift of these mountains occurred in five stages, the last one being during the late part of the early Pleistocene. The uplift caused three important environmental changes: (i) increase in the breadth of climatic gradient from a relatively uniform warm and humid stage (succeeded by cool-warm alternating oscillations) to that which now encompasses warm to extremely cold conditions with permanent snow cover at higher altitudes; (ii) continual but spasmodic and explosive surface modifications owing to the tectonic stresses; and (iii) creation of mountain barriers which influenced the distribution pattern of rainfall. The widening of the climatic gradient provided opportunities to several species to express their fullest range of elevational adaptability. Distributional ranges of other species were segregated along the altitudinal gradient. For example, during the later Pliocene there existed in the Kashmir valley at about 1700 m a mixed vegetation comprising species which now are widely separated in their elevational ranges (e.g., *Quercus glauca,* now occurring below 1800 m, and *Betula utilis,* around 3000 m, and *Litsea elongata,* occurring around 2000 m, and *Quercus semecarpifolia,* above 2500 m), grew together. This may indicate that either the climatic requirements of these species were different in the geological past from those they exhibit now, as suggested by Vishnu-Mittre (1984), or those earlier taxa were paleo-ecotypes of the modern species, if identification of these species were unquestionable. It is also possible that the population centers of these species were dispersed with time as a result of competitive interactions superimposed on the evolutionary changes induced by the changing gamut of environmental factors.

Repeated ingress of new species from time to time and build-up of additional biomes, such as alpine and subalpine, where the central Asian (Chinese and Euro-Siberian) species immigrated and established during the early Pleistocene, were other consequences of the evolution of a wide environmental gradient.

The mountain barriers not only created some of the most conspicuous rain-shadow zones and rendered the inner valleys drastically drier than the outer valleys, they also influenced the monsoonal pattern of precipitation over extensive areas, resulting in a greater winter precipitation in the form of snow. In the Kashmir valley this situation resulted from the rise of the Pir Panjal ranges by at least 1800 m after the early Pleistocene. The establishment of the drier conditions in the inner valleys led to the development of xeric vegetation consisting mostly of the species earlier confined to xeric sites of the otherwise mesic climatic regime. The change in the pattern of precipitation in the Kashmir valley during the Pliocene led to the establishment of Mediterranean floristic elements.

The cyclic warming and cooling phases (often accompanied by glaciation; there were more than four glaciations during the Quaternary alone) superimposed upon the widening climatic gradient stemming from the increasing elevation, caused profound changes in the vegetation of the Himalaya. Several species became extinct. Original communities were replaced by new ones consisting of already existing species which endured the changed environment, as well as of new arrivals. For example, in the western Himalaya during the end of the Miocene the humid tropical *Dipterocarpus–Anisoptera* forests of the lower slopes vanished, and the subtropical and temperate forests were transformed into less mesic types. Some of the original taxa of the relatively humid and warm climate, such as *Engelhardtia, Cinnamomum, Bauhinia, Ficus,* and *Litsea* could, however, adjust to the changed conditions. Maybe this adjustment involved genetic changes resulting in formation of new genotypes, ecotypes, or even species. However, *Podocarpus neriifolius,* a conifer of the Southern Hemisphere, vanished from the western Himalaya.

It is apparent from the foregoing that several destructive forces repeatedly obstructed and even reversed the natural course of species-enrichment. It is possible that several times in a given area the rate of extinction of the species was higher than the rate of immigration of new species plus the evolution of the species out of the original stock through speciation. On the other hand, the moderate disturbances in the intervening periods, as they often do (Whittaker, 1975), could enable the formation of a wide successional spectrum of communities, increasing thereby the species richness.

V. Structural Aspects

A. FOREST FORMATIONS

We classify the forest vegetation of the Himalaya into 11 formations (Fig. 3). Basic information was derived from the classical descriptions of Champion and Seth (1968a). However, qualitative and semiquantitative descriptions (Champion, 1923; Dobremez, 1972, 1973; Dobremez & Jest, 1971; Dobremez & Shakya, 1975; Dobremez et al., 1975; Dudgeon & Kenoyer, 1925; Ghosh, 1956; Gorrie, 1933; Gupta 1963; Hooker, 1852; Kenoyer, 1921; Mohan & Puri, 1956; Mohan et al., 1956; Numata, 1965; Osmaston, 1922; Puri, 1960a, 1960b; Schweinfurth, 1968; Shrestha, 1982; Singh, 1929; Troll, 1939), and quantitative phytosociological investigations of our group (Ralhan et al., 1982; Rawat et al., 1983; Saxena, 1979; Saxena & Singh, 1982a, 1982b; Saxena et al., 1978; J. S. Singh & Goel, 1983; J. S. Singh & Singh, 1984a, 1984b, 1984c; Tewari, 1982; Tewari & J. S. Singh, 1983; Tewari & S. P. Singh, 1981, 1985; Tiwari et al., 1983; Upreti, 1982; Upreti et al., 1985) were also used. Degraded forms, pioneer stages, and local communities are not considered, unless they are extensive enough to warrant recognition. While recognizing the formation types, emphasis is on leaf characters (leaf drop pattern, leaf size, texture, shape) and the elevational factor. In part, terms of UNESCO's (1973) classification of vegetation and those of the physiognomic-ecological plant classification of Mueller-Dombois and Ellenberg (1974) have been used. High montane (3000–3500 m) and very high montane (3500 m and up to timber line) replace subalpine and alpine categories of Champion and Seth (1968a). The term "evergreen seasonal forest" of Mueller-Dombois and Ellenberg (1974) has been replaced by "forests with concentrated summer leaf drop," in certain cases (e.g., hemisclerophyllous forests having oaks). This term characterizes the most conspicuous attribute of the phenology of these forests (Ralhan et al., 1985a).

Categories recognized by Champion and Seth (1968a) that fall within our 11 formation types are indicated in Table I. A brief description of the formation types follows.

1. Submontane Broadleaf Ombrophilous Forest

This formation (below 1000 m), which is broadly similar to tropical rain forest, is confined to the eastern Himalaya. While the rainfall (2300–4000 mm yr^{-1}) is as great as reported for the typical tropical rain forests,

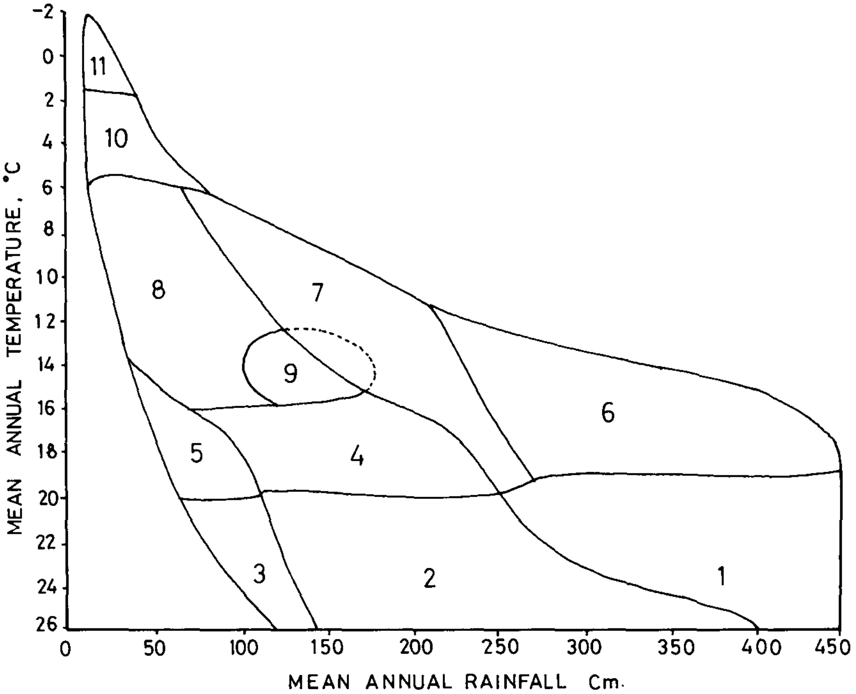

Fig. 3. Forest formations of the Himalaya in relation to rainfall and temperature. 1, Submontane broadleaf ombrophilous forest; 2, Submontane seasonal broadleaf forest; 3, Submontane broadleaf summer deciduous forest; 4, Low-montane needle-leaf forest with concentrated summer leaf-drop; 5, Low-montane sclerophyllous evergreen broadleaf forest; 6, Mid-montane broadleaf ombrophilous forest; 7, Low to mid-montane hemi-sclerophyllous broadleaf forest with concentrated summer leaf-drop; 8, Mid-montane needle-leaf evergreen forest; 9, Mid-montane winter deciduous forest; 10, High-montane mixed stunted forest; and 11, Very high-montane scrub.

it is comparatively less evenly distributed across the year. Most of the annual rainfall occurs during May–September, and the number of months with less than 50 mm rainfall varies from two to four. Luxuriance of these forests, their evergreenness, high species richness, multistratal structure, preponderance of buttressed trees 50 m or more tall, are the features which make these forests comparable to tropical rain forests. The Meliaceae and Anacardiaceae and the genera *Dipterocarpus, Artocarpus, Syzygium, Mesua,* and *Myristica* are well represented. In mature forests, *Dipterocarpus macrocarpa* and *Shorea assamica* account for a majority of the emergent trees, often attaining more than 50 m in height. Palms and tree ferns may be frequent in certain areas. On biotically disturbed sites, bamboos (e.g., *Dendrocalamus* spp.) predominate as second growth species.

Table I

Formation-types recognized in the Himalaya compared with the vegetation-types recognized by Champion and Seth (1968a)

Formation-type	Equivalent groups, subgroups, and categories of Champion and Seth (1968a)
Submontane broadleaf ombrophilous forest	Northern tropical wet evergreen forest (1B) and mesic part of northern tropical semi-evergreen forest (2B), lower part of northern subtropical broadleaved wet hill forest (8B)
Submontane seasonal broadleaf forest	Drier part of 2B and moist parts of the mixed deciduous forest (3C/C_3)
Submontane broadleaf summer-deciduous forest	Northern dry mixed deciduous forest (5B/C_2), and, dry Siwalik sal forest (5B/C_{1a}), moist mixed deciduous forest (3C/C_3)
Low-montane needle-leaf forest with concentrated summer leaf-drop	Subtropical pine forest (9)
Low-montane sclerophyllous evergreen broadleaf forest	Subtropical dry evergreen forest (10C/C_1)
Mid-montane broadleaf ombrophilous forest	East Himalayan wet temperate forest (11B/C_1), higher part of northern subtropical broadleaf wet hill forest (8B)
Low to mid-montane hemi-sclerophyllous broadleaf forest with concentrated summer leaf-drop	Lower western Himalayan temperate forest (12/C_1) and upper west Himalayan temperate forest (12/C_2), excluding coniferous categories and deciduous category
Mid-montane needle-leaf evergreen forest	Coniferous categories of lower western (12/C_1) and upper west (12/C_2) Himalayan temperate forests and east Himalayan moist temperate forest (12/C_3)
Mid-montane winter-deciduous forest	Moist temperate deciduous forest category of lower western Himalayan temperate forest (12/C_{1e})
High-montane mixed stunted forest	Subalpine forest (14)
Very high-montane scrub	Alpine scrub (15)

Because species richness is high and a single species may generally not account for more than one-fourth of the total importance value of the forest stand, it is not possible to recognize distinct dominant types in any real sense. However, as given below, there are instances where one or two to three species can show substantial dominance.

(i) *Dipterocarpus–Mesua* forest

This forest gains its best expression on undulating old alluvium at about 500–600 m. Individuals of *Dipterocarpus macrocarpus* and *Shorea assamica* emerge above the canopy layer consisting of *Mesua ferrea, Michelia* spp., and numerous other species. About six vertical layers are distinguishable.

(ii) *Kayea assamica* forest

Clear-cut dominance of *Kayea assamica* (relative density about 69%) and absence of *Dipterocarpus* are distinguishing features of this type, distributed on the north bank of the Bramhaputra valley.

(iii) *Mesua* forest

This is a four-storied forest of small stature (average height 30 m). *Ailanthus grandis, Echinocarpus* sp., *Michelia doltsopa, Quercus lamellosa,* etc., are some of the important canopy species, in addition to *Mesua* spp. It occurs on well-drained deep and porous soils between 200 and 800 m.

(iv) *Mesua–Dipterocarpus–Palaquium* forest

Structurally, it is similar to *Mesua* forest. It is found on lower slopes of the Cachar and Jainti hills around the Surma valley, upon old alluvial red sand, clay, and gravel.

All the above forests consist almost entirely of evergreen species. In some of the variants, certain canopy species, particularly the giant ones, are deciduous for a short period during the dry and warm portion (March–May) of the year (e.g., *Terminalia* spp., *Tetrameles, Stereospermum*). Such forests have been referred to as the semi-evergreen type by Champion and Seth (1968a). However, since the overall appearance of the forests remains evergreen, because the undercanopy is entirely evergreen, and many of the canopy species are also evergreen, these forests have not been separated into another formation. Further, many of the genera (*Dipterocarpus, Syzygium, Artocarpus*) and members of the Magnoliaceae assigned to the evergreen forests of Champion and Seth are found also in these forests.

2. *Submontane Seasonal Broadleaf Forest*

Distributed mainly in eastern and central parts, *Shorea robusta* (accounting for 60–90% in the top canopy) is the dominant and most extensively distributed species. However, in the eastern Himalaya *S. assamica* shares dominance with *S. robusta* in many areas. From the plains of northern India, sal forest ascends the Siwaliks up to 1000 m or occasionally more. It covers a wide range of soils and rock types that are encountered from the eastern Himalaya to western Himalaya, excepting Kashmir. Soil may vary from deep loamy sand to shallow residual mountain soil.

These dominant species, although they exhibit concentrated leaf drop in summer (dry season), the simultaneous leafing-out never renders their populations completely naked. However, the foliage mass of the canopy becomes markedly thin during the summer. The tree layer and shrub layers consist of a mixture of evergreen and deciduous species. The canopy is fairly close; crown density can be above 80%. Sal trees can grow up to 40 m in favorable environments, and can withstand frequent surface burning. The middle tree layer is relatively less developed and bamboos are generally absent. The mean annual temperature (MAT) ranges between 21 and 26°C; however, during the winter, frost may occur frequently. The annual rainfall varies from about 1000 to 1400 mm, but seasonality is well developed, for dry months (with less than 50 mm rainfall) may vary from 4 to 7 months. *Schima wallichii, Stereospermum personatum, Sterculia* spp., *Caschela microcarpa, Lagerstroemia parviflora, Terminalia* spp., *Machilus villosa,* and *Anogeissus latifolia* are some of the common canopy associates.

3. *Submontane Broadleaf Summer Deciduous Forest*

This type attains its predominance on nutrient-poor and dry sites, although it is also found in relatively moist areas of western Himalaya on skeletal soil. Unlike the previous type, species dominance is not marked, for diversity is relatively high. These forests are of an open-type, assuming woodland conditions on drier sites. They may contain *Shorea robusta,* but with much lower relative importance. In Bhabar of Kumaun Himalaya, *Albizia procera, Adina cordifolia, Terminalia tomentosa, T. bellerica, Toona ciliata,* and *Anogeissus latifolia* form the canopy, and *Mallotus philippensis* (a member of sal undercanopy) and *Ougeinia oogeinensis* form the understory tree layer. In the hills of Kumaun, Kenoyer (1921) recognized a *Bauhinia* forest with open canopy, where *B. retusa, B. variegata,* and *B. vahli* prevail. Generally, the relative density of single species does not exceed 10%; however, in certain areas of the Punjab hills, *Anogeissus latifolia* may show a clear-cut dominance.

The duration of deciduousness may vary from a short period of early summer (April) on relatively mesic sites to a period extending from winter to early summer on drier sites. Tree height may range from 30 m in relatively favorable environment to not above 15 m in stressful conditions.

4. *Low-montane Needle-leaf Forest with Concentrated Summer Leaf Drop*

It is found all along the Himalaya, with the exception of Kashmir, between altitudes of 1000 and 1800 m. In eastern Himalaya the formation is represented by *Pinus kesiya* and in central and western Himalaya by *P. roxburghii.* The trees attain 30–35 m height, the canopy is open, with crown density below 60%, the shrub layer is poor, and grasses predominate in the ground flora because of frequent burning (Saxena, 1979). Possibly this is not the potential natural climax forest, and its extensive occurrence today would not have been possible, had there not been continuing disturbances such as landslides, burning, deforestation, etc. (Champion & Seth, 1968a, 1968b). However, these forests are now stabilized over a large area and are regarded as a permanent feature.

5. *Low-montane Sclerophyllous Evergreen Broadleaf Forest*

Its distribution is confined to the western part in drier areas, where the effect of the monsoon is weakened. *Olea cuspidata* is the dominant species. Height is generally below 10 m, and shrubs grow abundantly.

6. *Mid-montane Broadleaf Ombrophilous Forest*

This type is confined to the eastern Himalaya between 1500 and 3000 m. Conditions are very mesic because rainfall is not less than 2000 mm and may be up to 4000 mm or more, and temperatures are low (MAT = 11°–18°C). This is considered to be the most species-rich forest between 2000 and 3000 m. In general, none of the species accounts for more than 12% of the relative importance. Compared to ombrophilous forests of lower elevations (formation type 1), boles are far less clean, height of trees is lower, and stratification is less developed. Tall emergent trees rising above the canopy layer, a common spectacle of lower ombrophilous forests, are not seen in this formation. While dipterocarps predominate in lower forests, oaks and *Castanopsis* prevail in these forests. Common species are members of the Lauraceae, *Machilus edulis, Michelia cathertii, Magnolia* spp., *Quercus lamellosa, Q. serrata, Castanopsis* spp., *Acer campbelli,* etc. The forests form a close canopy and, unless very dense, have a thick growth of dwarf bamboos; climbers are woody but they are not conspicuous. Conifers are not found in these forests. In some areas, particularly in higher elevations (2400–2700 m), dominant types such as *Quercus pachyphylla* and *Q. lamellosa* forests are recognizable. But in general, although names of tree species have been used to designate the forest types (Bor, 1938; Cowan, 1929; Deb, 1960), dominants are not readily apparent.

Between this type and the submontane broadleaf ombrophilous type, transitional evergreen broadleaf forests sharing species of both types are found. In these, dipterocarps are mixed with oaks and chestnuts (*Castanopsis* spp.). *Schima wallichii, Engelhardtia spicata, Alnus nepalensis,* and *Cinnamomum* spp. are some of the associates. A middle tree story is well developed; climbers and epiphytes, including orchids, grow luxuriantly, and shrubby undergrowth prevails. Toward higher elevations, approaching 3000 m, in the humid pockets, although trees become stunted, stratification, and an abundance of mosses, lichens, and vascular epiphytes, as found in lower forests, persist. These forests approximate the conditions of elfinwoods, which occur in the subalpine zone on tropical mountains.

7. *Low to Mid-montane Hemi-sclerophyllous Broadleaf Forest with Concentrated Summer Leaf Drop*

This type is best expressed in central and western Himalaya (between 1500 and 3000 m). Because of multiple leafing and longer longevity of leaves, the degree of evergreenness is greater than in low montane needleleaf forests (formation 4) or submontane seasonal broadleaf forest (formation 2). Leaves are leathery, but not as tough-textured or as small as in the forests of the Mediterranean regions of the world. They generally occupy mesic to sub-mesic areas with annual rainfall between 1000 and 2500 mm. The MAT ranges from 13 to 16°C and winter snowfall is quite frequent above 2000 m. In the past, the lower elevational limit of this formation was similar to that of the pine forests, but because of disturbance (frequent burning), the lower limit has risen considerably from less than 1000 m to 1500 m or so, during the last century. The canopy is closed (more than 80%) when undisturbed; shrub growth is conspicuous and the less developed herb layer does not include grasses. The height generally ranges from 25 to 30 m. Species-richness is low, for generally one or two species predominate; hence dominant types are easily recognizable: (i) *Quercus leucotrichophora* (banj oak) forest, which covers extensive areas in lower elevations (1500–2100 m); (ii) *Q. lanuginosa* (rianj oak) forest, which forms an almost pure stand in some pockets between 1800 and 2200 m; (iii) *Q. floribunda* (tilonj oak) forest, is also distributed in limited areas, between 2000 and 2300 m; (iv) *Q. semecarpifolia* (kharsu oak) forest is the predominant oak forest between 2400 and 3000 m; and (v) *Q. leucotrichophora–Q. floribunda* forest, which occurs between 2000 and 2200 m. From this account, the altitudinal variation in oak species is a feature worth noting. At 2000 m and less, *Q. leucotrichophora* may exhibit 80% dominance (in terms of relative basal area), between 2000 and 2200 m it may share dominance with *Q. floribunda,* whereafter it disappears gradually. In small patches between 2100 and 2300 m, *Q. floribunda* may show clear-cut dominance; with further increase in elevation, *Q. floribunda* is replaced by *Q. semecarpifolia,* which may show more than 70–80% dominance in oak forest stands located above 2400 m. *Rhododendron arboreum, Lyonia ovalifolia,* and *Ilex dipyrena* are the common understory species of the oak forests. Conifers frequently mix with oaks, particularly in the western Himalaya. Because of disturbances, chir pine (*P. roxburghii*) has extended into banj oak forest considerably. In contrast, in the eastern Himalaya, oaks do not mix with conifers, and forests seldom exhibit a clear-cut dominance of single species. Several other broadleaf species may show importance values similar to that of the oaks.

The oak forests are often rich in epiphytes. Singh and Chaturvedi (1982) reported that the contribution of the epiphytic flora to total community chlorophyll may be equal to or more than that of the herb and shrub layer.

8. *Mid-montane Needle-leaf Evergreen Forest*

This formation includes a part of the east Himalayan moist temperate forests as well as of the west Himalayan moist temperate forests of Champion and Seth (1968a). Dominant species are mostly needle-leaved, viz., *Cedrus deodara* (deodar) and *Pinus wallichiana* (blue pine). *Abies pindrow* (silver fir) and *Picea smithiana* (spruce) are in the western part, and *Abies delavayi, A. hylium,* and *Tsuga dumosa* (hemlock) in the eastern part. Although floristically distinct, physiognomically the eastern and western conifer forests are indistinguishable. They occupy wide ranges of habitats from mesic to xeric conditions. Therefore, separation into dry and moist types, as done by Champion and Seth, is not reasonable. Temperatures and annual rainfall are in the range found for formation 7. The role of fire has been limited.

Compared to the broadleaf species of similar elevations, the conifers grow taller (30–35 m). While deodar, fir, and spruce form a nearly complete canopy, blue pine, as with the chir pine, forms open forests. Species richness is low. Several local communities occur in response to changes in soil conditions, altitude, drainage, topography, etc. Some of the important communities are enumerated below: western Himalaya: (i) *Cedrus deodara* (deodar) forest (1700–2500 m), (ii) *Abies pindrow* (silver fir) forest (2500–3000 m or more), (iii) *Picea smithiana* (spruce) forest (2500–2800 m) in limited areas, (iv) *Pinus wallichiana* (blue pine) forest (2300–3000 m), but in some small pockets, (v) *Picea–Cedrus–Abies pindrow–Pinus wallichiana* forest; (vi) *Abies pindrow–Picea* forest, etc. Eastern Himalaya: (i) *Abies hylium–Tsuga dumosa* (hemlock) forest (2300–3000 m), characterized by copious growth of epiphytes, particularly ferns; (ii) *Abies delavayi* (a Chinese element) forest (around 2700 m) forming a pure stand of small trees (20 m or less) of great girth (2 m or more).

9. Mid-montane Winter Deciduous Forest

It occupies generally the moist places of limited areas along the streams, in the region assigned to mid-montane hemi-sclerophyllous and needleleaf evergreen forests. The common species are *Aesculus indica, Acer pictum, A. caesium, Carpinus viminea, Ulmus wallichiana, Betula alnoides, Pyrus lanata, Juglans regia,* and *Fraxinus micrantha.* It is much like the temperate broadleaf deciduous formation of Europe and North America. The species are temperate elements which immigrated into the Himalaya during the geological past (Puri, 1960a). Tree height ranges between 20 and 30 m, the canopy is open enough to permit the growth of undercanopy trees and a shrub layer, which are also deciduous. Species richness is fairly high, but less than that of the submontane deciduous forests. Nevertheless, dominant types are unrecognizable.

10. High-montane Mixed Stunted Forest (Above 3000 m)

The monsoon effect is markedly diminished, and plants mainly depend on snowmelt for their water requirement. Deciduous birch or bhojpatra (*Betula utilis*), evergreen fir (*Abies spectabilis*), evergreen oak (*Q. semecarpifolia*) are common species in the central and western Himalaya. Beneath them *Rhododendron campanulatum* (3–10 m) is the most common species. In hollows, the taller species are absent and almost pure *Rhododendron* stands occur. *R. lepidotum* and *R. arboreum* (of lower elevations) are the other species of the understory. In the eastern Himalaya, the conditions are relatively mesic. The fir is *Abies densa,* often mixed with *Juniperus wallichiana.* Several species of *Rhododendron* are found, of which *R. wightii* and *R. lepidotum* are common. Trees become stunted and low (generally below 15 m) and densely branched with marked contortion. Branching may start from less than one meter above the ground level. However, birch is able to maintain its clean bole and may grow taller. But the boles generally are bent due to heavy snowfall and strong winds. Between the forest stands there may be pastures of varying sizes.

11. Very High-montane Scrub (Above 3500 m and up to 4900 m)

All taxa named in the previous type are usually present, except for *Abies* species. On drier sites, pure *Juniperus* scrub (also called juniper steppe) of less than 1 m height is a common feature. *Juniperus recurva* is common in the eastern Himalaya, *J. wallichiana,* and *J. communis* in the western Himalaya. The common herbaceous associates are species of *Caragana* and *Artemisia.* On mesic sites, *Rhododendron,* with some birch and other deciduous species (e.g., *Sorbus foliolosa*), may form a thicket, difficult to penetrate. *R. campanulatum* (1.5–3 m), *R. hypenanthum* (15–50 cm), and *R. lepidotum* (15–100 cm) are common species of the western Himalaya, and *R. campanulatum, R. campylocarpus, R. wightii, R. setosum, R. lanatum,* and *R. nivale* are common in the eastern Himalaya. On such sites, a thick humus layer is typically present on the soil.

Low height (usually not more than 2 m), a high density of branches and their contorted form are characteristic physiognomical features. They develop in response to excessively windy conditions with substantial amounts of radiation of shorter wavelengths. Precipitation is almost entirely in the form of snow, and melting snow is the principal source of water to plants.

In extremely xeric conditions, as often found in the westernmost region, a vegetation approaching the miniature semi-desert scrub found in the alpine zone of the White Mountains of California may be formed.

B. BROAD COMMUNITY PATTERNS

Because of the diversity of the climatic, elevational, geological, topographical, and anthropological factors that have influenced the development of vegetation on these mountains, it is difficult to express the relationship of community structure to environment in a simple framework. Following the concepts of gradient analysis, that is, to relate the communities to climate in a broader way (Whittaker, 1975), Singh and Singh (1985) identified two major environmental gradients: (i) that of decreasing temperature from low to high elevations; and (ii) that of decreasing moisture from east to west.

In response to these environmental gradients, two major coenoclines are discernible; this is represented as a pattern of formation types in relation to climate (rainfall and temperature) in Figure 3. For a number of reasons, the boundaries between the types, in such a representation as this, are approximate: (i) Several formation types integrate continuously, showing broad overlaps. For example, the climate characterized by MAT of 21°–26°C and the annual rainfall of about 2000 mm in the submontane zone (<1000 m elevation) can support both ombrophilous forests and seasonal broadleaf forests. Similarly, the overlap between hemi-sclerophyllous broadleaf forests and the needle-leaf forests is broad. (ii) Adaptations of different growth-forms in different regions are not perfectly convergent. For example, in the similar climatic regimes within the midmontane belt, evergreen oak and broadleaf winter-deciduous communities may develop in different regions, although soil conditions may also be similar. (iii) Climate does not solely determine the formation-type; soil and frequency of burning can alter the influence of climate. Development of chir pine (*Pinus roxburghii*) forest in the low montane belt of the entire central and western Himalaya in a climate which normally would have supported oak forest, is a typical example of the effect of recurrent burning. (iv) Interaction of the same MAT and the amount of rainfall can lead to different climatic-types, such as the development of the Mediterranean climate in Kashmir valley owing to winter rainfall. As a consequence, in the Kashmir valley, oak and chir pine forests, which typically develop in the areas with summer rainfall, are not found. Thus, the effect of climate is rather loose, and the pattern in Figure 3 is a considerable simplification. Nevertheless, some broad relations of communities to the climate become apparent in this figure. The two climatic factors, rainfall and temperature, are interrelated to a certain extent. The upper limit of rainfall (400–450 cm) remains approximately the same from MAT 26° to 12°C, whereafter it diminishes sharply with the decline in temperature until the precipitation is entirely in the form of snow. Thus, this pattern shows marked divergence from that of the world average, where a more or less uniform decline in upper limit of precipitation occurs from higher to lower temperatures (Whittaker, 1975). The sudden decline in rainfall with the drop below the MAT of 12°C in the Himalaya is related to elevation. Up to about 2500 m altitude, the monsoon, in general, is not affected by increase in the elevation, whereafter it is weakened markedly. The actual mesicness increases from foothills to 2500 m because of the decline in temperature and consequently in evapo-transpiration. Thus, the same amount of rainfall causes more mesicness at lower temperatures than at higher temperatures. In response to this, as an example, the evergreen ombrophilous forests of high diversity are found up to 12°C MAT, corresponding to more than 2500 m elevation, in the eastern Himalaya. This means that the luxuriance of vegetation, as expressed by height and massiveness of the trees and vertical stratification of communities, remains roughly the same up to a considerable elevation. In fact, some of the tallest and largest trees in the Himalaya occur between 2500 and 3000 m (e.g., *Abies pindrow, Picea smithiana*). However, with further rise in elevation, in response to a sudden decline in the rainfall, and in severely cold and windy conditions, tree height (Fig. 4), stratification, diversity, and canopy density are reduced drastically. The species that constitute the communities of high montane belts are selected because they are adapted to survive in harsh climate, while in ombrophilous forests of lower elevations selection of the species is largely for the characters that enable them to withstand competitive interaction with other species.

The east-to-west trend of decreasing climatic moisture is most pro-

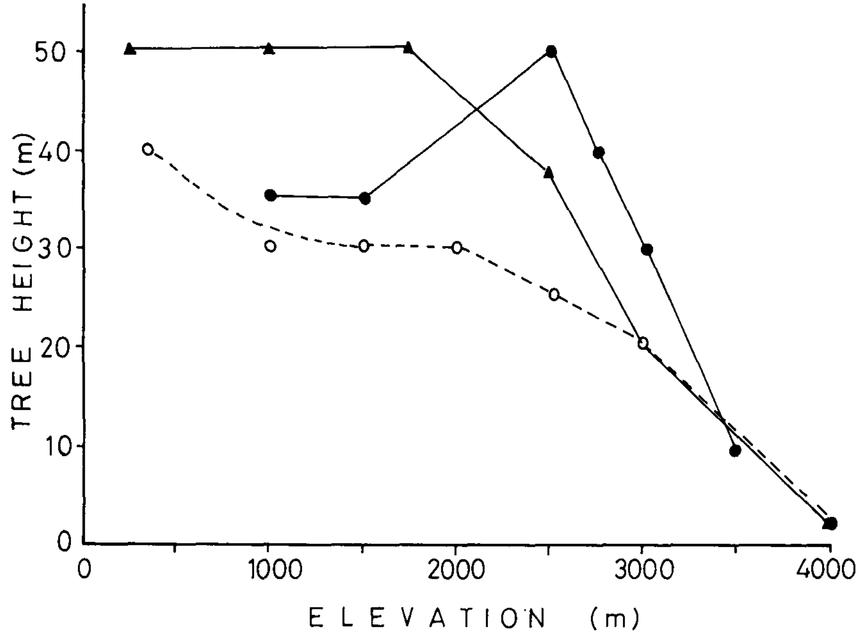

Fig. 4. Maximum tree height along the elevational gradient in the Himalaya. Triangles connected with solid line represent broadleaf species of eastern Himalaya, circles connected with broken line represent broadleaf species of central and western Himalaya; circles connected with solid line represent conifer species of central and western Himalaya.

nounced in the submontane belt, therefore the trends in vegetational changes described below pertain to this belt. Along the east-to-west gradient of decreasing climatic moisture, the diminishing effect of the Pleistocene glaciation is also noticed. Because of the relatively stable (destruction of vegetation was less severe under the comparatively moderate spell of glaciation) and favorable conditions (high humidity), the order of diversity in the eastern Himalayan forests is higher (Table II) than in the central and western Himalayan forests. As pointed out earlier, the relative stability allowed greater speciation of various taxa than in other regions, where the impact of glaciation was severe.

Although the difference in diversity at a regional level is well marked, the relationship between diversity and moisture gradient is not straightforward. Diversity is by far the highest in ombrophilous forests of the eastern region, but is low in the fairly mesic forests, that is, the seasonal forests where sal (*Shorea robusta*) predominates. Compared to seasonal forests, diversity is higher in the summer-deciduous forests of relatively drier conditions, but is lowest in the low-montane sclerophyllous evergreen broadleaf forests of the driest areas in the westernmost part. The summer deciduousness is maximum in the middle part of the moisture

Table II

Tree diversity (Simpson's diversity index) for certain eastern and central Himalayan forests located between foothills and 3000 m altitude (based on Tewari, 1982; S. P. Singh & J. C. Tewari, unpubl.)

Elevational belt in m	Eastern Himalaya		Central Himalaya	
	Location of forest	Stand diversity	Location of forest	Stand diversity
Submontane (<1000)				
	Submontane broadleaf ombrophilous forest			
	Lower slope of Cachar hills	0.95	—	—
	Duling Reserve,[a] extreme east on the north bank of Brahmaputra River	0.51	—	—
	South bank of Brahmaputra River, Assam	0.95	—	—
	North bank of Brahmaputra River, Assam	0.94	—	—
	Lower hill slope, Kalimpong, West Bengal	0.89	—	—
	Submontane seasonal broadleaf forests			
	Teesta Valley Kurseong, West Bengal	0.72	Ranibagh, Naini Tal	0.51
	Buxa, West Bengal	0.74	Siwaliks, Saharanpur	0.67
	Goalpara, Assam	0.48	—	—
	Submontane broadleaf summer-deciduous forests			
	Buxa, West Bengal	0.89	Siwaliks, Saharanpur	0.72
Low-montane (1000–2000)				
	Low-montane needle-leaf forest			
	Kalimpong, West Bengal site II[b]	0.79	Khurpatal, Naini Tal	0.10

Table II
Continued

Elevational belt in m	Eastern Himalaya		Central Himalaya	
	Location of forest	Stand diversity	Location of forest	Stand diversity
	Mid-montane broadleaf ombrophilous forests			
Mid-montane (2000–3000)	Kalimpong, West Bengal site I	0.82	Mixed forest Jeolikote,	
			Naini Tal site I[c]	0.63
			site III[c]	0.76
	Low- to mid-montane hemi-sclerophyllous broadleaf forests with concentrated summer leaf-drop			
	Kalimpong, West Bengal site III[b]	0.85	–	–
	Kalimpong, West Bengal		Maheshkhan, Naini Tal	0.41
	site I	0.91	Kilbari, Naini Tal	0.63
	site II	0.77		

[a] Complete absence of Dipterocarpaceae and predominance of *Kayea assamica* make it an unusual forest.

[b] These sites represent transition between submontane and mid-montane ombrophilous forests.

[c] Transition between sal and oak/pine forests, far less luxurious than the ombrophilous forests; they however, occupy similar altitudes and are species-rich.

gradient, the forests of either extreme are evergreen, although they differ markedly in leaf texture. With the decreasing mesicness, the forests become increasingly open, short-statured, and simpler in structure, with little vertical stratification.

C. COMMUNITY PATTERNS AT A REGIONAL LEVEL

As pointed out earlier, the impact of climate on community development is rather loose and several factors, such as burning, geology, soil, cultural practices, and nonhuman disturbances [e.g., surface removals due to natural landslides, which are rather frequent (J. S. Singh et al., 1983)], may modify the straightforward relations of climate to community patterns in a given region. Some preliminary studies to interrelate these factors, discussed below, have been made for the central Himalayan region (eastern part of the central Himalaya), within 300–2500 m elevation (Saxena, 1979; Saxena & Singh, 1982a, 1982b; Saxena et al., 1982; J. S. Singh & Singh, 1984b, 1984c; Tewari, 1982; Tewari & S. P. Singh, 1981, 1985; Upreti, 1982).

Along the elevational gradient (from 300 to 2500 m), the following continuously intergrading forest communities (dominant-types) are recognizable: *Shorea robusta* (sal); mixed *Shorea robusta–Pinus roxburghii* (chir pine)–*Toona ciliata* (tun); *Pinus roxburghii*–mixed broadleaf; *P. roxburghii*; mixed *Quercus leucotrichophora* (banj oak)–*P. roxburghii*; *Quercus leucotrichophora*; mixed *Q. floribunda* (tilonj oak)–*Q. leucotrichophora*; mixed *Q. floribunda–Q. lanuginosa* (rianj oak); *Q. lanuginosa*; mixed *Q. lanuginosa–Q. semecarpifolia* (kharsu oak); and *Q. semecarpifolia*. With some variations, such as local preponderance of conifers (e.g., *Cupressus torulosa,* the surai cypress forest), this pattern holds true for the entire central Himalaya.

Indirect ordination of forest stands (based on tree composition) following Bray and Curtis (1957) by and large indicates a continuity of communities, with stands of forest types overlapping on one or more axes (Fig. 5). Overlap in the distribution of species importance values along the elevational gradient becomes apparent also from the direct ordination (Fig. 6). The species populations show a hill-shaped pattern of distribution, importance values of species decreasing in all directions away from the peak in the two-dimensional ordination field (Figs. 7 and 8). The centers of species importance values become scattered rather than clustered in the ordination field. As shown in Figure 5, the x axis tends to separate the stands along the altitudinal gradient, the stands of sal forest, located in the lowest elevation (600–1200 m) occupying its lower extremity and those of higher elevation oaks (2300 m or more), viz., kharsu and rianj oak, occupying the higher extremity of the x axis. Separation of

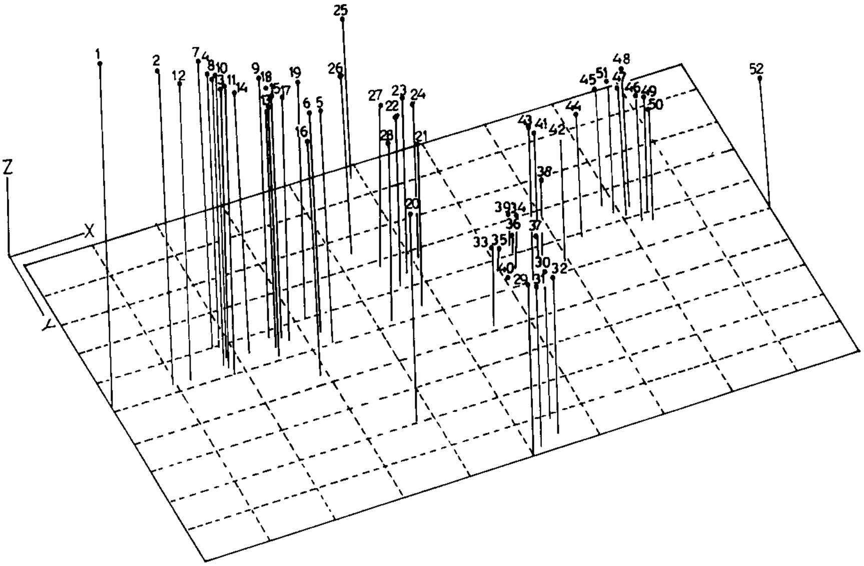

Fig. 5. Three-dimensional ordination model of forest stands of central Himalaya based on tree (>31.5 cm cbh) basal cover. Numbers above bars represent stands of different communities: 1–12, *Shorea robusta* forest; 13–20, mixed *Shorea robusta–Pinus roxburghii–Toona ciliata* forest; 21–28, *Pinus roxburghii*-mixed broadleaf forest; 29–32, *Pinus roxburghii* forest; 33–40, *Quercus leucotrichophora* forest; 41–44, *Cupressus torulosa* forest; 45–52, mixed *Quercus lanuginosa–Q. semecarpifolia* forest.

stands on the *y* axis appears to be in response to the multiple environmental forces, which result from the varying extents and kinds of disturbance and subsequent progress of secondary succession. The stands of early successional chir pine forest, are located farther on the *y* axis with respect to the stands of banj oak forest, the climatic climax forest of the mid-elevations (1500–2000 m), and those of chir pine–mixed broadleaf forest, representing the intermediate stages of succession, are located between the stands of the banj oak and chir pine forests. The tendency of chir pine to form pure stands after encroaching into adjacent forests as a consequence of disturbance is apparent in the ordination graph based on sapling composition (Fig. 9). For example, in the ordination based on tree composition, the stands of sal–pine–tun forest and of sal forest were intermixed to a marked extent, while in the ordination based on sapling composition, the stands of one forest became separated from those of the other. Thus, the disturbance and concomitant expansion of chir pine is likely to cause a discontinuity in the pattern of vegetation along the elevational gradient, in the future.

There is sufficient evidence to indicate that originally the above ele-

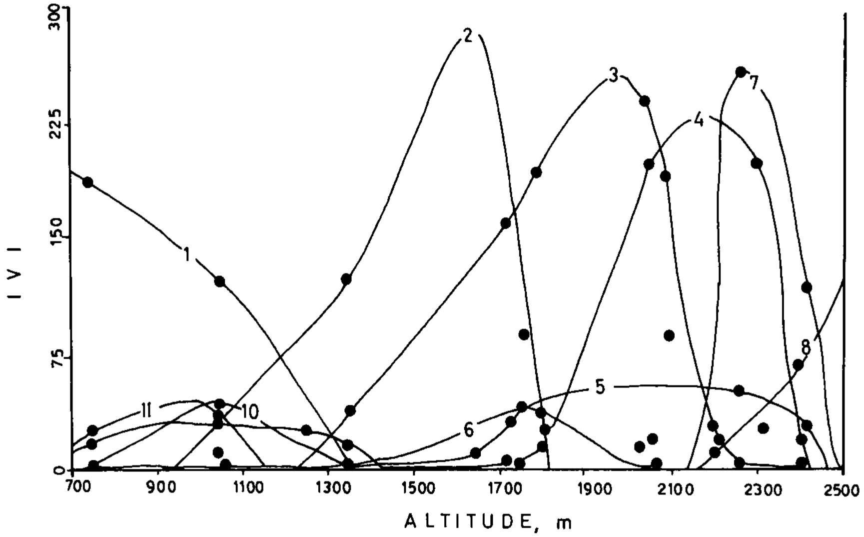

Fig. 6. The IVI (Importance Value Index) of major tree species along an elevational gradient of the central Himalaya. 1, *Shorea robusta*; 2, *Pinus roxburghii*; 3, *Quercus leucotrichophora*; 4, *Q. floribunda*; 5, *Rhododendron arboreum*; 6, *Persea odoratissima*; 7, *Quercus lanuginosa*; 8, *Q. semecarpifolia*; 9, *Syzygium cumini*; 10, *Toona ciliata*; 11, *Mallotus philippensis* (based on J. C. Tewari & S. P. Singh, unpubl.).

vational transect was divisible into two major regimes: the sal regime towards the lower elevations, characterized by a warmer climate; and the oak (various *Quercus* spp.) regime towards the higher elevations. For example, remnant forest stands of sal and oak in mid-elevations of the transect (1200–1500 m) still exist; while banj oak can descend as much as 600 m, sal can ascend up to 2000 m in certain localities; and around 1200 m banj oak forest can be found on undisturbed ridge tops, a site considered by many to be most suitable for chir pine. According to Whittaker (1973), a central or most extensive (steady-state in undisturbed condition) community type, called climatic climax or prevailing community (that which comprises the largest share of climax stands in the area and occupies the largest share of habitats that are not special or extreme for the area), is usually recognizable. The sal and oak forests are such climatic climax communities, respectively, of warmer and cooler climates within the present elevational transect. However, because of disturbances (natural, such as landslides, as well as man-made, such as burning, selective exploitation of biomass, management practices), chir pine has widened its area markedly towards higher as well as lower elevations, and has now stabilized as the most extensive community in the middle elevations. Following Clements' terminology, chir pine forest has

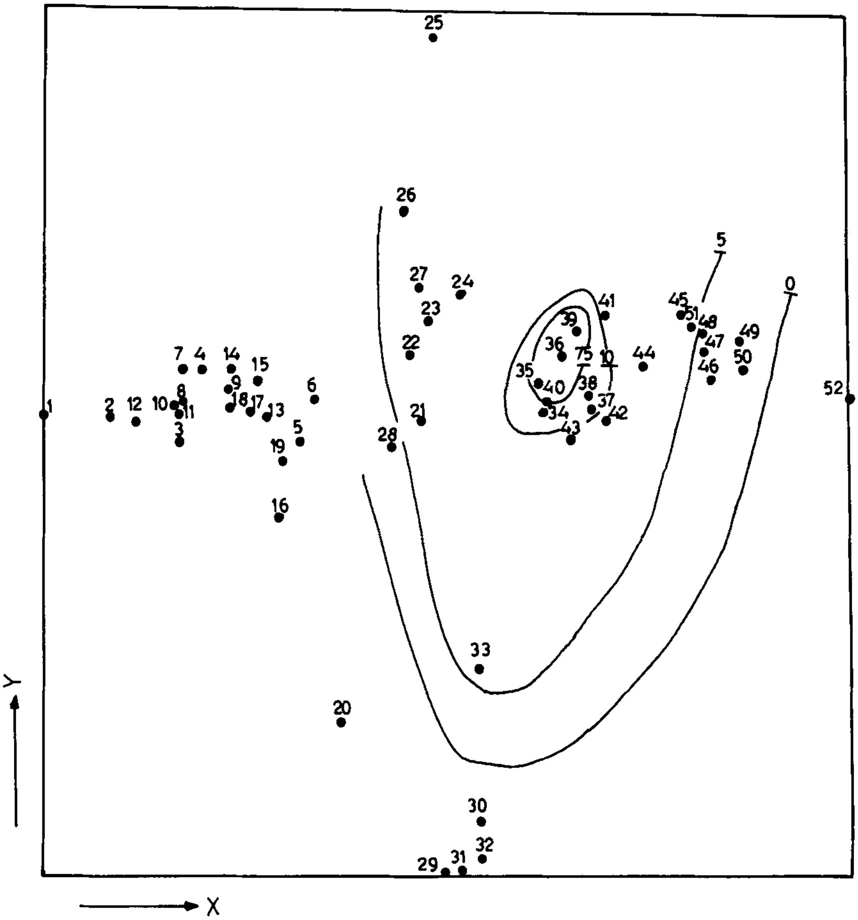

Fig. 7. Quantitative distribution of widely distributed *Quercus leucotrichophora* in terms of relative basal area. Contour lines represent patterns of distribution of relative basal area of the species in 52 stands. For explanation of numbers of stands (closed circles) see Figure 5.

been referred to as an edaphic climax or preclimax (a stable community on exceptionally unfavorable sites in an area) (Dudgeon & Kenoyer, 1925), or subclimax (stability due to human disturbance, including burning) (see Champion & Seth, 1968b; Gupta & Singh, 1962). Our observations suggest that it is a pioneer species exhibiting properties attributable to the "inhibition model" of Connell and Slatyer (1977), thus able to occupy the site for long periods corresponding to the age of the populations. Most of the recent landslide sites of the middle elevations show a preponderance of chir pine in the tree layer (Singh & Goel, 1983). Chir pine often colonizes bare sites immediately after landslides, provided a seed source exists. On

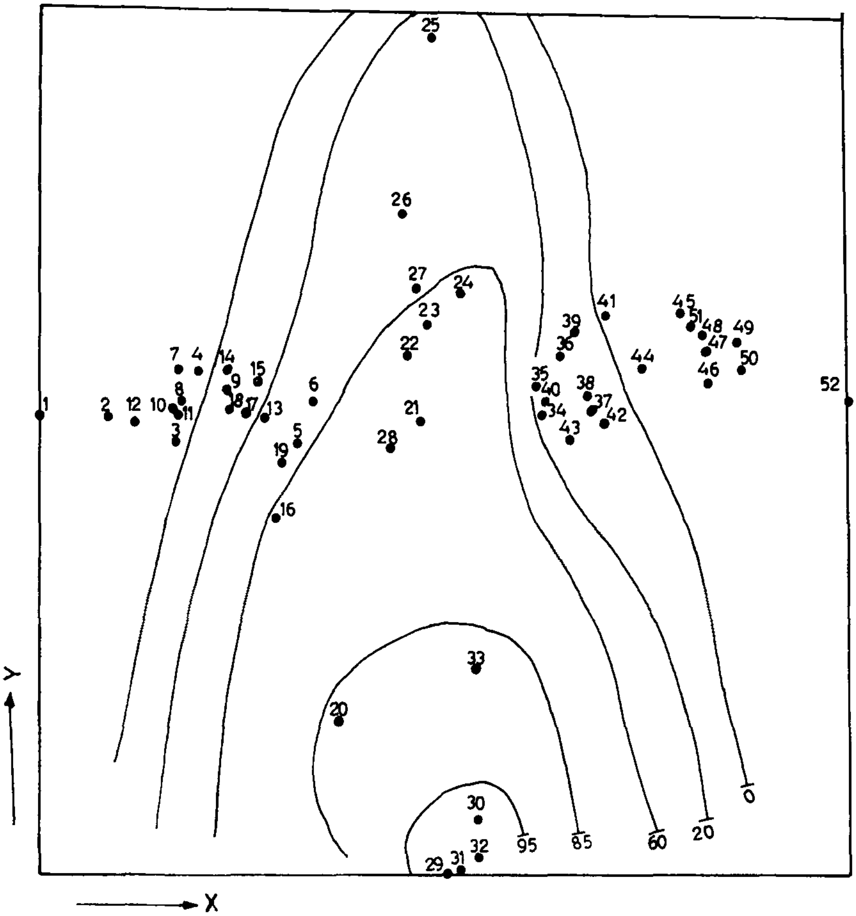

Fig. 8. Quantitative distribution of widely distributed *Pinus roxburghii* in terms of relative basal area. Contour lines represent patterns of distribution of relative basal area of the species in 52 stands. For explanation of numbers of stands (closed circle) see Figure 5.

the basis of its growth responses along light and moisture gradients, Rao (1984) and J. S. Singh and Singh (1984b) identified chir pine as an early successional, stress-tolerant type, for it shares characters attributed to ruderals as well as the stress-tolerants of Grime (1977).

All forests can form a closed canopy (with crown density >80%), with the exception of chir pine (crown density <80%) and transitional communities such as chir pine–mixed broadleaf forest in the middle part of the elevational transect (Tewari & J. S. Singh, 1983; Tiwari et al., 1983). Shrubs dominate the undergrowth of oak and sal forests, while herbs, particularly grasses (due to recurrent burning) predominate in the undergrowth of the chir pine forest.

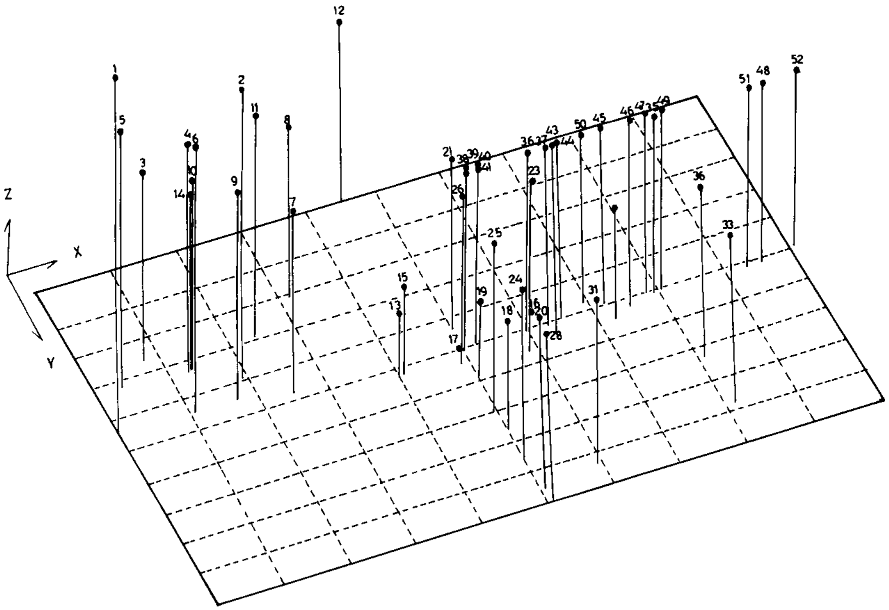

Fig. 9. Three-dimensional ordination model of forest stands based on sapling (<31.5 cm cbh) density. Stands not shown lacked saplings. For explanation of numbers see Figure 5.

Floristic comparison between these forests also elucidates that, although by and large patterns of continuity are evident, they are weakened at certain points. About 50% of the tree species encountered within the elevational transect are present in pine–mixed broadleaf forest as well as in sal–pine–tun forest; in others the percentages are generally lower than 26 (Table III). Obviously, the above two communities are transitional, encompassing species of relatively lower as well as of higher elevations. Interestingly, about 50% of the species found in oak forest of higher elevation (above 2300 m) are found in the pine–mixed broadleaf forest of comparatively much lower elevation (1200–1500 m). Obviously, the overlap in distribution of some species populations on the elevational gradient is considerable. More species of oak forests are common to pine–mixed broadleaf forest than to chir pine forest located in adjacent sites. However, more species of chir pine forest than of chir pine–mixed broadleaf forest are present in oak forests. This indicates that the chir pine community has emerged as a result of disturbance, its presence is not in conformity with the general pattern along the elevational gradient that the climate determines.

A sizeable proportion (37–38%) of tree and shrub species are confined to single forests, and all such trees belong to understory species or are members of subordinate species with negligible importance values.

Table III

Reciprocal floristic commonness[a] of tree species in different forests (values are in terms of percentage) of Kumaun Himalaya located within 600–2500 m (based on J. C. Tewari & S. P. Singh, unpubl.)

Forest	Sal	Sal–chir pine–tun	Chir pine–mixed broad-leaf	Chir pine	Banj oak	Surai cypress	Rianj oak–kharsu oak
Sal (*Shorea robusta*)	100	65.4	28.6	25.0	14.3	0	0
Sal–chir pine (*Pinus roxburghii*)–tun (*Toona ciliata*)	85.0	100	46.4	25.0	14.3	0	0
Chir pine–mixed broadleaf	40.0	50.0	100	87.5	50.0	71.4	55.6
Chir pine	10.0	7.7	25.0	100	35.7	57.1	33.3
Banj oak (*Quercus leucotrichophora*)	10.0	7.7	25.0	62.5	100	57.1	66.7
Surai cypress (*Cupressus torulosa*)	0	0	19.9	50.0	28.6	100	55.6
Rianj oak (*Quercus lanuginosa*)–kharsu oak (*Quercus semecarpifolia*)	0	0	17.9	37.5	42.8	71.4	100

[a] Commonness was calculated as given in del Moral (1979).

If the chir pine (which tends to form nearly pure stands) community is excluded, the tree diversity (alpha) peaks in middle elevations, declining both towards the higher and the lower elevations, but more rapidly towards the former. Within the middle elevations, the species diversity is greater in the mid-successional stages. This is consistent with the observation of Loucks (1970). However, it may be pointed out that the pine–mixed broadleaf forest, which represents a mid-successional stage, is also disturbed continually and this might have promoted its diversity.

Values of total tree basal cover for the above forests are compared with those of other regions in Table IV. Our values (>60 m^2 ha^{-1}) for several oak forests are markedly higher than those reported for oak forests of temperate regions (16–40 m^2 ha^{-1}). The sal forests realize two to five times greater basal area than do similar forests located in the Vindhyan hills. The main difference here is in regard to climatic humidity, the conditions being more mesic in Kumaun Himalaya than in the Vindhyas. However, the values for chir pine forests are lower than those for conifer forests of temperate and subalpine zones. In Kumaun Himalaya, chir pine is maintained with the assistance of human interference, which also involves continual harvest of biomass (in the form of thinning, pruning, and removal of other species).

D. STRUCTURAL AND FUNCTIONAL FEATURES

Recently some studies on structural and functional features at the community-level have been reported for Kumaun Himalayan forests. Saxena et al. (1982) have brought out the differences between the chir pine and oak forests, and have indicated how the biological spectrum of the regional flora differs from that of Raunkiaer's normal spectrum. Tewari (1982) and Tewari and S. P. Singh (unpubl.) have tried to elucidate patterns along an elevational transect (300–2600 m). The following conclusions emerge from these studies.

(i) In the entire Kumaun Himalayan region the percentage of therophytes (about 25%) is markedly higher (Table V) than in the Raunkiaer's normal spectrum (13%). This is a reflection of frequent natural and man-induced surface removals [particularly in the chir pine forests, where therophytes represent the predominant life-form (50.8%)] and grazing. In contrast, in oak forests, phanerophytes prevail (55–60%) and therophytes are poorly represented (11–14%). The biological spectrum of oak forests is similar to that of the subtropical warm-temperate forests of other areas (Whittaker, 1975).

(ii) The flora of Kumaun Himalaya can be categorized as "therohemigeophytic." Compared to this, in a region of Jammu-Kashmir, where temperatures are relatively lower and the climate approaches the Mediterranean-type, the flora is geochamaephytic (Kaul & Sarin, 1976).

(iii) In the three major elevational belts, while the percentages of therophytes, geophytes, and chamaephytes remain more or less constant, that of phanerophytes decreases markedly from 44.8%, between 300 and 1500 m, to 7.3% between 3450 and 5550 m, and that of hemicryptophytes increases from 18.5% in the lowest belt to 37.4% in the highest belt (Table V).

(iv) In response to increasing elevation, the relative density for evergreens (percentage of the total density) increases. If only the broadleaf species were to be considered, the proportion of megaphanerophytic individuals (>30 m tall) declines with increasing elevation. However, this pattern is confounded when conifers are also considered, for chir pine, deodar (*Cedrus deodara*), and surai cypress (*Cupressus torulosa*), which represent the megaphanerophyte life-form, can occupy higher elevations (Fig. 10). The pronounced apical dominance of conifers may largely enable them to attain such heights in conditions where broadleaf trees can only grow much less tall.

(v) Although almost all shades of leaf-form are represented in the region, trees with larger leaves (megaphyll and macrophyll) are mostly confined to lower than 1200 m elevation (Fig. 10). In higher elevations needle-leaf, microphyll, and mesophyll types are well represented.

Table IV

A cross section of data on forest basal area

Forest	Locality	Dominant species	Total forest basal area (m^2 ha^{-1})	Reference
Central Himalayan forests:				
Sal forest	Ranibagh	*Shorea robusta*	63.15	Tewari (1982)
Sal–chir pine–tun forest	Dogaon-Dolmar	*Shorea robusta*	59.43	Tewari (1982)
Chir pine–mixed broadleaf forest	Kalona	*Pinus roxburghii*	69.49	Tewari (1982)
Chir pine forest	Khurpatal	*Pinus roxburghii*	37.34	Tewari (1982)
Banj oak forest	Kailakhan	*Quercus leucotrichophora*	35.57	Tewari (1982)
Surai cypress forest	Naini Tal	*Cupressus torulosa*	33.82	Tewari (1982)
Rianj oak–kharsu oak forest	Kilbari	*Quercus lanuginosa*	62.36	Tewari (1982)
Chir pine forest	Champhi, Sattal	*Pinus roxburghii*	30.24	Saxena and Singh (1982a)
Mixed forest	Sattal	*Quercus leucotrichophora*	35.99	Saxena and Singh (1982a)
Banj oak forest	Maheshkhan	*Q. leucotrichophora*	53.02	Saxena and Singh (1982a)
Rianj oak forest	Maheshkhan	*Q. lanuginosa*	83.78	Saxena and Singh (1982a)
Tilonj oak forest	Maheshkhan	*Q. floribunda*	39.41	Saxena and Singh (1982a)
Subalpine forests:				
Subalpine communities	Enchantment Lakes basin, Washington, U.S.A.	unidentified	0.13–39.89	del Moral (1979)
Tsuga/moss communities	Yatasugatake and Chichilu Mountains, Japan	*Tsuga diversifolia*	64.00–81.00	Franklin et al. (1979)
Abies/herb communities	Mount Ontake and Mount Fuji, Japan	*Abies veitchii*	51.00–65.00	Franklin et al. (1979)

Table IV
Continued

Forest	Locality	Dominant species	Total forest basal area (m^2 ha^{-1})	Reference
Temperate forests:				
Oak forest—east facing slope	North Dakota, U.S.A.	*Quercus macrocarpa*	40.00	Killingbeck and Wali (1978)
West facing slope	North Dakota, U.S.A.	*Q. macrocarpa*	32.60	Killingbeck and Wali (1978)
Oak forest	North-eastern North Dakota, U.S.A.	*Q. macrocarpa*	24.90	Wikum and Wali (1974)
Oak forest (45–50 yr old)	Minnesota, U.S.A.	*Q. ellipsoidalis*	26.50	Reiners (1972)
Oak–hickory forest	Central Missouri, U.S.A.	*Quercus* sp.	22.30	Rochow (1972)
Mixed oak forest	Belgium	—	21.20	Duvigneaud and Denaeyer-DeSmet (1970)
Oak forest (38–45 yr old)	New York, U.S.A.	*Quercus alba, Q. coccinea*	15.60	Whittaker and Woodwell (1969)
Steward Wood	South-western Wisconsin, U.S.A.	*Quercus* sp.	24.14	Cottam (1949)
Tropical forests:				
Tropical rain forest	Silent Valley Upland forest, Kerala, India	—	102.71	J. S. Singh, Singh, Saxena, and Rawat (1984)
Kerangas forest	East Kalimantan, Indonesia	—	10.73	Kartawinata (1978)
Deciduous forest (Fenced)	Chandra Prabha Sanctuary, Varanasi, India	*Anogeissus latifolia*	17.99	K. P. Singh and Misra (1978)
(Open)	Chandra Prabha Sanctuary, Varanasi, India		15.20	K. P. Singh and Misra (1978)
Dry deciduous forest	Chakia forest, Varanasi, India	*Shorea robusta*	12.80	R. P. Singh (1974)
Dry deciduous forest	Chakia forest, Varanasi, India	*Shorea robusta*	30.62	Bandhu (1971)

Table V
Biological spectra of Himalayan forests (% of total species)

Region	Th	G	H	CH	Ph
Kumaun Himalaya[a]					
Altitudinal zones					
300–1500 m	24.1	7.3	18.5	5.4	44.8
1500–3450 m	24.9	8.9	36.5	5.2	24.5
3450–5550 m	25.2	5.6	57.4	4.7	7.3
Forests, with elevations					
Chir pine forest (1300 m)	50.8	1.5	24.6	6.2	16.9
Mixed forest (1340 m)	37.1	1.6	9.7	8.1	43.5
Banj oak forest (1980 m)	14.0	0	27.9	2.3	55.0
Rianj oak forest (2010 m)	13.2	2.6	26.3	5.3	52.6
Tilonj oak forest (2160 m)	11.4	5.7	22.9	0	60.0
Entire region, average	24.9	7.8	33.1	3.9	27.3
Western Himalaya[b]					
Bhaderwah mountainous tract (1500–4200 m)	11.4	9.0	18.0	25.0	25.8
Bhaderwah mountainous tract (3000 and 3500 m)	6.1	12.2	32.6	27.4	15.2
Raunkiaer's normal spectrum[c]	13.0	6.0	26.0	9.0	46.9

Th = therophytes, G = geophytes, H = hemicryptophytes, CH = chamaephytes, Ph = phanerophytes; authors—[a] Saxena et al. (1982), [b] V. Kaul and Sarin (1976), [c] Raunkiaer (1934).

(vi) Regardless of the elevation, vernal flowering and anemophily (conditions are warm and dry) prevail in the region. The vernal flowering enables the species to take advantage of the rainy season, since by that time seeds may start falling on the ground and thus get adequate moisture for germination.

(vii) Relative density for thick-barked (>20 mm) and fire-resistant species declines rapidly above 1800 m, where the frequency of burning is negligible (J. S. Singh & Singh, 1984a). The two dominant species of the elevational range 300–1800 m, sal and chir pine, are fire-resistant. The above characters, viz., thick bark and fire resistance, are associated with a megaphanerophyte life-form and sun-demanding nature.

(viii) Biotic seed-dispersal is prevalent at higher elevations (particularly in oak forests), while an abiotic mode of seed dispersal is typically found in forests of relatively lower elevations, including chir pine. This is why several crown-inhabiting mammals (e.g., the giant red flying squirrel,

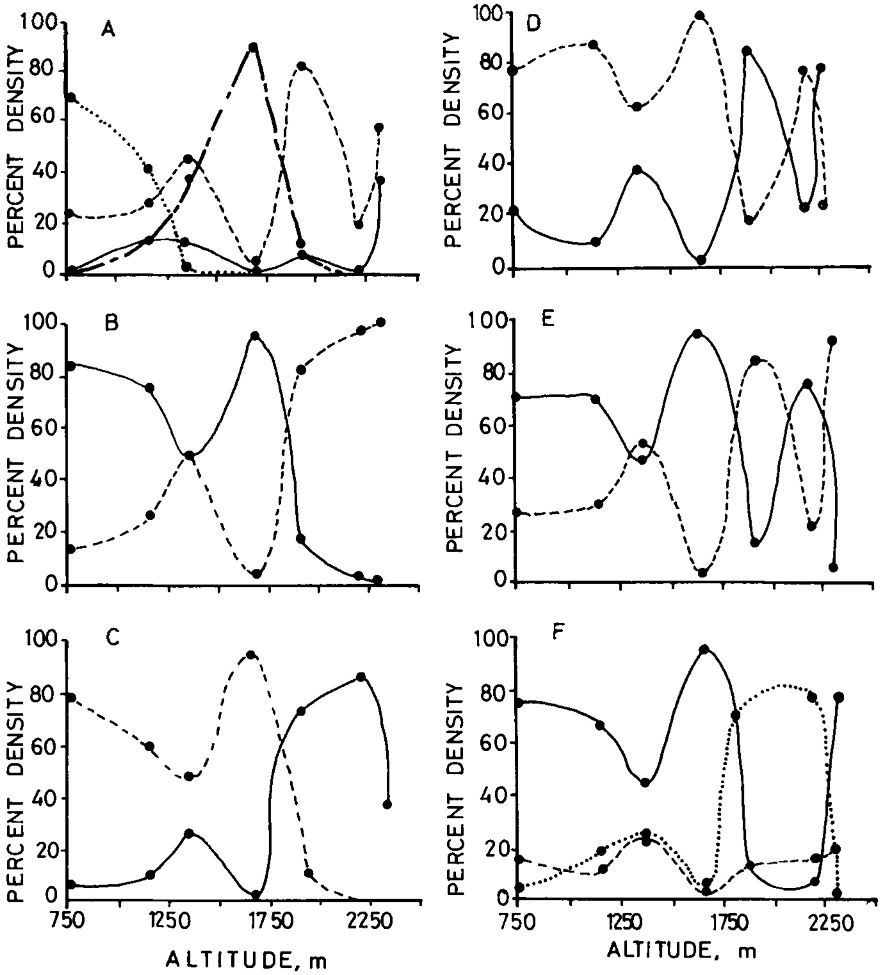

Fig. 10. Patterns of the structural and functional features of trees along an elevational gradient in central Himalaya. A. Leaf size after Raunkiaer (1934); ●——● microphyll; ●– –● mesophyll; ●·····● macrophyll; ●—·—● needles and scales. B. Response to fire; ●——● fire resistant; ●– –● fire susceptible. C. Bark thickness, ●——● 5–10 mm; ●– –● more than 20 mm. D. Pollination mechanism; ●——● biotic; ●– –● abiotic. E. Life form; ●——● megaphanerophyte (more than 30 m high); ●– –● mesophanerophyte (8–30 m high). F. Response to shade; ●——● sun demanding; ●– –● shade demanding; ●·····● shade tolerant (based on Tewari, 1982).

Pataurista petusista albiventer, and the black-faced Himalayan langur, *Presbytis entellus*) or those which can forage in the crown (e.g., the Himalayan black bear, *Solenarctos thibetanus*) are abundantly found in oak forests.

Little is known about the structural and functional features of the eastern

Himalayan region and those of above 2500 m altitude in the entire Himalaya. However, some qualitative inferences can be derived from our studies (J. S. Singh & Singh, 1984a, 1984b, 1984c) and from the literature available on silvicultural aspects (Champion & Seth, 1968b; Troup, 1921) for higher elevations in the central and western regions. Between 2500 and 3000 m, the forests are mainly composed of evergreen broadleaf species, viz., kharsu oak, *Rhododendron* spp., and several needle-leaf evergreen conifers, viz., fir, deodar, spruce, and kail pine (*Pinus wallichiana*). Therefore, evergreenness is preponderant, except in some localities where winter-deciduous forests consisting of *Aesculus indica, Acer villosum, A. acuminatum, A. pectinatus, A. pictum, Prunus cornuta, Juglans regia, Salix wallichiana, Betula alnoides,* etc., exist. Forests consist primarily of fire-susceptible species. As far as life-form is concerned, both megaphanerophytes (represented by conifers) and meso-phanerotypes (represented by broadleaf species) may form distinct communities as well as mixtures. The broadleaf species are likely to be shade-tolerant, for they can grow under the canopy of the former. Some broadleaf species which are shade-intolerant, such as *Q. lanuginosa* (which can reach 2500 m elevation, but is generally found below it), form only pure stands and fail to survive under the canopy of megaphanerophytes. The biotic mode of seed dispersal is largely represented by oaks. However, as at lower elevations, anemophily is likely to prevail in higher elevations also. Studies pertaining to structural-functional features of trees are particularly needed in the eastern Himalayan region, for they may prove to be useful in characterizing and classifying the species-rich vegetation, where dominant types are not recognizable.

In the Himalayan region, with pronounced exploitation of species for fodder and fuel (J. S. Singh, Pandey & Tiwari, 1984), species with nutrient-poor leaves, or with unpalatable leaves and those with nonflammable wood have a better chance for survival, if biotic pressures were to continue unabated. Survival of *Rhododendron arboreum* and *Lyonia ovalifolia,* and the local disappearance of oaks in the central and western regions are related to biotic stress (Champion & Seth, 1968b). Weeds, including exotics (e.g., *Lantana camara*) tend to expand until destruction of vegetation impairs the basic fabric of the productive environment. Local examples have emerged, such as the stress-tolerant cactoid, *Euphorbia royleana* becoming a dominant species.

E. POPULATION STRUCTURE AND REGENERATION

1. Population Structure

Saxena et al. (1984) have interpreted the structure and regeneration of Kumaun Himalayan forests over a large area (about 8000 ha, distributed between 300 and 2500 m altitude) on the basis of the density-diameter distribution of trees (individuals with dbh 10 cm and above). One major conclusion is that there has been a large scale replacement of old-growth forests by more even-aged, successional forests. As shown in Figure 11, a density-diameter curve ($d - d$ curve) for the entire area assumes an overall convex appearance (largely, second derivative negative). It is likely to be constituted as a result of exploitation practices, which maximize the even-agedness, and the proportion of intermediate-age stands. Obviously, the relatively shade-tolerant oak species are failing to regenerate and shade-intolerant species, such as pine, are regenerating abundantly in younger forest stands. The overall total forest structure thus gives an impression of an early successional forest. The exploitive management practices and the biotic stress exerted by the hill population (grazing, lopping, felling for firewood) on oak species have encouraged the pine in various ways to intrude into oak forests. Even in pine and sal forests, a population of intermediate-age trees appear to be promoted. Thus, the old-growth all-aged multilayered forests are being removed at a faster rate than they are being reconstituted. The exploitation cycles appear to be shorter than they should be to promote uneven-aged forests.

2. *Regeneration*

For the tree species of central Himalayan forests preliminary observations are available on seed characteristics, seed germination in response to various environmental factors, growth of seedlings along shade and moisture gradients, and population dynamics of certain species in natural forests (Rao, 1984; Saxena & J. S. Singh, 1982a, 1984; J. S. Singh & Singh, 1984b; Tewari, 1982; Upreti, 1982; Upreti et al., 1985).

Broadleaf species with larger seeds (>50 mg dry wt/seed) mostly occur at relatively higher elevations. The largest seeds are those of *Aesculus indica* (7.2 g dry wt/seed) and of *Quercus semecarpifolia* (2.4 g dry wt/seed), which occur above 2000 m (the latter ascends above 3000 m). The large seeds enable these species to attain greater initial shoot heights in the dense shade of the undercanopy environment, and deeper root penetration, since due to slow decomposition a considerable amount of litter and humus accumulates at these elevations. The two major species of lower elevations (<2000 m), viz., *Shorea robusta* and *Pinus roxburghii* bear much smaller seeds (less than 1 g dry wt/seed). However, because of frequent surface fire the litter deposition is negligible. Further, the canopy is quite open in chir pine forest. In laboratory conditions, when stored in polyethylene bags at room temperatures, the seeds of all species lose viability within one year, though the duration of viability in soil is not known for most of the species. Seed viability is of exceptionally short

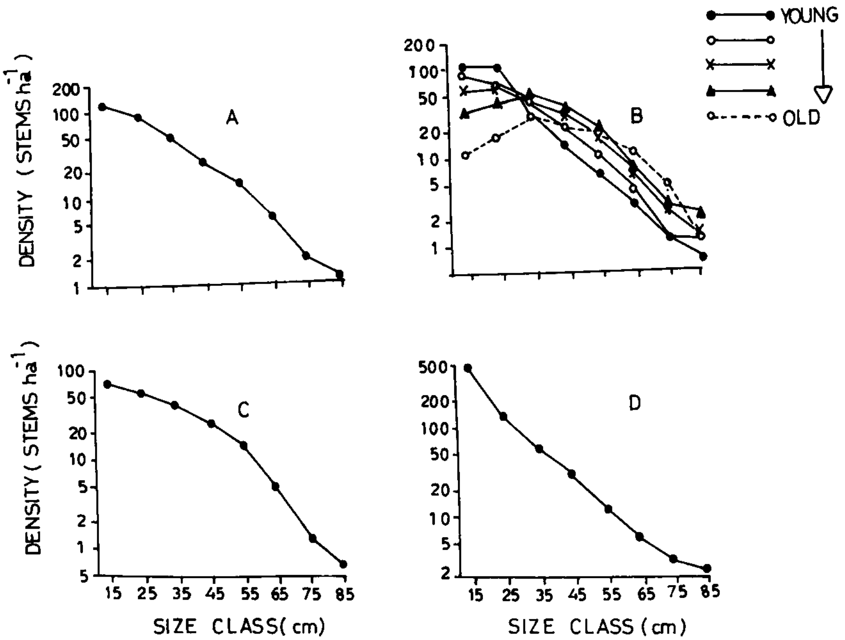

Fig. 11. A. Density-diameter distribution curve for all species within the whole Kumaun Himalaya. B. Population structure of all species in Kumaun Himalaya across the age sequence. Diameter strata: 10–24 cm (solid circles connected by solid line), 24–29 cm (open circles connected by broken line), 29–34 cm (X's connected by solid line), 34–39 cm (triangles connected by solid line), and 39–44 cm (open circles connected by broken line). C. Density-diameter distribution curve for all species in *Pinus roxburghii* forest. D. Density-diameter curve for all species in *Quercus floribunda* forest (based on Saxena et al., 1984).

duration in *Shorea robusta* and *Populus ciliata* (<2 weeks), even in soil. But their germination is synchronized with the commencement of rainy season. The seeds of the latter species require rain storms for dispersal from the fruits. In general, seeds lack clear-cut dormancy, but in species whose seeds fall after rainy season, winter chilling promotes the rate of seed germination (e.g., *Quercus leucotrichophora, Pinus roxburghii, Fraxinus micrantha,* etc.).

Germination capacity under conditions of adequate moisture and temperature is high for about half of the tree species investigated (Table VI). These include most of the dominant species, *Cedrus deodara* and *Abies pindrow* being the notable exceptions.

Most native tree species show a wide response breadth for germination on the temperature gradient (average Levins's response breadth, B = 0.929, Table VII). Evidently, the elevational range of these species is not restricted by temperature at the germination stage. Germination in all oak species was almost insensitive to variations in temperature within

Table VI

Germination capacity (percentage of seeds) under conditions of adequate moisture and temperature for the central Himalayan trees. Observations are based on 39 species (based on R. N. Kaul & Ganguli, 1961; J. S. Singh & Singh, 1984b)

Capacity	Percentage of total species	Typical examples
High (<75%)	51	*Quercus* spp., *Shorea robusta, Pinus roxburghii, Bauhinia variegata.*
Intermediate (51–75%)	21	*Betula alnoides, Cupressus torulosa, Pinus wallichiana, Fraxinus micrantha.*
Low (26–50%)	18	*Cedrus deodara, Abies pindrow, Toona ciliata, Rhododendron arboreum.*
Very low (25% and less)	10	*Alnus nitida, Cassia floribunda.*

15° to 30°C ($B = 0.979$–0.998). Wider response breadths are found for sal ($B = 0.944$) and chir pine ($B = 0.969$). *Aesculus indica* showed the narrowest response breadth among the native species. In this species, normally found above 2000 m, germination was drastically reduced at high temperatures (30°–35°C).

On average, most of the native species show wide response breadth (average $B = 0.928$) on a light (quality) gradient also (Table VII). In *Erythrina arborescens,* a species with wide elevational range and occurring outside the close-canopied forests, germination is entirely insensitive to light variations. In comparison, the response breadths on a moisture gradient (average B for most native species = 0.769) are narrower, indicating a more vital role of moisture in controlling the germinability. Some of the species usually localized to mesic habitats, such as *Fraxinus micrantha* ($B = 0.415$) and *Olea glandulifera* ($B = 0.299$) have especially narrow response breadths on the moisture gradient. Among the oaks, seed germination of *Q. leucotrichophora* ($B = 0.698$) is most vulnerable to hydric deficiency. Compared to this, chir pine can withstand higher water stress ($B = 0.872$). A markedly wide response breadth for germination on the moisture gradient for sal (*Shorea robusta*) ($B = 0.899$), suggests a good potential for the production of seedlings, though the exceptionally short period of seed viability requires a synchronization of seed fall with the advent of the rainy season. A delay in the monsoon can thus drastically inhibit the recruitment of seedlings. Those oak species which shed seeds during the rainy season (*Q. floribunda* and *Q. semecarpifolia*) show vivipary, which may help in the establishment of seedlings on ground overstocked with herbage cover.

Table VII

Levins's response breadth (*B*) for seed germination of the central Himalayan trees on certain environmental gradients (based on J. S. Singh & Singh, 1984b)

	Environmental gradients		
	Temperature	Light quality	Moisture
Average of native species (25)	0.902	0.885	0.721
Major native species			
Pinus roxburghii	0.969	0.872	0.872
Quercus floribunda	0.996	0.985	0.996
Quercus leucotrichophora	0.979	0.963	0.698
Shorea robusta	0.944	0.977	0.899

Levins's response breadth (B) = $1/(\sum_{i=1}^{s} p_i^2)S$ where p_i is the proportion of seed germination in state i and S is the total number of states (treatments). The resulting measure B is a scale from 0 to 1 with 1 being the widest breadth.

Observations on seedling growth along a shade gradient (from full sunlight to 18% of full sunlight) indicates that generally species attain their maximum growth at 70% sunlight. In contrast to the general opinion that the early successionals show wider response breadth on the environmental gradients than the late successionals (Odum, 1969; Zangerl & Bazzaz, 1983), *Quercus leucotrichophora,* a climax species, shows wider response breadth on the shade gradient than *Pinus roxburghii* and other early successional species (Table VIII). This suggests that the replacement of *Q. leucotrichophora* by *P. roxburghii* under disturbed conditions has not occurred as a consequence only of greater availability of light on the ground floor. Seedlings of the former exhibit a distinctly wider response breadth than that of the latter on the moisture gradient (Table VIII).

Age structures indicate that the three climax species, banj oak (*Quercus leucotrichophora*), kharsu oak (*Q. semecarpifolia*), and sal (*Shorea robusta*) are failing to regenerate adequately over large areas. On the other hand, chir pine is regenerating copiously (Saxena & J. S. Singh, 1984; J. S. Singh & Singh, 1984a). Cutting of all trees but a few seed-bearers (15–25 seed bearers ha^{-1}), frequent fires, and cutting of broadleaf species left after fire are the essential techniques used to promote the regeneration of chir pine (Champion & Seth, 1968b). Once the species has established, its ability to sequester the available soil N excludes the reinvasion of broadleaf species, which are generally high N-demanders (J. S. Singh, Rawat & Chaturvedi, 1984).

As far as the oaks are concerned, the regeneration problem is principally due to severe biotic stress. Excessive lopping, consequent reduction in

Table VIII

Levins's response breadth (*B*) for seedling growth of central Himalayan trees on certain environmental gradients (based on P. B. Rao, 1984)

	Environmental gradients	
	Shade	Moisture
Acer oblongum	0.678	0.986
Aesculus indica	0.900	0.997
Cupressus torulosa	0.637	0.959
Eucalyptus globulus[a]	0.678	0.766
Eucalyptus hybrid[a]	0.743	0.975
Olea glandulifera	0.654	0.920
Pyrus pashia	0.649	0.983
Pinus roxburghii	0.662	0.982
Quercus floribunda	0.856	0.996
Quercus leucotrichophora	0.817	0.962

[a] Exotic species.

seed production and increased insect infestation of seeds and possible decline in winter rainfall (when seeds reach the ground) over the last two to three decades, are some of the factors attributed to failure of regeneration of *Q. leucotrichophora* (Saxena & J. S. Singh, 1984; Upreti, 1982). Coppicing, which involves sprouting of shoots from the buds of stumps left after cutting, is quite frequent in oaks (Champion & Seth, 1968b).

The Forest Department seems to consider that sal has failed to regenerate in the "bhabar belt," and its replacement by teak (*Tectona grandis*), a timber species of southern and central India, and by several eucalypts and poplars has been initiated (R. P. Singh, pers. comm.). A study of the population dynamics in two adjacent sal stands in the submontane belt (Rao, 1984; Rao & S. P. Singh, 1985) throws some light on the pattern of sal regeneration (Fig. 12). One, called the old-growth stand, was characterized by the presence of uneven-aged trees, up to very old ones and the other called seedling-coppice stand was characterized by the preponderance of even-aged young trees. The canopy of the former was broken and that of the latter was almost complete. In the old-growth stand the regeneration of sal was quite active from short seedlings (10 cm or less tall) to small sapling size-class (>30 cm tall and circumference at ground level 10 cm or less), but was arrested from this size-class to large sapling size-class (cbh more than 10 cm–30 cm). On the other hand, in the seedling-coppice stand the regeneration was arrested from a very early stage (i.e., the medium size-class seedlings; 10 cm–20 cm tall). However, once the individuals reached the large sapling size-class (cbh > 10 cm–

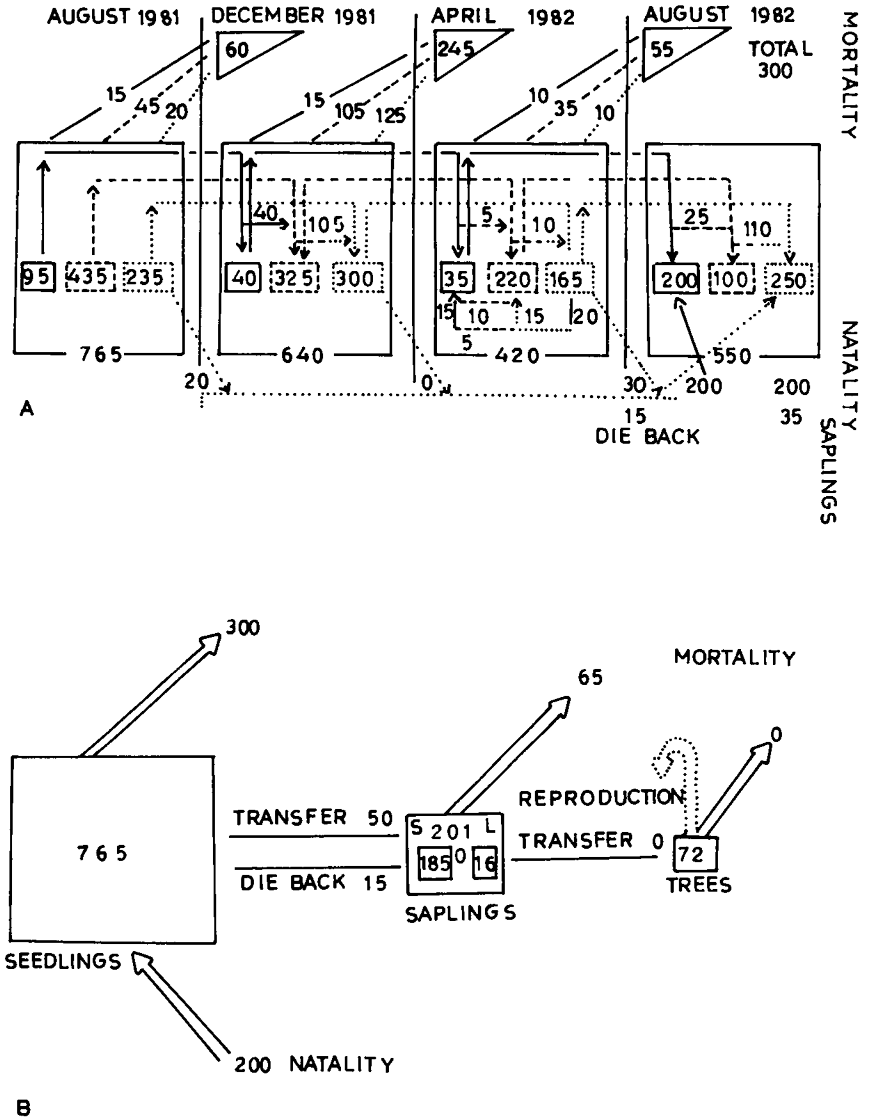

Fig. 12. A. Population dynamics of seedlings in a plot of 0.2 ha of sal old-growth stand (OGS), located in submontane belt of central Himalaya, August 1981 to August 1982. Solid line boxes represent seedlings (<10 cm high), broken line boxes represent medium size seedlings (10–20 cm high) and dotted line boxes represent tall size seedlings (20–30 cm high). Triangles represent mortality; arrows indicate transfer of individuals from one to another size class; and populations of each size class are given in smaller boxes and that of total, outside the small boxes. B. Population dynamics of seedlings, saplings, and trees per 0.2 ha of sal old-growth forest stand, August 1981 to August 1982. Within the sapling box, the small S box represents small saplings (<30 cm height and up to 10 cm dbh) and small L box large saplings (10–30 cm dbh). The population size at the beginning of study is given inside these small boxes; the arrow indicates transfer from small to large saplings (based on P. B. Rao, 1984).

30 cm) they become immune to die-backs and mortality. Thus, the successful regeneration of sal largely depends on the ability of individuals to attain about 10 cm cbh (large saplings), after which the individuals withstand the stressful conditions successfully. Die-back seems to be an inherent property of the species, which helps it to survive the adverse conditions, such as frost and hydric-deficiency. The regeneration will also depend on the "good seed year cycle" which is reported to be 3–5 years (Pande, 1956) and the synchronization of a good seed year with timely rainfall, which may happen every 25–30 years (Champion & Seth, 1968b).

Information on the regeneration of other species is fragmentary and inconclusive. Among the species studied so far, the longest cycle of good seed year (10 yr) is reported for *Abies pindrow* and the shortest (1–2 yr) for two successional species of the submontane zone, viz., *Acacia catechu* and *Dalbergia sissoo.* For *Cupressus torulosa,* it is 7–8 years, for *Picea smithiana* 5–6 years, for *Pinus roxburghii* 4–5 years, for *P. wallichiana* 2–3 years, and for *Terminalia tomentosa* 3–4 years (Pande, 1956).

VI. Functional Aspects

A. HYDROLOGICAL CYCLE

Results from studies on the hydrological cycle of Himalayan forests have been reported by Dabral and Subba Rao (1968), Dabral et al. (1963), Pandey et al. (1983), Pathak (1983), and Pathak et al. (1983). Detailed studies on six central Himalayan forests listed in Table IX are now available (Pathak et al., 1984, 1985).

Frequency distributions of shower size and rainfall intensity show that 59–74% of rainfall events are of small size (<20 mm) and only 1.2–7.5% are of >80 mm each. Rainfall intensity is ≤ 4 mm/30 min for 62–84% of storms, and less than 5% of the storms are of >8 mm/30 min intensity (Pathak et al., 1984). Stem flow accounts for 0.28 to 0.89%, throughfall 74.7 to 91.5%, and canopy interception 8.1 to 25.0% of the gross rainfall (Table X). The overland flow is generally less than 1% of the gross rainfall (Pandey et al., 1983; Pathak et al., 1984, 1985). Singh et al. (1983) suggest that these Himalayan catchments are subsurface-flow systems and therefore are markedly prone to landslips and landslides.

B. RECOVERY OF DAMAGED FOREST ECOSYSTEMS

The Himalayan forest ecosystems have been repeatedly damaged in the geological past, because of the inherent vulnerability of these young mountains to landslides caused by tectonic stresses. Man has accelerated this process through deforestation, cultivation, and road-building activities (Pandey & J. S. Singh, 1984a; Pandey et al., 1983; Pathak et al., 1984; J. S. Singh et al., 1983). Shifting cultivation has been a predominant practice

Table IX

Certain site characteristics of central Himalayan forests studied in detail for ecosystem functions

Forest types	Altitude (m)	Predominant lithology	Average annual rainfall (mm)	Average temperature (°C)	Dry season P-E index[a]		Dominant species
					Summer	Winter	
Sal forest	350	Sandstone associated with slates	2076	23.0	2.33	6.23	*Shorea robusta* *Mallotus philippensis*
Pine–mixed broadleaf forest	1350	Sandstone associated with slates	2005	17.5	3.30	5.29	*Pinus roxburghii* *Quercus leucotrichophora*
Pine forest	1750	Slates and dolomites	2185	15.8	4.92	3.55	*Pinus roxburghii* *Myrica esculenta*
Mixed oak–pine forest	1850	Mica schist and gneisses	1313	15.8	5.10	8.71	*Quercus leucotrichophora* *Pinus roxburghii*
Mixed oak–rianj dominated forest	2150	Dolomite limestone and conglomeratic sandstone	2488	15.0	6.40	13.20	*Quercus lanuginosa* *Q. floribunda*
Mixed oak–tilonj dominated forest	2150	Quartzite and slates	2488	15.0	6.40	13.20	*Quercus floribunda* *Q. leucotrichophora*

[a] Calculated according to Thornthwaite (1931): Mesicness increases with increasing value of P-E index.

Table X

Apportionment of monsoon rainfall (mm) in central Himalayan forests (based on Pathak et al., 1984, 1985)

Forest	Gross rainfall	Stand through-fall	Stand stem-flow	Stand inter-ception	Litter inter-ception	Over-land flow	Ground vegetation intercep-tion + infiltra-tion
Sal forest	1153	950	10	193	113	8	839
Pine–mixed broadleaf forest	1179	1079	5	95	85	15	984
Pine forest	1234	922	3	308	89	10	727
Mixed oak–pine forest	915	758	3	154	81	5	675
Tilonj dominated–mixed oak forest	1364	1155	5	204	128	7	1026
Rianj dominated–mixed oak forest	1240	1002	11	227	114	2	897

in the eastern region for centuries. The present information regarding the recovery processes is largely derived from two sets of studies, one dealing with the recovery subsequent to shifting cultivation (Mishra & Ramakrishnan, 1983a, 1983b; Ramakrishanan & Toky, 1981; Toky & Ramakrishnan, 1983a, 1983b), and the other dealing with the recovery of oak forest damaged due to landslide (Pandey & Singh, 1985).

1. Recovery Processes Following Shifting Cultivation

Shifting cultivation involves cutting the forest vegetation, burning the debris and cropping for a year or more before abandoning the land and allowing a fallow to develop. The interval before recultivating the same site (called the fallow cycle) used to be 20–30 years in the past but now, it is generally 4–5 years (Toky & Ramakrishnan, 1983a). Thus, the site is recultivated before secondary succession has moved to a tree stage. A 5-year fallow with a number of years of cultivation before abandonment is dominated by *Eupatorium odoratum,* a non-sprouting perennial herb (i.e., depending entirely on seeds for reproduction) at lower elevations (about 100 m) in eastern Himalaya, because the rhizomes of the sprouting species are removed by repeated hoeing during the cultivation period. On the other hand, *Imperata cylindrica,* a sprouting perennial shares dominance with *Eupatorium* when the field is abandoned after only one year of cultivation. Obviously, cultivation for one year is insufficient to eradicate the rhizomes of this species, which sprout copiously with the temporary enrichment of the fields with nutrients and solar radiation. A 10-year fallow shows clear-cut dominance by *Imperata.* After 5 years of abandonment, the bamboo, *Dendrocalamus hamiltonii* appears and dominates the vegetation between 10 and 20 years. In 20 years, a number of shade-intolerant trees (*Terminalia bellerica, Vitex glabrum, Schima wallichii, Dillenia pentagyna,* etc.) also share dominance with *Dendrocalamus.* Since some of these tree species are also members of mature forests (Champion & Seth, 1968a), it is suggested that the succession is fairly rapid. Accumulation of live biomass rises exponentially until 5 years (from 0.5 kg dry wt m^{-2} in 1 yr to 2.3 kg dry wt m^{-2} in 5 yr), and continues to rise rapidly thereafter until 20 years of succession, to about 15 kg m^{-2}. The proportions of live biomass in various plant groups also shift rapidly (Fig. 13). Herbs, which account for 63% of the biomass at 5 years are almost completely replaced by the bamboo and shrubs and trees by 10 years. From here, until the 20th year, the two groups (viz., bamboo and tree plus shrubs) account for about equal proportions of live biomass. The increase in biomass is also accompanied by a rapid increase in species diversity (Shannon-Wiener index) (from less than 1 at 1 yr to about 2.5 at 20 yr), litter fall (from 0.1 kg dry wt to 1 kg dry wt m^{-2} yr^{-1}) and net primary production (from 0.5 kg dry wt to 1.8 kg dry wt m^{-2} yr^{-1}). The increase in net production is conspicuous between 5 and 10 years, which coincides with the establishment of *Dendrocalamus.* This species plays a prominent role in nutrient cycling, particularly that of K. It conserves this element, which is highly susceptible to losses after slash and burn, by accumulating it in significantly high concentrations. From the 10th to the 20th year, more than two-thirds of the total K in the ecosystem is accumulated in plant biomass. Consequently, the decline in the total ecosystem K from the first to the 10th year is followed by a rapid rise from the 10th to the 20th year (Fig. 14). *Dendrocalamus* accounts for 54–60% of the total K accumulated in the live biomass. This role is reported to be similar to that of *Musanga cecropioides* in early succession of fallows in Yangambi (Belgian Congo) region (Bartholomew et al., 1953). Interestingly, K is predominant over Ca in live biomass, which is the reverse of the situation generally found for mature forests (e.g., Golley et al., 1975; Grubb & Edwards, 1982).

The concentration of all elements in soil, except N, tends to be higher in a 1-year fallow as compared to more aged ones (Fig. 14). This is due to the nutrient release following slash and burn. Rapid accumulation of nutrients in live biomass during 5–10 years causes a rapid depletion of nutrients in soil. This is followed by a phase during which nutrient return through litter fall builds up the soil nutrient pool. On the other hand, N is lost from the soil through volatilization due to burning and due to the adverse effect of fire on the N-fixing microbial populations. However,

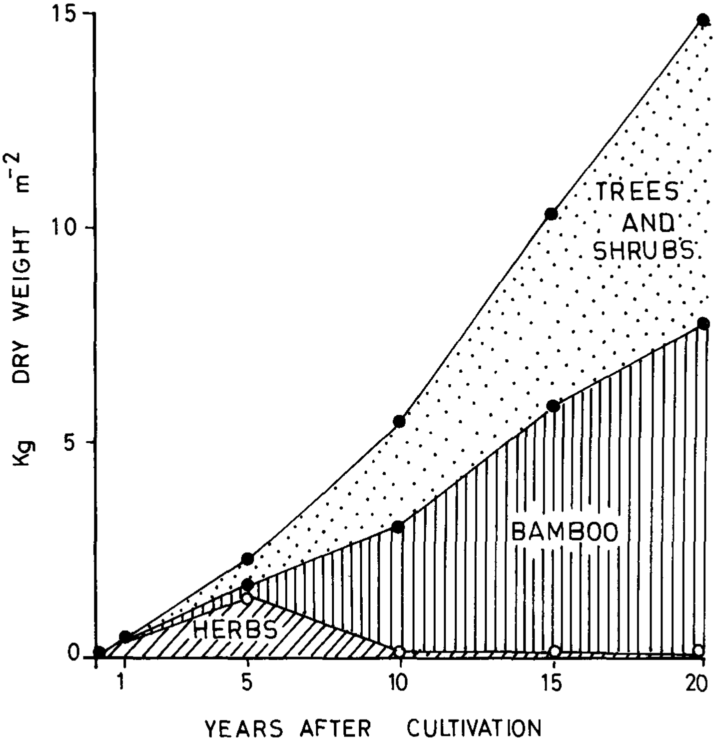

Fig. 13. Live biomass accumulation during succession following shifting cultivation in northeastern Himalaya (developed from data in Toky & Ramakrishnan, 1983a).

soon after the fire, as micro-environmental conditions improve, N-fixation presumably is resumed and the N content increases during the rest of the first 10 years of succession (see Ahlgren & Ahlgren, 1965; Rice, 1974; Smith et al., 1968).

In their study of recovery in the Hubbard Brook Forest ecosystem following clear-cutting of part of the forest, Bormann and Likens (1979) recognized a "reorganization phase" for 15 years after clear-cut during which total biomass in the system (live biomass + dead wood biomass + forest floor + soil organic matter) showed a net loss. Thereafter, for the next 155 years, an aggradation phase occurred during which the total biomass increased. However, in the case of succession following slash and burn agriculture, the soil biomass (increasing N pool is assumed to reflect increasing soil organic matter and biomass) and the live plant biomass increase rapidly within the first 10 years (Fig. 15). Here the aggradation phase is thus initiated as soon as 1 year after the abandonment of cultivation, with the reorganization phase being confined to a period of less than 1 year.

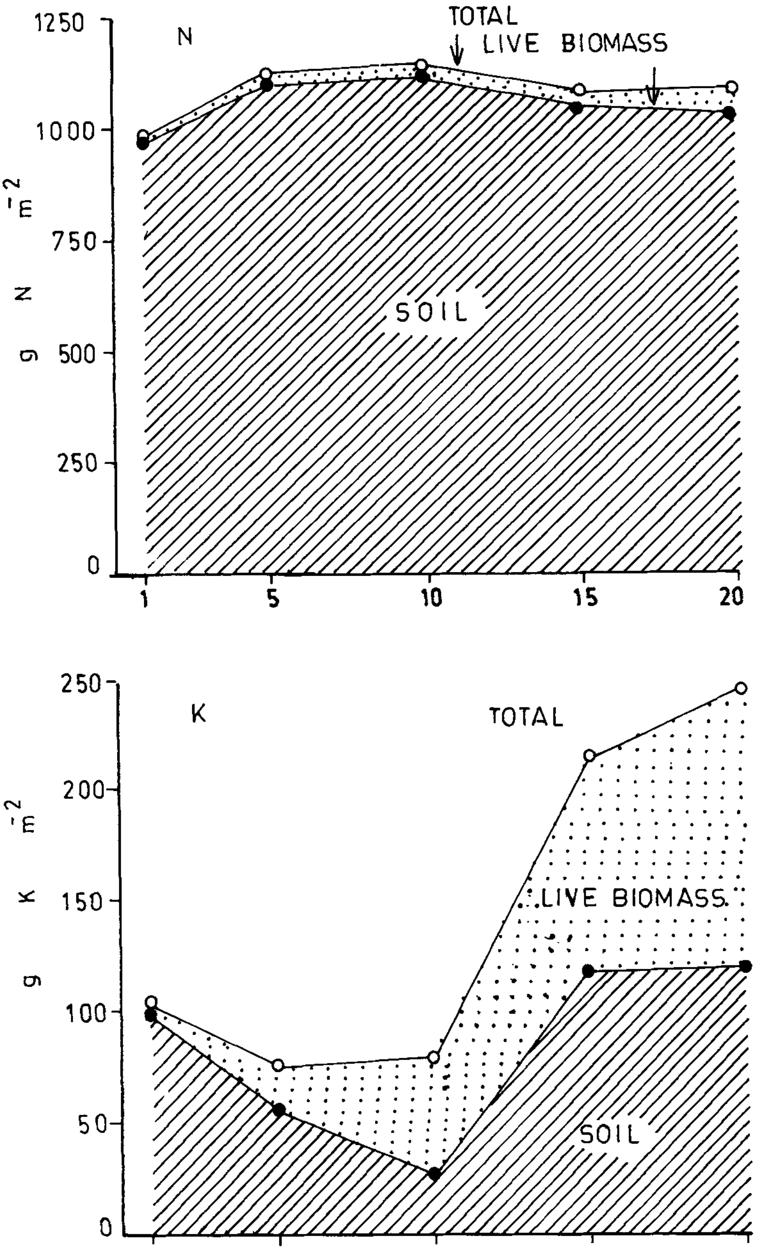

Fig. 14. Density of nutrients in different components of the ecosystem during 20 years of succession following shifting agriculture in Meghalaya, north-eastern Himalaya (developed from data in Toky & Ramakrishnan, 1983b).

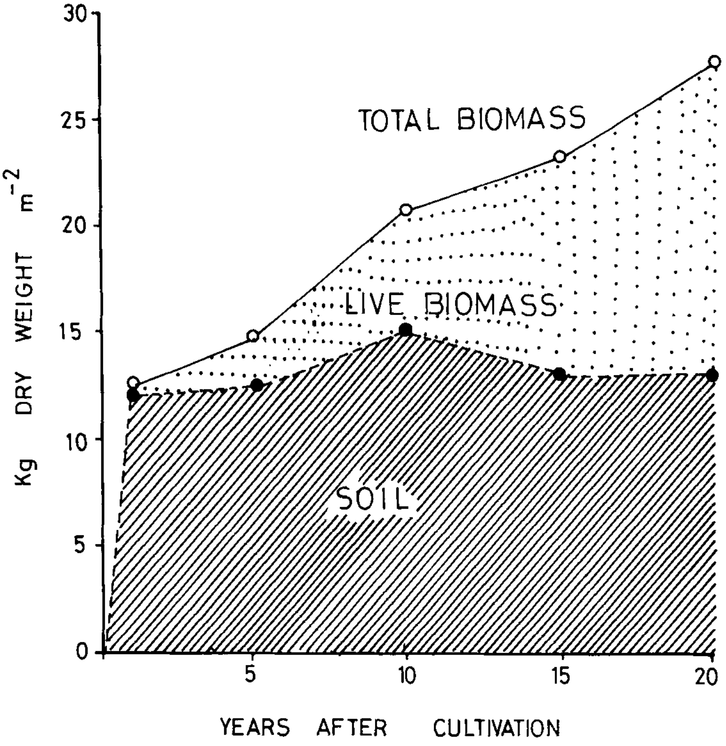

Fig. 15. The accumulation of total biomass during the aggradation phase of ecosystem development (after shifting cultivation) following a decline during the short phase (approximately 0–1 year) of reorganization (R). Broken line connected with closed circles indicates biomass of floor litter. Organic matter in mineral soil was calculated from N density in soil using C:N ratio of 7, as given in Mishra and Ramakrishnan (1981) (for others, data from Toky & Ramakrishnan, 1983a, 1983b were used).

At relatively higher elevation (1500 m), successional patterns are similar to those described above, with some variations (Mishra & Ramakrishnan, 1983a, 1983b). In the absence of species like *Dendrocalamus hamiltonii* conservation of K is less efficient in the succession. Here *Pinus kesiya* becomes the dominant species at 15 years of secondary succession and the net primary production due to regrowth of vegetation remains lower (5 kg ha^{-1} yr^{-1}) than at lower elevations.

2. *Recovery of Forest Ecosystem Damaged due to Landslide*

A massive landslide prepares the ground for primary succession, while landslides of low-to-moderate scale may create a mosaic of microsites with and without traces of original vegetation. Observations were collected from seven sites of different ages (from 1 yr to 90 yr old following a landslide event) located within an area of radius 3 km at around 1900 m altitude where banj oak (*Q. leucotrichophora*) and tilonj oak (*Q. floribunda*) form natural potential vegetation. The landslides were massive enough to remove almost all the existing vegetation.

Development of vegetation.—Annuals (e.g., *Achyranthus bidentata, Justicia simplex, Polygonum amplexicaule*), which can readily arrive at the bare sites from adjacent areas through massive seed production and efficient seed-dispersal mechanisms, accounted for 98% of the total plant cover on 1- to 6-year-old sites (Fig. 16). From the 6th to the 13th year, a number of perennials were recruited, and these shared dominance with the annuals, whereafter dominance shifted largely to perennials. The adjacent undisturbed forests contributed substantially to the herbaceous flora of the damaged sites. The chrono-sequence of herbs seems to represent a situation similar to "relay floristics" of the "facilitation model" of Connell and Slatyer (1977). By the 21st year, the herbage cover was 78.6% of the undisturbed reference site and by 40 years it was 95.2%.

The shrubs appeared at a 13-year-old site and their composition became highly similar to an adjacent undisturbed site by 40 years.

Seedlings of *Sapium insigne,* an early successional tree species, appeared as early as 1 year after the landslide. This was immediately followed by *Alnus nepalensis,* an efficient nitrogen-fixer (Sharma & Ambasht, 1984). Interestingly, seedlings of the climax species, *Q. leucotrichophora* and *Q. floribunda* appeared at a 21-year-old site, and at a 40-year-old site their young trees had established themselves. Thus, although some degree of improvement seems to be prerequisite for the recruitment of these climax species, they are able to establish directly on disturbed sites without following a well-marked stage of shade-intolerant species. It should, therefore, be possible to shorten the time lag in the appearance of the climax oak species through suitable management practices, such as dibbling of seeds and establishment of an adequate herbage cover.

Biotic regulation of biochemical flux.—Soil erosion is a major destabilizing force in damaged ecosystems. Such erosion might revert the ecosystem from a partially developed state to an extremely earlier stage. Since these systems are predominantly subsurface-flow systems, the amounts of overland flow are low from all stages. Even the vegetal cover of a 21-year-old site was large enough to reduce the overland flow to a minimal level of 0.45% of the incident rainfall. Similarly, soil loss (which was positively related to overland flow) declined from 81 kg ha^{-1} from a 6-year-old to 37 kg ha^{-1} from a 40-year-old site. There was a significant inverse relationship between loss of N and plant biomass ($r = -0.95$, $P < 0.01$). A similar relationship was found for other nutrients.

Fine-soil content (<0.02 mm) increased with time and attained an equilibrium by 40 years. Similarly, concentration of various nutrients in

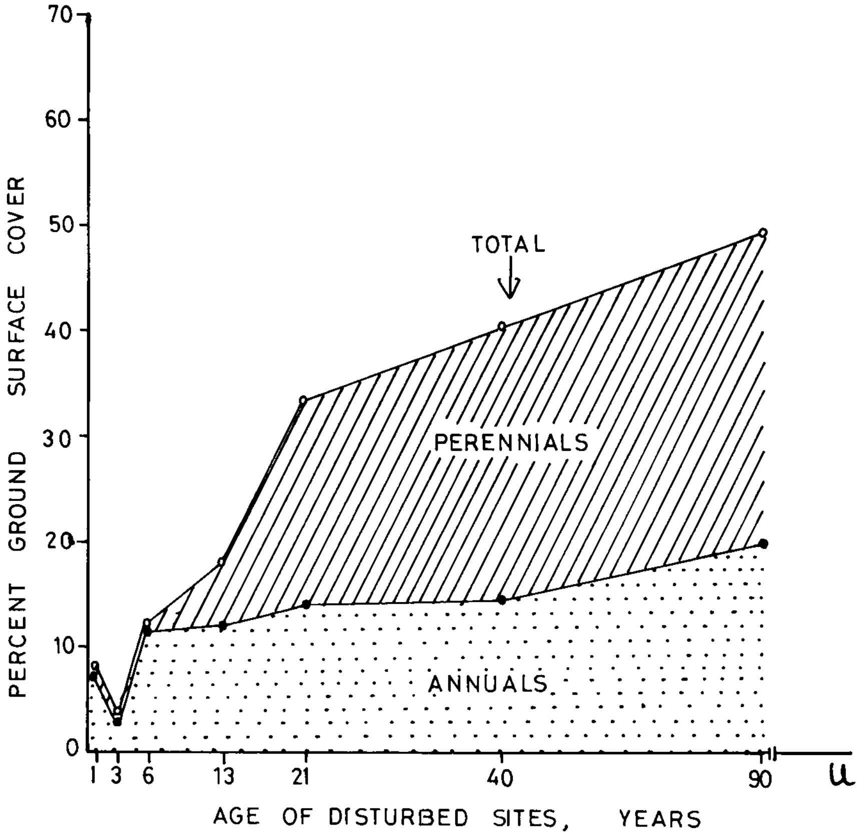

Fig. 16. Percent cover of herbaceous vegetation in succession following landslide in an oak forest zone of central Himalaya (data of J. S. Singh & Singh, 1984a used).

soil increased significantly with time (Fig. 17). However, the rate of change in nutrient concentration declined with the progress of succession, as also reported by Mellinger and McNaughton (1975). In fact, the nutrient level in soil stabilized by 40 years or earlier. Interdependence between soil nutrients and plant biomass is indicated by significant positive relations between soil nutrient concentrations (total N, available P, exchangeable Ca and N, and organic carbon) and plant biomass (e.g., for soil N and plant biomass, $r = 0.917$, $P < 0.01$). It is suggested that the added carbon from the developing vegetation stimulates the immobilization of nutrients, which are constantly generated from geological weathering and added by rainfall. This would counteract the process of leaching, and release the nutrients at a slower but stabilized rate for recycling by the vegetation. Evidently, the climax oak forest can bounce back to its original state within a short period even after massive destruction due to landslide.

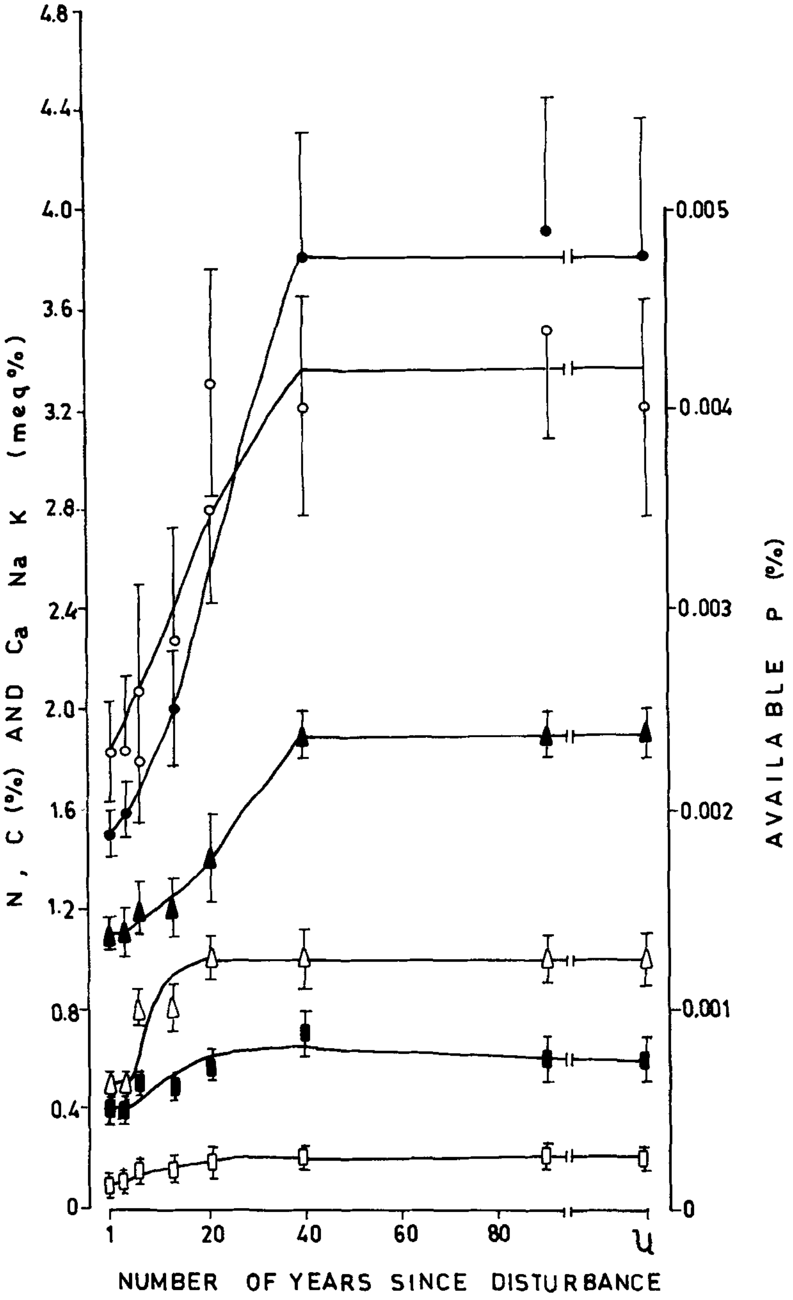

Fig. 17. Soil nutrients across the development sequence following landslide in an oak forest zone of central Himalaya after 1, 3, 6, 13, 21, 40, and 90 years. U represents undisturbed forest site. Vertical bars represent ± 1 SE. In some cases SE is shown only on one side (based on A. N. Pandey & Singh, 1985).

Oaks are excellent coppicers and this helps in the rejuvenation of the forest even after clear felling (S. P. Singh, P. K. Ralhan & J. C. Tewari, 1985), provided the site is kept free from burning and grazing. Thus, if stability were to be compared in terms of resilience, most conveniently measured by the speed with which a community returns to its original state after disturbance (Horn, 1974), the potential natural oak forests would seem to be fairly stable. Perhaps they have developed their resilience in response to frequent periodic disturbances in the geological past. It seems that Horn's view that climax communities are inherently fragile does not hold true for the Himalayan oak forests. Considering the development of total vegetation and continuity in soil improvement, Connell and Slatyer's (1977) "tolerance mode" appears more applicable in this situation, although both holistic and reductionist approaches are needed to completely explain the pattern of secondary succession.

C. BIOMASS AND PRODUCTIVITY

Some data on biomass and primary productivity of central Himalayan forests are now available (Chaturvedi & Singh, 1982, 1984; Negi et al., 1983; J. S. Singh & Chaturvedi, 1982; J. S. Singh & Singh, 1984b; S. P. Singh & Singh, 1985; Singh, Rawat & Chaturvedi, 1984; Tiwari & Singh, 1984).

In *Pinus roxburghii,* the dry weight of each component of the tree (i.e., bole, branch, foliage, root) increases with age and the total aboveground biomass in a 128-year-old tree was 1939 kg. The largest proportion of the production was accounted for by the tree crown and fine roots, while the largest biomass resided in the bole. The maximum current biomass increment was attained at the age of 39 years. The relationship of bole and shoot production per annum to leaf area and fine roots for different age periods indicated a significant spurt during 36–39 years, and a secondary limited spurt during 97–103 years in the life history (Chaturvedi & Singh, 1982). Energy stored by trees was assessed at four sites of all-aged *P. roxburghii* forest (Chaturvedi & Singh, 1984). Total biomass and net production averaged 210.8 t ha^{-1} and 15.0 t ha^{-1} yr^{-1}, respectively. The total energy stored as biomass and fixed during one year were 3.738 T J ha^{-1} and 0.26 T J ha^{-1} yr^{-1}, respectively. Energy capture efficiency was 0.779 and 0.873% of photosynthetically active radiation, respectively, for the aboveground and total tree vegetation.

Negi et al. (1983) reported 197.2 to 322.8 t ha^{-1} aboveground tree biomass for the oak forest, and the component-wise distribution of biomass indicated that the evergreen oak forest of the central Himalaya was more similar to the evergreen conifer forest than was the temperate deciduous oak forest. J. S. Singh, Rawat, and Chaturvedi (1984) found that annual net production equalled 8% of tree biomass in pine forest and 4% in the oak forest.

Attempts have been made to map the forest biomass using aerial photographs and satellite images (Tiwari & J. S. Singh, 1984; Tiwari et al., 1985). Over a large area, the aboveground tree biomass ranged from less than 80 t to more than 400 t ha^{-1} depending upon the forest type and basal cover.

More recently, a coordinated study on a number of forests along an altitudinal gradient (Table IX) was completed (J. S. Singh & Singh, 1984a, 1984b, 1984c) and the results are summarized in Table XI. The biomass of a majority of forests (163–787 t ha^{-1}) falls within the range (200–600 t ha^{-1}) given for many mature forests of the world (Whittaker, 1966, 1970). Biomass is much affected by the age of the dominant plants and since the age differs among the forests, the relationship between productivity and the biomass is rather loose (Lieth, 1975). Among the central Himalayan forests, in general, lower biomass was recorded for the successional chir pine and chir pine–mixed broadleaf forests than for the climax forests (Table XI). The variation in age of the same forest community results in considerable variation in the biomass. For example, the biomass of sal forest in old-growth stand can be about one and one-half times greater than in seedling–coppice forest (Table XI).

The net primary productivity (Table XI) ranges from 11.0 (chir pine–mixed broadleaf forest) to 27.4 t ha^{-1} yr^{-1} (mixed oak–tilonj dominated). Most of the values, however, lie within the range of about 16–25 t ha^{-1} yr^{-1}. Values for a number of forests exceed the range (12–15 t ha^{-1} yr^{-1}) reported for mature stable temperate forests of favorable environments (Whittaker, 1975). In fact, the production of certain stands of each of the major forest types is comparable with the range (20–30 t ha^{-1} yr^{-1}) given for highly productive communities, such as tropical rain forests, marshes and successional communities of favorable environments (Lieth, 1975; Whittaker, 1975). Around 15°C mean annual temperature, Lieth (1975) indicated that net primary productivity ranges from about 10 to 25 t ha^{-1} yr^{-1}. Values of the productivity in certain stands of mixed oak forests are toward the higher side of this range.

Herbaceous components, which account for less than 1% of the total forest biomass contribute about 6.6–16.7% to the forest productivity (Table XI).

The relation of biomass to productivity, which is conveniently expressed as the biomass accumulation ratio, ranges from 20 to 50 for mature forests (Whittaker, 1975). Values for the central Himalayan chir pine (10.9–12.6) and chir pine–mixed broadleaf forests (15.8) are lower than values in the above range, while for the remaining forests they lie

Table XI

Total biomass (t ha^{-1}) and net primary productivity (t ha^{-1} yr^{-1}) for certain forests in the central Himalaya. Values for net primary production include litter fall and root production. Species names as in Table IX

Forest	Biomass	Net primary productivity	Proportions[a] (%)			Biomass[a] production ratio	Reference
			Tree	Shrub	Herb		
Central Himalaya							
Chir pine	115.2–286.2	11.0–23.0	83.7	0.8	15.5	12.6	Chaturvedi (1983)
Oak forests	197.2–322.8	15.9–20.6	81.2	8.6	10.2	24.7	Y. S. Rawat (1983)
Sal old growth	330.7–716.9	16.0–18.9	77.4	6.0	11.6	37.9	J. S. Singh and Singh (1984b)
Sal coppice growth	291.5–460.4	17.9–21.1	89.1	4.3	6.6	21.8	J. S. Singh and Singh (1984b)
Chir pine–mixed broadleaf	199.0–222.9	12.6–13.0	70.6	12.7	16.7	15.8	J. S. Singh and Singh (1984b)
Chir pine	200.8–377.1	18.5–24.5	93.0	0.5	6.5	10.9	J. S. Singh and Singh (1984b)
Mixed oak–chir pine	163.4–432.6	14.4–18.9	84.7	6.3	9.0	22.9	J. S. Singh and Singh (1984b)
Mixed oak–rianj dominated	268.0–562.2	17.1–21.4	83.2	3.3	13.5	26.3	J. S. Singh and Singh (1984b)
Mixed oak–tilonj dominated	205.7–786.7	16.8–27.4	90.6	1.4	8.0	28.7	J. S. Singh and Singh (1984b)

[a] Computed for the stands of higher net primary productivity.

within the range. Evidently, chir pine and chir pine–mixed broadleaf forests represent immature communities.

Bormann and Likens (1979) indicated that about 35% of the current net primary productivity (NPP) was incorporated as net increase in live biomass of the ecosystem in a 55-year-old second growth northern hardwood forest. They (Bormann & Likens, 1979) suggested that this rate of net accumulation in live biomass is relatively high and is indicative of young, rapidly changing forest. This value ranged between about 24 and 29% of NPP for sal old-growth, mixed oak–pine and mixed oak forests, 44 and 64% of NPP for sal seedling–coppice, pine–mixed broadleaf, and pine forests in central Himalaya. Evidently the latter represent rapidly changing forests.

D. LITTER FALL AND LITTER DECOMPOSITION

Literature on this aspect includes Boojh and Ramakrishnan (1982), Chaturvedi (1983), Mehra and Singh (1985), Mehra, Pandey, and Singh (1983), Mehra et al. (1985), Pandey and Singh (1981a, 1981b, 1982), Y. S. Rawat (1983), J. S. Singh and Singh (1984b), J. Singh and Ramakrishnan (1982a, 1982b), Subba Rao et al. (1972), Tewary et al. (1982), Upadhyay and Singh (1985a, 1985b), and Upadhyay et al. (1985).

In the forests of the central Himalaya (Table XII) the annual litter fall ranges between 2.1 and 3.8 t C ha^{-1} yr^{-1} (carbon assessed as 50% of dry matter). Except for the pine–mixed broadleaf forest, the litter fall is higher than 2.7 t C ha^{-1} yr^{-1}, reported as the mean value for warm temperate forests by Bray and Gorham (1964). In the sal forest, the annual litter fall (3.3 t C ha^{-1} yr^{-1}) is towards the lower range of 3.45–3.95 t C ha^{-1} yr^{-1} reported for the Indian tropical deciduous forests (Bandhu, 1973; V. K. Sharma, 1971; R. P. Singh, 1974) but is higher than the estimate (2.4 t C ha^{-1} yr^{-1}) of Jordan and Murphy (1978), and distinctly lower than the estimates of Proctor et al. (1983) (4.4–6.0 t C ha^{-1} yr^{-1}) for other tropical forests. A value (4.5 t C ha^{-1} yr^{-1}) toward the lower side of the range given by Proctor et al. (1983) is reported from an ombrophilous broadleaf forest located at 1900 m in eastern Himalaya (Boojh & Ramakrishnan, 1982).

The litter fall for the chir pine forest (2.2–3.8 t C ha^{-1} yr^{-1}, based on five stands) is generally higher than for a number of other pine forests (2.2–2.4 t C ha^{-1} yr^{-1}) (DeAngelis et al., 1980) and is lower than 3.9 t C ha^{-1} yr^{-1}, reported for a loblolly pine forest in coastal South Carolina (Gresham, 1982). The litter fall in the oak-dominated forests (2.7–3.8 t C ha^{-1} yr^{-1}) approaches the upper side of the range of 1.9–3.5 t C ha^{-1} yr^{-1} reported for *Quercus ilex* forest in southern France (Rapp, 1969), but is distinctly higher than the estimates (1.75–2.4 t C ha^{-1} yr^{-1}) for

Table XII

Total litter fall in certain forests of the Himalaya

Forest	Elevation (m)	Total litter fall (t C ha^{-1} yr^{-1})	Reference
Central Himalaya			
Sal seedling–coppice	350	3.3	Mehra et al. (1985)
Chir pine–mixed broadleaf	1350	2.1	Mehra et al. (1985)
Chir pine (average of 5 stands)	1400–1750	3.5	Mehra et al. (1985), Chaturvedi (1983)
Mixed oak–chir pine	1850	3.2	Mehra et al. (1985)
Banj oak forest	1950	2.9	Y. S. Rawat (1983)
Mixed oak–rianj dominated (average of two stands)	2150–2194	3.0	Y. S. Rawat (1983), Mehra et al. (1985)
Mixed oak–tilonj dominated (average of two stands)	2194–2250	3.9	Y. S. Rawat (1983), Mehra et al. (1985)
Mixed oak–conifer	2050	2.8	U. Pandey and Singh (1981b)
Eastern Himalaya			
Bamboo–mixed broadleaf[a]	100	4.8	Toky and Ramakrishnan (1983a)
Sal forest[b]	760	1.7	J. Singh and Ramakrishnan (1981)
Ombrophilous evergreen	1900	4.5	Boojh and Ramakrishnan (1982)

[a] Successional community, 20 years after shifting cultivation.
[b] 13-year-old plantation.

several mixed oak and oak forests studied elsewhere (DeAngelis et al., 1980; Ovington et al., 1963; Reiners, 1972; Whittaker & Woodwell, 1969).

Tree leaves account for 54–82% of the total litter fall in the Himalayan forests. This is within the range of 40–85% reported for temperate forests (Rodin & Bazilevich, 1967). The contribution of wood to the total litter fall (9–20%) compares with 10–36% reported for different forests of the world (Bray & Gorham, 1964; Christensen, 1975; Killingbeck & Wali, 1978; R. P. Singh, 1979).

Data on the rate of litter decomposition (by using the litter bag method) are available only for the central Himalayan forests (for those forests listed in Table XI) and for a mixed oak–conifer forest located at about 2000 m).

Results of a study in which the same leaf litter species (viz., *Quercus leucotrichophora*) was placed at different forest sites located along an elevational gradient (300–2200 m), indicate that an interaction of several factors determines the rate of decomposition. Decomposition of this species is fastest at the sal forest site (Table XIII), where temperatures are distinctly warmer than at other sites. At this site, size of both microbial and micro-arthropod populations are largest (Singh & Singh, 1984b). The next fastest rate of decomposition occurs at the pine–mixed broadleaf forest and mixed oak forest sites. The former is located at relatively lower elevation, so temperatures, therefore, are warmer than at other sites except for the sal forest site. On the other hand, at the mixed oak forest site, at the highest elevation, temperatures are lowest but the site is most mesic. Decomposition is slowest at the pine forest site (located in mid-elevations), although climatic conditions are quite favorable (rainfall about as high as at the mixed oak forest site, and temperatures quite warm). Poverty of microorganisms and microarthropods in the native floor litter, which is characterized by a high C:N ratio and lignin content, are some of the factors which retard the decomposition at this site (J. S. Singh & Singh, 1984b). To conclude, temperature, moisture, C:N ratio of soil and of native litter and lignin : N ratio of the native litter interact in a complex way to cause the differences in decomposition rate of the *Quercus leucotrichophora* leaf litter placed at different sites.

Differences in initial lignin content or lignin : N ratio and C:N ratio appear to explain a large part of the variation in the rates of decomposition of leaf litter of different species (Upadhyay & Singh, 1985a). The relationship of these parameters with decomposition rate is inverse. Species initially having 17% or more lignin immobilize significantly more N during decomposition than the species with lower lignin contents. Because of these factors, marked interspecific variations in the rate of decomposition may occur within the same community. U. Pandey and Singh (1982) identified two groups of species in a mixed oak–conifer forest. One group consisted of canopy species, *Cedrus deodara, Cupressus torulosa, Quercus floribunda, Q. leucotrichophora,* and *Aesculus indica,* and the other of understory species, viz., *Daphne cannabina* and *Ilex dipyrena.* The first group reflects a nutrient pool which turns over slowly, while the second group represents a pool with rapid turnover. Such variations in the rate of decomposition would cause pulsed nutrient release, with lesser chances of nutrient leakage from the ecosystem.

The rates of decomposition of leaf litter (0.253–0.274% day^{-1}; Table XIV) of the major species of the two lowermost forest sites are comparable to those given for some tropical rain forest species (Edwards, 1977; Tanner, 1981; Wiegert, 1970). For oak forests the values are higher (0.150–0.193% day^{-1}) than most of the values reported for temperate oak forests

Table XIII

Rate of decomposition of *Quercus leucotrichophora* leaf litter placed at different forest sites of central Himalaya (based on J. S. Singh & Singh, 1984b)

Forest sites	Elevation (m)	Rate (% day^{-1})
Sal forest	330	0.253
Pine–mixed broadleaf forest	1350	0.192
Pine forest	1750	0.165
Mixed oak–pine forest	1850	0.165
Mixed oak–rianj dominated forest	2150	0.183

(Jenny et al., 1949; Shanks & Olson, 1961; Witkamp, 1966; Witkamp & Olson, 1963). However, for pine the rate of decomposition is similar to the values reported for several pine species of the temperate zone (Kärenlampi, 1971; Thomas, 1968; Witkamp, 1966).

Recently, some preliminary analysis of microbial population on decomposing leaf litter of central Himalayan forests has been made (J. S. Singh & Singh, 1984b). Most of the leaf litter fungi (97%) belong to Deuteromycetes, of which 87% are Moniliales. Markedly different fungal communities develop on even the same leaf litter (*Quercus leucotrichophora*) placed at different forest sites (Table XV). Comparison of leaf litter of dominant species of respective forest sites indicates that the fungal communities developed on chir pine leaf litter are most dissimilar to those of other litters (Table XV). A conspicuously higher C:N ratio and lignin content in the chir pine leaf litter is responsible for this dissimilarity. This is also supported by the observation that at a given site the fungal communities developed on leaf litter of different species are similar, with the exception of the chir pine forest site.

The succession of fungi seen on decomposing leaf litter indicates that *Fusarium* spp. are common colonizers, and are not found at later stages. *Trichoderma viride* and *Mortierella subtilissima* are common late successional species. These species show a remarkably wide elevational range. Species diversity (Shannon-Wiener's index) of litter fungi peaks at three months following litter placement, whereafter it declines sharply and levels off at later stages of decomposition. The fungal species diversity and the fungal counts were positively correlated (significant at $P < 0.01$ level), and in contrast to the general pattern of higher plant succession (Odum, 1969), both were higher in initial rather than late stages of decomposition. Furthermore, the dominance-diversity curve assumes a lognormal form at an early stage and a geometric form at a later stage.

The rate of litter decomposition is positively related with temporal beta

Table XIV

Rates of decomposition for major leaf litter species of the central Himalayan forests and for certain other forests (with genera common to the central Himalayan forests)

Vegetation	Place	Rate of decomposition (% day^{-1})	Authors
Lyonia ovalifolia	Central Himalaya	0.253	J. S. Singh and Singh (1984b)
Mallotus philippensis	Central Himalaya	0.274	J. S. Singh and Singh (1984b)
Pinus alba	Tennessee, U.S.A.	0.110	Witkamp (1966)
P. roxburghii	Central Himalaya	0.126	J. S. Singh and Singh (1984b)
P. sp.	England	0.083	Kärenlampi (1971)
P. taeda	Tennessee, U.S.A.	0.120	Thomas (1968)
Oak forest	California, U.S.A.	0.016–0.032	Jenny et al. (1949)
Quercus alba	Eastern United States	0.107	Shanks and Olson (1961)
	Eastern United States	0.126	Witkamp and Olson (1963)
	Tennessee, U.S.A.	0.150	Witkamp (1966)
Q. floribunda	Central Himalaya	0.193	U. Pandey and Singh (1982)
		0.172	Y. S. Rawat (1983)
		0.150	J. S. Singh and Singh (1984b)
Q. glauca	Central Himalaya	0.274	J. S. Singh and Singh (1984b)
Q. lanuginosa	Central Himalaya	0.182	Y. S. Rawat (1983)
		0.150	J. S. Singh and Singh (1984b)
Q. leucotrichophora	Central Himalaya	0.193	U. Pandey and Singh (1982)
Q. leucotrichophora	Central Himalaya	0.183	J. S. Singh and Singh (1984b)
Q. leucotrichophora	Central Himalaya	0.196	Y. S. Rawat (1983)
Q. robur	Rothamsted, England	0.240	Heath et al. (1966)
Shorea robusta	Central Himalaya	0.253	J. S. Singh and Singh (1984b)

diversity of litter fungi (significant at $P < 0.01$ level). The latter varies from 4.0, for the slowest decomposing pine leaf litter, to 5.7, for the fastest decomposing sal leaf litter (Table XVI). Temporal beta diversity expresses the rate of species change in time, which seems to be related to the rate of structural and chemical changes in the decomposing material. Further, the rate of decomposition is also positively related to the mean (across months) microbial count (sum of fungi, bacteria, and Actinomycetes; Table XVII) and the mean microarthropod population (each significant at $P <$

Table XV

Values of community coefficient among fungal communities developed on decomposing standard leaf litter (*Quercus leucotrichophora* leaf litter), placed at different forest sites (as in Table IX) and between those developed on decomposing leaf litter of dominant species of respective forests of the central Himalaya (based on J. S. Singh and Singh (1984b)

Decomposing material	Community coefficient (%)
For standard leaf litter between different forest sites	
Sal forest vs. mixed broadleaf forest	52.6
Sal forest vs. pine forest	18.4
Sal forest vs. oak–pine forest	32.4
Sal forest vs. mixed oak forest	39.9
Pine–mixed broadleaf forest vs. pine forest	38.2
Pine–mixed broadleaf forest vs. oak–pine forest	20.3
Pine–mixed broadleaf forest vs. mixed oak forest	23.8
Pine forest vs. oak–pine forest	34.0
Pine forest vs. mixed oak forest	19.3
Oak–pine forest vs. mixed oak forest	39.2
Between dominant species' leaf litter at respective forest sites	
P. roxburghii vs. *Quercus lanuginosa*	19.70
P. roxburghii vs. *Q. leucotrichophora*	24.70
Quercus leucotrichophora vs. *Q. lanuginosa*	41.20
Shorea robusta vs. *Pinus roxburghii*	20.00
S. robusta vs. *Quercus lanuginosa*	29.80
S. robusta vs. *Q. leucotrichophora*	34.40

0.01 level). The mean microarthropod population on sal leaf litter, as an example, was about seven times larger than on the slow decomposing chir pine leaf litter (Table XVII); within a mixed oak–conifer forest the broadleaf litter harbored more microarthropods than the conifer litter (Sharma et al., 1984), and the soil-litter respiration in broadleaf tree stands was greater compared to conifer stands (Tewary et al., 1982).

E. NUTRIENT CYCLING

Studies on the nutrient cycling have been undertaken for the central Himalayan forests only (Chaturvedi, 1983; Mehra et al., 1985; Negi et al., 1983; U. Pandey & Singh, 1984b; Y. S. Rawat, 1983; J. S. Singh, Rawat & Chaturvedi, 1984; J. S. Singh & Singh, 1984b).

A. N. Pandey et al. (1983) and Pathak et al. (1984), have assessed the

Table XVI

Beta diversity of fungal communities in different forests of central Himalaya (based on J. S. Singh & Singh, 1984b)

Forest	Oak leaf litter	Dominant tree leaf litter
Sal old-growth forest	5.71	5.70
Pine–mixed broadleaf forest	5.07	5.00
Pine forest	4.31	4.00
Oak–pine forest	4.36	4.36
Mixed oak–rianj dominated forest	5.04	4.70

input of nutrients through rainfall and output through overland flow and sediment movement for a number of sites. Data for six forests are summarized in Table XVIII. The precipitation input during the monsoon period was maximum for Ca and least for P on all sites. Among the sites, input of nutrients varied primarily according to the total amount of rainfall received. Loss of nutrients through overland flow and sediment output was considerably higher on sites 1–3 compared to sites 4–6. Among the nutrients, more Ca, Mg, K, and C was lost through sediment output but more N and P through overland flow. However, maximum loss (as percent of input through rainfall) occurred for Mg, and least for K, N, and P. The nutrients can be arranged in decreasing order of loss as: Mg > C > Ca > K = N = P.

The nutrient concentration of wood samples from a substantial number of tree species of Himalayan forests was markedly higher compared to those from temperate forests. For example, N concentration in wood was in the range of 0.48–0.63% in these forests compared to 0.011–0.28% in the temperate forests. Because of the higher nutrient concentration in wood, a greater proportion of nutrients is accumulated in the biomass component of the Himalayan forests than in the temperate forests (S. P. Singh et al., 1985). In this respect, these forests resemble the mesic tropical forests (Table XIX). The accumulation of nutrients in the perennial biomass enables these forests to conserve nutrients, since the soil pool (small because of the presence of a substantial proportion of boulders and stones in the soil profile) is vulnerable to nutrient losses through runoff, leaching, and landslides.

As the leaf nutrient concentrations are similar to those of temperate species, the ratios of nutrient concentration between leaf and bole are significantly higher in temperate forests than in the Himalayan forests (Table XX). For example, the leaf-bole ratio for N concentration ranged

Table XVII

Average (of 12 sample dates during 1982–83) microbial counts (values in terms of 10^4 g^{-1} for fungi, 10^4 g^{-1} for bacteria, and 10^6 g^{-1} for actinomycetes on decomposing leaf litter and microarthropod population (individuals m^{-2}) in different forests of the central Himalaya (based on J. S. Singh & Singh, 1984b)

	Sal old-growth forest	Chir pine–mixed broadleaf forest	Chir pine forest	Oak–chir forest	Mixed oak–rianj dominated forest
Microbials					
Fungi	32.42	30.50	21.02	25.93	26.36
Bacteria	51.91	48.85	31.18	35.23	39.22
Actinomycetes	7.12	6.39	3.21	5.05	4.81
Microarthropods					
Total population	7413.0	3259.0	1171.0	4672.0	5301.0
Percent contribution by					
Acarina	73.3	73.4	65.1	66.5	60.8
Collembola	16.9	15.9	23.6	20.4	29.9
Others	9.8	10.7	11.2	13.1	9.4

between 2.5 and 4.2 in the central Himalayan forests, and between 4.6 and 29.6 in the temperate forests. Values similar to those of the central Himalayan forests have also been reported for the eastern Himalayan forests (J. Singh & Ramakrishnan, 1982a), and some tropical forests of other countries (Bartholomew et al., 1953; Greenland & Kowal, 1960; Jordan, 1977; Nye, 1958; Rodin & Bazilevich, 1967; Stark, 1971).

Although litter fall was the major route through which nutrients returned from the biomass to the soil pool, a substantial amount (11–46%) reached the soil pool via throughfall and stemflow (Table XXI). Since the nutrients returned through the rain water are in "available" form, as opposed to "bound," such return plays a significant role in the nutrient cycling (Pathak & Singh, 1984). The return of N through leaf litter fall was 41–48% of the annual uptake in three forests which were studied in detail (Table XXII).

Substantial proportions of N and P were reabsorbed from old leaves before abscission in chir pine (Table XXII). This proportion was markedly lower for oaks, while sal represented an intermediate situation. For example, the reabsorption value from senescing leaves for N was 53.5% in pine, 38.6% in sal, and 21.5% in oak. Consequently, the C:N ratio of the

Table XVIII

Seasonal input of nutrients through rainfall and loss through overland flow and sediment output on different forest sites located in central Himalaya based on 1981 and 1982 monsoon data (based on Pathak et al., 1984)

	Sites					
Nutrients	Sal forest	Pine–mixed broadleaf forest	Pine forest	Mixed oak–pine forest	Mixed oak–tilonj dominated forest	Mixed oak–rianj dominated forest
	Rainfall input (kg ha^{-1} yr^{-1})[a]					
N	6.1	5.9	7.4	4.8	8.2	6.3
Ca	16.5	16.7	18.2	14.1	22.1	20.2
Mg	10.5	12.5	12.1	9.8	13.9	9.7
K	12.2	14.1	12.9	8.6	14.0	14.2
P	1.4	1.4	1.7	1.2	1.6	1.2
Org. C	7.7	9.4	6.2	5.0	14.7	12.0
	Loss through overland flow (kg ha^{-1} yr^{-1})					
N	0.13	0.12	0.10	0.04	0.06	0.07
Ca	0.18	0.36	0.21	0.08	0.12	0.15
Mg	0.11	0.21	0.11	0.04	0.06	0.08
K	0.11	0.18	0.10	0.04	0.06	0.07
P	0.03	0.05	0.02	0.01	0.02	0.02
Org. C	0.12	0.17	0.10	0.04	0.06	0.07
	Loss through sediment output (kg ha^{-1} yr^{-1})					
N	0.14	0.09	0.08	0.02	0.04	0.04
Ca	1.08	0.68	0.50	0.22	0.29	0.35
Mg	0.81	0.55	0.46	0.20	0.37	0.32
K	0.50	0.55	0.28	0.10	0.19	0.15
P	0.02	0.02	0.02	0.01	0.01	0.01
Org. C	0.90	0.61	0.40	0.26	0.29	0.25

[a] Snow is not included.

leaf litter was much higher in pine (48) than in oak (23) or sal (36.8). Thus, the efficiency of litter production per unit of N was in the order pine > sal > oak.

The high C:N ratio of litter as well as of the soil in pine forest, reduces the rate of litter decomposition and thus increases the fuel load of the forest. Furthermore, the decomposers on litter with a high C:N ratio immobilize available N from the soil solution. It is suggested that this, in addition to the fire promoting character, is the main strategy through which pine invades a disturbed oak area and is partially able to hold the

Table XIX

Percentage of the total ecosystem nutrient accumulated in plant biomass of the central Himalayan forests, tropical forests, and temperate forests. Values are averages of 14 samples for central Himalayan forests, 17 for tropical forests, and 19 for temperate forests

	Nutrients				
Forest	N	P	K	Ca	Mg
Central Himalayan	30.14	46.83	66.54	27.28	23.88
Tropical	24.25	46.38	69.95	54.14	52.50
Temperate	12.35	27.14	37.24	30.34	36.75

site against a possible reinvasion by oak (J. S. Singh, Rawat & Chaturvedi, 1984). Both oak and sal are high N-demanders and cannot succeed in N-poor soil. Through the return of N-rich litter and rapid mineralization, oaks maintain a high soil fertility. The heavy lopping of oaks for fodder and cutting for fuel reduces the N return through litter fall, and over the years the soil becomes gradually depauperate. In such situations the low N-demanding pine has a definite advantage.

A study of 13 major woody species occurring between 300 and 2500 m altitude in central Himalaya indicated that the retranslocation of nutrients from the leaves before abscission, on average, was distinctly greater for deciduous species than for the evergreens (46.7% vs. 32.0% N, 58.6% vs. 33.7% P, 42.9% vs. 28.8% K, 21.0% vs. 9.4% Ca) (J. S. Singh & Singh, 1984b). While the canopy species *P. roxburghii* showed low nutrient concentration in leaves and higher retranslocation of nutrients, the understory species, *Myrsine semiserrata,* in the same forest, showed higher nutrient concentration in leaves, but lower retranslocation of nutrients. Further, in mixed oak forests, the understory species *Viburnum cotinifolium,* maintained twice as much retranslocation of nutrients as did the oaks which made the canopy. The soil of this forest was rich in nutrients. Thus, members of certain communities, regardless of soil nutrient level may show widely different levels of nutrient retranslocation from the senescing leaves.

The forest floor, a major reservoir of nutrients and organic matter, is quite dynamic. The turnover rates and the turnover times for dry matter and selected nutrients in central Himalayan forests are given in Table XXIII. The rate of replacement of the floor of the chir pine forest is slowest, and that of the oak-dominated forests highest. Among the nutrients, the rate of replacement varies from 33% yr^{-1} (Ca, Mg in chir pine forest) to 77% yr^{-1} (P, in mixed oak forest). These turnover rates, on

Table XX

Ranges for the ratio of leaf to wood nutrient concentration for trees of Himalayan and temperate regions

Region	Nutrients					Reference
	N	P	K	Ca	Mg	
Himalayan	2.5–5.1 (3.2)	1.7–7.3 (3.7)	1.3–7.0 (2.7)	0.7–3.1 (1.7)	1.9–5.5 (3.1)	S. P. Singh et al. (1985)
Temperate	4.6–29.6 (16.6)	2.2–100 (20.3)	1.8–29.5 (10.3)	1.5–45.6 (9.0)	3.0–32.1 (9.0)	Bartos and Johnston, 1978; Hingston et al., 1980; Johnson and Risser, 1974; Jokela, 1981; O. N. Kaul and Srivastava, 1967; Madgwick et al., 1981; Ovington and Madgwick, 1959; Shelton et al., 1981; Whittaker, 1975; Whittaker et al., 1969; and Woodwell et al., 1975

average, are higher than the rates reported for temperate forests and more comparable to those of tropical forests (J. S. Singh & Gupta, 1977; Vogt et al., 1983).

F. SEASONAL RHYTHMS

Phenological studies (Table XXIV) on some representative central Himalayan forests listed in Table IX have been conducted (Ralhan et al., 1985a, 1985b; J. S. Singh & Singh, 1984b, 1984c). In these investigations, apart from documenting the general phenophases, such as leafing, leaf drop, flowering, and fruiting, the seasonalities of photosynthetic activity, rate of decomposition, and population of decomposers were also taken into consideration (Figs. 18–20). Data on phenophases are also available for a species-rich ombrophilous broadleaf forest at 1900 m elevation (Boojh & Ramakrishnan, 1981) and a low elevation (296 m) subtropical forest (Shukla & Ramakrishnan, 1982) of eastern Himalaya. The following accounts are based on these studies.

In all forests of the central Himalaya, evergreen woody species showing a concentrated summer (April, the warm and dry month) leaf-drop pattern prevail. This summer leaf-drop is accompanied by simultaneous leafing, which seems actually to precede the leaf-drop (and possibly induces it by causing demand for resources) in a majority of species. This closely approaches the situation exhibited by "leaf-exchanging" types of species of tropical rain forests (Longman & Jenik, 1974). By the time the rainy season commences, the forests, with fully developed foliage, are ready to take full advantage of the favorable conditions of the warm and wet period. Leafing during the warm and dry period is prevalent also in the eastern Himalayan forest (Fig. 21), but contrary to the situation in central Himalayan forests, the trees drop their leaves in greater quantities during a long period of December to March (cold, and warm dry periods). This situation is due to the presence of winter-deciduous species (18 out of 66 species) as well as the evergreen species with thin foliage dropping during winter and spring (44 out of 66 species). However, litter fall peaks in March, which represents the warmer month in the above period.

In forests of both regions, smaller secondary peaks for leafing during the warm-wet season (July–August) and autumn (October) are present because of the multiple leafing, which is more common in the eastern forest than in the central Himalayan forests (82% of the species in the former vs. 40% in the latter show this behavior). The percentage of species with multiple leafing is significantly greater in overstory than in understory. It appears that the lower availability of light limits the multiple leafing in the undercanopy environment.

Several advantages are attributable to multiple leafing: (i) it enables the

Table XXI

Annual input of nutrients by precipitation components (throughfall + stemflow) and litter fall (based on Mehra et al., 1985)

Nutrients	Input by precipitation components (kg ha^{-1})	Input by litter fall (kg ha^{-1})	Total input (rainfall + litter fall) (kg ha^{-1})	% input of nutrients by precipitation
		Sal forest		
N	9.1	69.8	78.9	12
P	1.7	5.4	7.3	23
K	15.2	31.4	46.6	33
Ca	18.2	80.7	98.9	18
Mg	11.99	N.A.	N.A.	N.A.
		Pine–mixed broadleaf forest		
N	7.9	47.7	55.6	14
P	1.7	4.1	5.8	29
K	16.5	22.8	39.3	42
Ca	17.8	50.8	68.6	26
Mg	15.8	N.A.	—	—
		Pine forest		
N	11.4	56.9	68.3	17
P	2.1	6.4	8.5	25
K	23.3	37.1	60.4	39
Ca	25.7	74.2	99.9	26
Mg	16.5	N.A.	N.A.	N.A.
		Mixed oak–pine forest		
N	8.5	69.4	77.9	11
P	1.4	4.4	5.8	24
K	16.1	28.5	44.6	36
Ca	18.2	86.3	104.5	17
Mg	12.9	N.A.	N.A.	N.A.
		Mixed oak–rianj dominated forest		
N	10.2	72.2	82.4	12
P	1.7	5.4	7.1	24
K	27.9	32.3	60.2	46
Ca	29.8	89.2	119.0	25
Mg	14.5	N.A.	N.A.	N.A.

Table XXI

Continued

Nutrients	Input by precipitation components (kg ha^{-1})	Input by litter fall (kg ha^{-1})	Total input (rainfall + litter fall) (kg ha^{-1})	% input of nutrients by precipitation
		Mixed oak–tilonj dominated forest		
N	11.2	70.0	81.2	14
P	1.9	5.8	7.7	25
K	26.9	31.9	58.8	46
Ca	28.6	91.6	120.2	24
Mg	17.7	N.A.	N.A.	N.A.

N.A. = not analyzed.

species to utilize efficiently the favorable periods of potentially unfavorable seasons, such as winter, (ii) it is a protective measure that ensures the presence of some leaves in case the leaves of the first flush are destroyed, (iii) it staggers the demand for nutrients in time and thus there is a need to deal only with a steady nutrient release in the soil instead of a concentrated demand in a short period, and (iv) it promotes staggered leaf-drop and staggered nutrient release, ensuring the availability of nutrients to support the multiple leafing, while minimizing the leakage of nutrients. The leaf-life for broadleaf species, on average, is longer for the eastern Himalayan trees (average for 12 dominant species = 20 months) than for the central Himalayan trees (average of six dominant species= 13 months). Phenological observations on individual leaves in Kumaun Himalayan forests indicate that the leaf expansion phase is longer for overstory species (average 6 weeks) than for understory species (average, 4.2 weeks), and for shrubs it is shortest (average, 2.5 weeks) (P. K. Ralhan, personal communication). The phase following the leaf expansion, during which leaf weight either increases or remains constant, appears to increase with increasing elevation, being about as long as 10 months for some oaks. The flowering peak also occurs during the warm and dry period for both the woody growth forms (trees and shrubs) of central Himalayan forests and for the trees of the eastern Himalayan forests. However, another equally larger peak is formed for the shrubs in the central Himalayan forests, either during the rainy season or in autumn. The trees of the eastern Himalayan forest show a smaller secondary peak in autumn. Among the trees of the central Himalayan forests, the three forests of relatively lower elevations show the peak for the standing crop of mature fruits during warm and dry period (May) (Ralhan et al., 1985a). Evidently, in

Table XXII

N and P budgets for the tree layer of the three Kumaun Himalayan forests. Values for sal forest are based on the average of two stands (stands located in sal old growth forest and sal seedling–coppice forest), those for pine forest based on five stands and those for oak forest based on six stands (based on J. S. Singh, Rawat & Chaturvedi, 1984 and J. S. Singh & Singh, 1984b)

	Sal forest		Pine forest		Oak forest	
	N	P	N	P	N	P
Compartment pools (t ha^{-1})						
Vegetation						
Foliage	0.178	0.014	0.141	0.011	0.253	0.016
Branch	0.556	0.053	0.257	0.031	1.282	0.086
Bole	1.599	0.150	0.655	0.089	1.028	0.072
Root	0.489	0.036	0.065	0.012	0.403	0.027
Total	2.822	0.253	1.118	0.143	2.966	0.201
Litter	0.113	0.008	0.140	0.012	0.118	0.006
Soil (30 cm)	4.401	0.140	4.744	0.236	6.331	0.214
Total	7.336	0.401	6.002	0.391	9.415	0.421
Accumulation in net production (t ha^{-1} yr^{-1})						
Foliage	0.092	0.0073	0.090	0.0071	0.0905	0.0059
Branch	0.024	0.0026	0.025	0.0028	0.0473	0.0032
Bole	0.024	0.0021	0.027	0.0039	0.0219	0.0016
Root	0.016	0.001	0.005	0.0051	0.016	0.0016
Total	0.156	0.013	0.147	0.0189	0.176	0.0123
Reabsorption before senescence (t ha^{-1} yr^{-1})	0.031	0.003	0.056	0.005	0.028	0.0021
Net uptake from soil (t ha^{-1} yr^{-1})	0.125	0.010	0.091	0.0139	0.148	0.0102
Return (t ha^{-1} yr^{-1})						
Leaf litter	0.060	0.005	0.045	0.004	0.068	0.005
Wood litter	0.012	0.001	0.009	0.0009	0.014	0.001
Removal from canopy in throughfall	0.0035	0.0005	0.004	0.0006	0.005	0.0004
Removal from canopy in stem flow	0.003	0.0002	0.00006	0.00003	0.0001	0.0001
Root mortality	0.006	0.0004	0.0023	0.0003	0.0066	0.0005
Total	0.0818	0.0071	0.0604	0.0059	0.0937	0.007
Retention in vegetation compartment (t ha^{-1} yr^{-1})	0.0432	0.0050	0.0306	0.010	0.0543	0.0032

Table XXII
Continued

	Sal forest		Pine forest		Oak forest	
	N	P	N	P	N	P
Ratios						
Reabsorption : accumulation	0.248	0.300	0.615	0.314	0.189	0.206
Return : vegetation pool	0.029	0.028	0.041	0.034	0.032	0.035
Litter : litter fall	1.569	1.333	3.205	3.000	1.439	1.000

these forests seed germination is synchronized with the commencement of the rainy season. On the other hand, in the forests of higher elevations the peak for the standing crop of mature fruits is formed during autumn. The seed germination of these species is staggered over a long period, because the seeds show partial dormancy to be broken by winter chilling (some seeds can germinate without winter chilling also). Both the above peaks for the mature fruits are found in the eastern Himalayan forest, and the species with the autumn peak also require winter chilling for seed germination. The shrubs of a great majority of central Himalayan forests show the peak standing crop of mature fruits in autumn (J. S. Singh & Singh, 1984b), however, data are not available on their seed germination.

Notwithstanding the differences in the temporal pattern of peaks, a majority of species of these forests show lengthy fruit retention, and fruits of one or the other species are available to wildlife throughout the year. In oak forests of the central Himalaya, *Q. leucotrichophora* alone bears acorns throughout the year (Ralhan et al., 1985a).

Studies on the central Himalayan forests indicate that the peak photosynthetic activity of one growth-form is separated from that of another in time (Figs. 18–20). Further, among the herbs, three major categories common across all forest types are distinguishable on the basis of the variation in the time of peak photosynthetic activity: (i) spring-perennials showing peak photosynthetic activity in spring; (ii) rainy season herbs consisting of a mixture of annuals and perennials, showing peak photosynthetic activity well after that of the woody species; and (iii) autumn or winter season perennial herbs showing peak photosynthetic activity when woody species enter the dormant phase or show limited photosynthetic activity. Such a time-separation in the growth behavior of species has several implications in regard to the functioning of the ecosystem. The spring-perennials, which are able to maintain rapid initial growth at the expense of food stored in the perennating organs, by restricting their

Table XXIII

Turnover rate (K) and turnover time (t, in yr) of forest floor in central Himalayan forests

Forest		Dry matter	N	P	K	Ca	Na
Mixed oak–conifer forest, Naini Tal[a]	t	1.30	1.59	1.36	–	1.39	–
	K	0.77	0.63	0.73	–	0.72	–
Sal old-growth	t	1.96	1.75	1.49	1.45	1.67	1.85
	K	0.51	0.57	0.67	0.69	0.60	0.54
Sal seedling–coppice	t	2.08	1.82	1.54	1.47	1.64	1.85
	K	0.48	0.55	0.65	0.68	0.61	0.54
Pine–mixed broadleaf	t	2.22	1.96	1.56	1.56	1.89	1.69
	K	0.45	0.51	0.64	0.64	0.53	0.59
Chir pine	t	3.03	2.94	2.78	2.63	3.03	3.03
	K	0.33	0.34	0.36	0.38	0.33	0.33
Mixed oak–pine	t	2.63	2.44	2.00	2.04	2.27	2.50
	K	0.38	0.41	0.50	0.49	0.44	0.40
Rianj dominated–mixed oak	t	2.33	1.89	1.47	1.49	1.79	1.92
	K	0.43	0.53	0.68	0.67	0.56	0.52
Tilonj dominated–mixed oak	t	2.44	1.85	1.61	1.72	1.92	2.38
	K	0.41	0.54	0.62	0.58	0.52	0.42
Chir pine[b]	t	1.87	2.43	2.50	1.89	2.17	1.56
	K	0.53	0.41	0.40	0.53	0.46	0.64
Mixed oak forest[c]	t	1.47	1.51	1.30	1.22	1.56	2.19
	K	0.68	0.66	0.77	0.82	0.64	0.84

[a] Based on U. Pandey and Singh (1981b); [b] Chaturvedi (1983); [c] Y. S. Rawat (1983); and the rest, J. S. Singh and Singh (1984b).

growth between snowmelt (or start of the frost-free period) and the renewal of foliage in canopy, are able to escape from the competitive effects of woody species. They utilize the greater light available on the ground because of the thinner foliage in canopy. Although these herbs contribute little to the productivity of the forest community, they immobilize the nutrients (particularly Mg, which is found in greater concentration in herbs than in woody plants) against the leaching that can occur due to the snowmelt or frequent spring storms. These herbs act as a short-term sink, by incorporating nutrients in biomass and releasing them as the shoots decompose during summer, when they become available to other plants. Thus, the nutrient capital of the ecosystem is conserved. A similar role is indicated for the spring herb, *Erythronium americanum,* in a 55-year-

Table XXIV

Peak values of certain ecosystem activities within the annual cycle in representative forests of central Himalaya

	Forests					
Activity	Sal	Pine–mixed broad-leaf	Pine	Mixed oak–pine	Mixed oak–rianj dominated	Mixed oak–tilonj dominated
Herb production g m^{-2}	77.4	77.0	69.9	71.4	74.6	74.8
Litter fall g m^{-2}	289.3	106.0	311.3	257.8	213.1	250.2
Microarthropod population m^{-2}	42,696	10,428	22,922	30,641	35,501	—
Microbial[a] population 10^4 g^{-1}	72.3	69.5	31.6	50.2	53.6	—
Decomposition, weight loss $month^{-1}$	15.8	13.9	12.6	19.4	14.7	13.9
No. of fruiting species	6(2)[b]	9(11)	4(6)	5(7)	3(7)	3
No. of flowering species	6(3)	13(10)	3(5)	5(5)	4(7)	5
No. of leaf-flushing species	7(4)	17(12)	4(10)	8(9)	4(7)	5
No. of leaf-drop species	7(4)	13(13)	3(9)	8(10)	4(10)	6

[a] Only fungi are considered here.

[b] Values in parentheses are for shrubs.

old northern hardwood forest at Hubbard Brook (Muller & Bormann, 1976). Muller and Bormann (1976) suggested that, although contributing less than 0.5% of the ecosystem's aboveground production, *E. americanum* acts as an efficient short-term sink or "vernal dam," with nutrients incorporated in accumulating biomass during the spring flushing period and released by shoot decomposition during the summer to be utilized by other species. The niche of rainy season herbs is characterized by greater adaptability to high shade levels, which reaches a maximum during the rainy season because of complete development of the canopy, and the cloudiness that prevails. Because of the availability of adequate moisture all annuals are able to germinate even in a highly competitive ground floor environment. Compared to trees the shrubs generally start their photosynthetic activity earlier. Thus, by shifting their growth activity to a relatively less favorable period (with respect to temperature and solar radiation), they minimize the competitive interaction with trees.

It is apparent that as a result of such subtle and rhythmic variations in

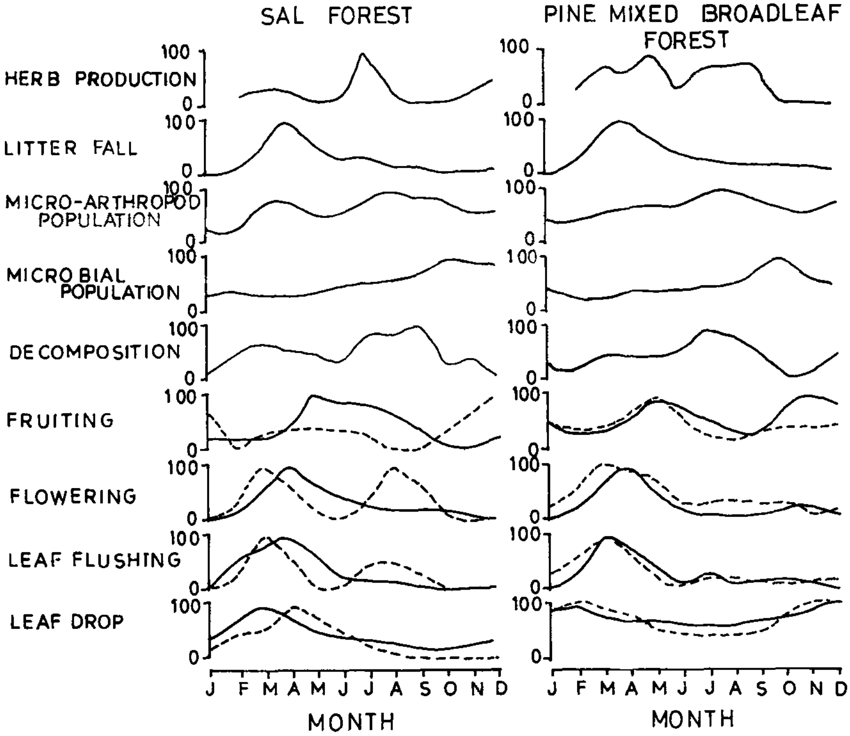

Fig. 18. A representation of periodicity of certain activities in sal and pine–mixed broadleaf forests. The peak value in each case is taken as 100, and all other values are computed in respect to that (peak values are given in Table XXIV). Broken curves indicate the same activity for shrubs and solid curves for trees. Herb production is in terms of g m^{-2} $month^{-1}$, litter fall values in terms of g m^{-2} $month^{-1}$, litter microarthropod population in terms of m^{-2}, microbial population (only fungi are considered here) in terms of 10^4 g^{-1}, decomposition as percent weight loss of litter $month^{-1}$, fruiting, flowering, leafing, and leaf-drop, in terms of number of species (based on J. S. Singh & Singh, 1984c).

the growth behavior of different plant groups a considerable quantity of green tissue is present in the ecosystem throughout the year.

In all forests, the microarthropod population peaks about four months after the peak leaf fall, that is, in the mid-rainy season. This is the period when the peak rate of weight loss in litter decomposition occurs. The microbial population, on the other hand, generally reaches a maximum immediately after the rainy season, i.e., in October, when ground litter is still quite moist. It is suggested that microarthropods play a predominant role during the early phases of biological decomposition, while the microbes predominate as decomposers when the residual material is rather more resistant yet moist.

Despite differences in the elevation and physiognomy, the central Hi-

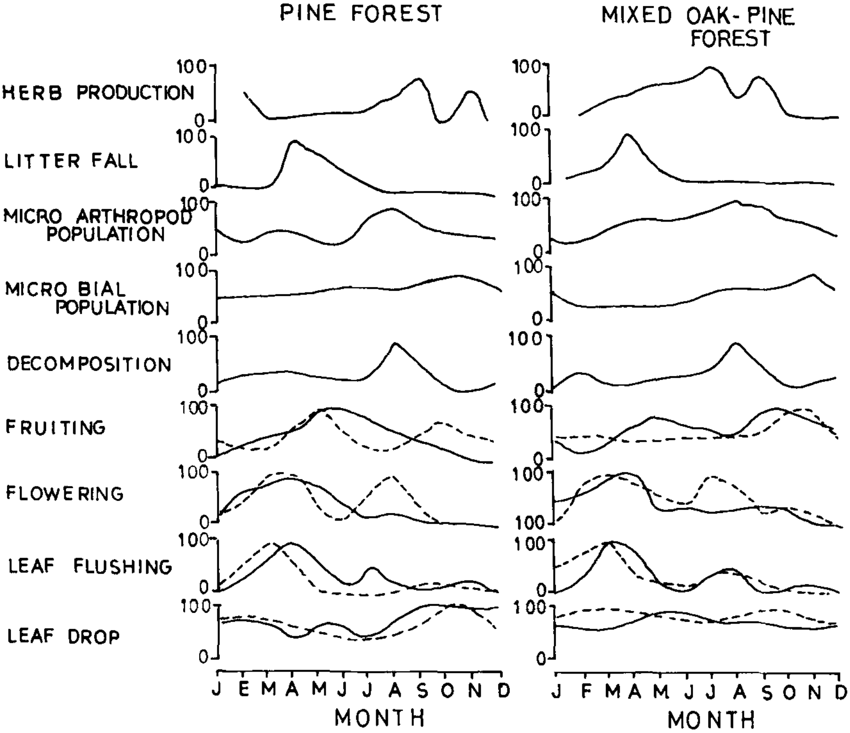

Fig. 19. A representation of periodicity of certain activities in pine and mixed oak–pine forest. See Figure 18 for explanation.

malayan forests of 300–2200 m elevation show a marked similarity to one another wth regard to seasonal periodicity of their various activities. Although the temperature differs, the magnitude of difference is not large enough to cause major differences in the phenological patterns. Summer temperatures at lower elevations are not high enough to curtail bud burst in trees or to stop herbaceous growth. Similarly, at higher elevations, the temperatures are not sufficiently low to hasten the process of dormancy. Further, many of the dominant species of the elevational range studied in central Himalaya occurred within a relatively much narrower elevational range in the mid-Miocene, as discussed earlier. Further selections in adaptational strategies have presumably occurred subsequently, in response to a wider range in climate, but many species have apparently retained a substantial part of their original character.

To sum up, these ecosystems seem to be geared to maximize the advantages of the monsoon period: (1) To take full advantage of the favorable period, the foliage of trees and shrubs is overhauled and fully developed prior to the commencement of the monsoon. In the eastern Himalayan

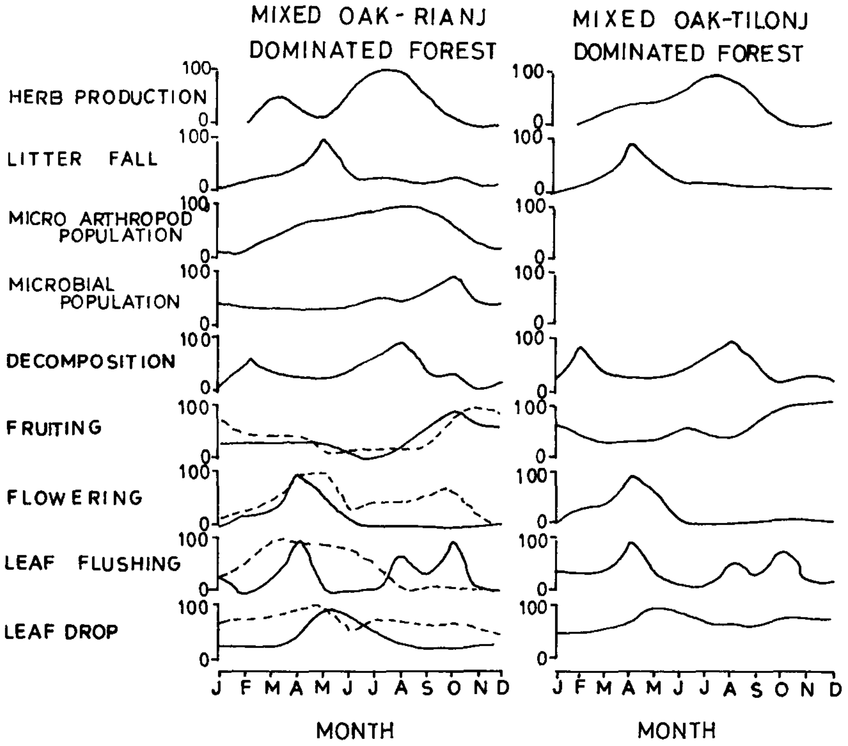

Fig. 20. A representation of periodicity of certain activities in mixed oak–rianj dominated and mixed oak–tilonj dominated forests. See Figure 18 for explanation.

forests, litter fall and leafing occur earlier. (2) A concentrated summer leaf-drop ensures rapid decomposition of litter during the subsequent rainy season when soil biota are the richest. (3) Possibly, the maturation of foliage prior to rainy season minimizes the losses due to insects, whose populations may show spurts in warm and wet conditions. (4) To take advantage of adequate moisture, the seeds of annuals germinate during the rainy season, even though they are disadvantaged by having to photosynthesize in the low light intensity of an environment under fully developed overhead foliage. (5) The maximum development of renewable forest canopy and the ground flora during the rainy season ensures immobilization of nutrients being released through rapid decomposition in order to check the leakage. Because of heavy rainfall, the majority of nutrients would otherwise be leached out or lost in surface runoff.

VII. Man and Forest

Major human activities in relation to forests are given in Table XXV. There are nomadic races, such as the Gujjars, who lead a pastoral life-

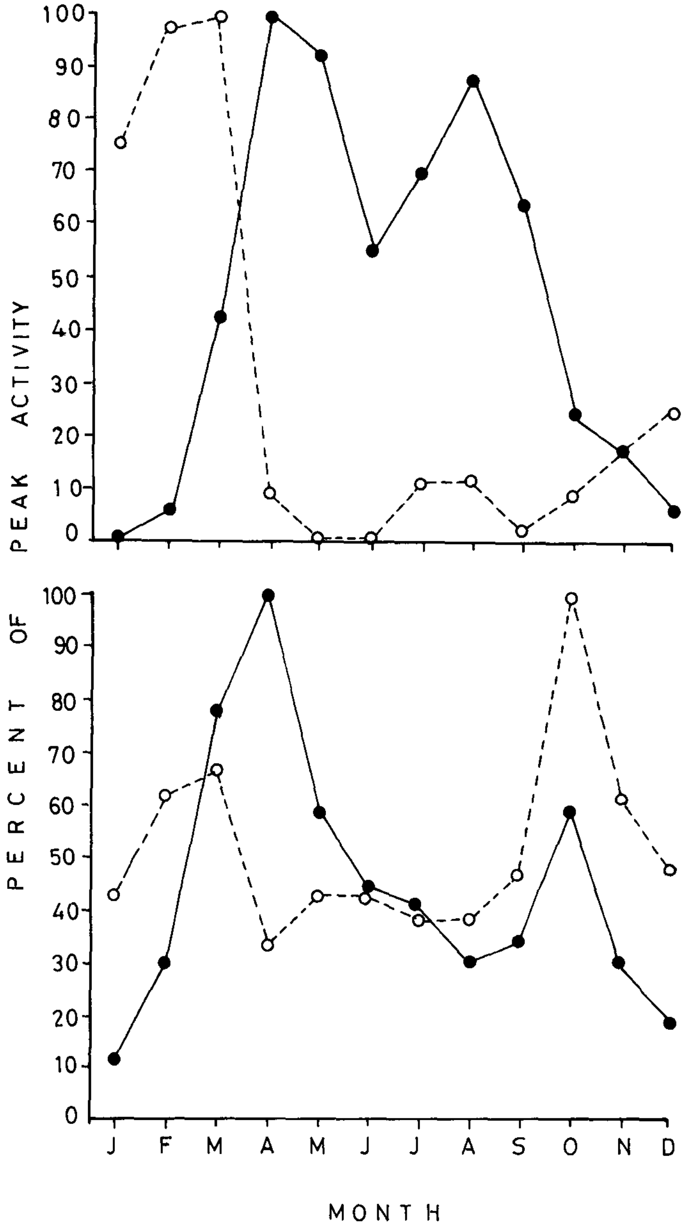

Fig. 21. Seasonal periodicity of certain activities in overstory trees of a mid-montane ombrophilous forest, eastern Himalaya. Top. Solid line with closed circles represents leafing and broken line with open circles leaf fall. Bottom. Solid line with closed circles represents flowering, and broken line with open circles fruiting (based on Boojh & Ramakrishnan, 1981).

Table XXV

Major human activities in relation to forests in the Himalaya

Life-style	Activity	Examples	Region
Nomadic	Pastoral	Gujjars, Sherpas in the past	Central and western Himalaya, particularly in high mountains
Semi-nomadic	Semi-pastoral	Bhujelas of Nepal	Central Himalaya, between 2000 and 4500 m
	The past form of jhuming[a]	Several tribes, e.g., Khasi	Eastern Himalaya, submontane to mid-montane
Settled	The present form of jhuming	Several tribes, e.g., Khasi	Eastern Himalaya, submontane to mid-montane
	Settled-agriculture	About 80% of population of region	Central and western Himalaya, in submontane to mid-montane belt
Industrial	Tea plantation and other industries	Urban societies	Central and eastern Himalaya, but more in the latter

[a] Jhuming, explained in text on page 169, means shifting agriculture.

style, traversing the entire elevational gradient that encompasses the vegetation, to graze their animals. The "bhujelas," as an example, exhibit semi-pastoralism (Hitchcock, 1977). At the higher elevational zone (2500–4500 m), animal husbandry is their predominant occupation. They migrate to lower altitudes (1800–2200 m) during the winter, where agriculture becomes their main occupation. In the eastern Himalaya, most of the tribal populations practice shifting cultivation. Earlier they led a semi-nomadic life, but now are getting settled in villages. In most of the areas outside the eastern Himalaya, settled agriculture is the main human activity of the population. Apart from these activities, the Himalayan forests have been subjected to commercial exploitation during about the last one and one-half centuries. In all the above activities, the populations in question have exploited forests, both by destroying the trees to clear the land for agriculture, and by harvesting the trees for fuel, fodder, and building materials on a sustained basis. In this section, we are mainly concerned with the impact of three major forms of existing activities that depend on the forest, viz., shifting agriculture, settled agriculture, and commercial exploitation.

A. SHIFTING AGRICULTURE

Shifting agriculture, or slash and burn agriculture, is locally called "jhuming." Practiced since time immemorial (originating during Neolithic times), it is still the major form of agriculture in the eastern Himalaya. Practiced by about half a million tribal families, it affects about 2.7 million ha, and about 0.45 million ha remain under shifting cultivation per year (Borthakur et al., 1980). This accounts for 85% of the land cultivated each year. Normally, shifting cultivation involves: (i) forest-cutting during December–January; (ii) burning of the slashed forest after removing tree trunks and large branches during mid-February to mid-March; (iii) cultivation of crops in April–May (cereals, vegetables, and oil-yielding crops) in various mixes by dibbling for one or two years; (iv) shifting to another forest site; and (v) returning to the original site (in earlier times after 20–30 yr) but currently, owing to the population pressure, after 5 years or even less. The only inputs are seeds and human labor. The only tools used are the chopping-knife, the dibbling-stick, and a small hoe for weeding.

Recently, some studies elucidating the functioning of this form of agriculture have been conducted (Mishra & Ramakrishnan, 1981, 1982; Ramakrishnan & Toky, 1981; Ramakrishnan et al., 1981; Toky & Ramakrishnan, 1981a, 1981b, 1982). The average size of a "jhum" in Khasi hills (at 1500 m in Meghalaya) is about 1.5–2 ha per family of five members each. Earlier, when the population was small and the jhum-cycle was circa 20–30 years, this size of jhum was small relative to the area under mature forests. Shortening of the jhum-cycle from 30 years to 5 years or less has resulted in the following consequences, which are somewhat related to one another: (i) a gradual decrease of the area under mature forest relative to that of jhum and concomitant fragmentation of the forests and local extinction of original forest species; (ii) the formation of increasingly continuous stretches of pioneer communities and the arrival and establishment of exotics (weeds) such as *Eupatorium adenophorum, Imperata cylindrica* (Table XXVI); (iii) a depletion of valuable timber species and firewood required for cooking, and consequently the destruction of forests not even being used for jhuming; (iv) a reduction in the subsidy in terms of nutrients and soil-building material from the slashed and burned vegetation, hence the introduction of the practices, initially of using organic manures and lately also of using chemical fertilizers; (v) an increase in soil and nutrient losses and deterioration in overall soil quality (Table XXVII); (vi) a reduction of species richness in the crop-system (Table XXVI) and its simplification from an integrated mixture of tuber crops (*Solanum tuberosum, Ipomoea batatas,* and *Colocasia esculentum*), cereals (e.g., *Zea mays*), legumes (e.g., *Phaseolus vulgaris*), and cucurbits (e.g., *Cucurbita maxima, Cucumis sativus*) in longer cycles to a crop-system of *Solanum tuberosum, Zea mays,* and *Brassica oleracea* in shorter cycles, which has led to a deterioration in food quality for humans; and (vii) a decrease in the output : input ratio of the crop-system, owing to an increasing input, as well as to a decline in output (Table XXVI). As the cycle is shortened, while less energy is expended on clearing the vegetation and crop-harvest, considerably more energy is required for fertilizing the soil and for weeding. In a 15-year cycle fertilizers are not used, in a 10-year-cycle organic manure is used, and in a 5-year cycle chemical fertilizers are used in addition to organic manure. The difference in energy inputs (per ha) among the different cycles (about 370,000 kcal between the 15-yr and 5-yr cycles and about 119,000 kcal between the 10-yr and 5-yr cycles) is due to the decrease in subsidy from the vegetation that develops subsequent to jhuming and to the deterioration of the system in response to the shortening of the jhum-cycle.

The present situation is frightening, as most of the original forests in accessible areas have been replaced by successional communities, which too are not being allowed to progress beyond a weed-stage over large areas. Only some forested islands in the form of "sacred groves" left for religious purposes, bear some similarity to the potential natural forests. Since more than 50% of energy required for cooking is derived from forests other than being slashed for jhuming, deep inroads have been made into secondary forests also. Consequently, the original ground-flora has been replaced by weeds, which arrived in the region owing to intensive jhuming.

Table XXVI

Impact of shortening of jhum-cycle on various aspects of the crop system in the eastern Himalaya (at about 1600 m) (based on Mishra & Ramakrishnan, 1981)[a]

Parameters	Jhum-cycle		
	15 years	10 years	5 years
Basal area of weeds ($cm^2\ m^{-2}$)	–	17.4	28.4
Total of N, PO_4-P, K, Ca, Mg in soil ($g\ m^{-2}$)	426	416	365
Number of crop species	13	13	3
Agronomic yield ($kg\ ha^{-1}\ m^{-2}$)	2443	1614	975
Total energy			
($kcal\ ha^{-1}\ yr^{-1}$)—input	340,139	581,200	709,857
—output	3,708,157	5,729,131	3,287,054
Output: input ratio	25.6	9.8	4.6

[a] Jhum-cycle explained in the text on page 169.

Chirapunji, the wettest place of the world, with an annual rainfall of over 1000 cm bears today a vegetation far removed in structure from the potential natural ombrophilous forests. Here weeds, bushes, and cacti prevail and soil and nutrients have been swept away.

B. SETTLED AGRICULTURE

Our information on the energy relations of settled agriculture which is practiced in most of the areas outside the eastern Himalaya, is based on a case study of three villages located within the low-montane belt (1000–2000 m) of the central Himalaya (U. Pandey & Singh, 1984a, 1984c; J. S. Singh, Pandey & Tiwari, 1984) (Fig. 22). The crops are raised on the terraces carved out of the hill slopes. For a majority of the households (of 6–7 members each), the average cultivated land is 0.5 ha. On average, two crops are taken in three years. Three major conclusions are immediately obvious: (i) The agronomic production is based largely on the adjacent forest ecosystems. (ii) The amount of food produced from agriculture is inadequate to meet the minimal demands of the resident population. (iii) The area of the "village forests" (all the forests in which villagers have a right to harvest) is far less than required to meet the firewood and fodder demand. Consequently, even the "reserved" forests (under the control of the State Forest Department) are being damaged.

Each unit of the agronomic energy produced entails about seven units of energy from the adjacent forests in terms of fodder, firewood, and litter (for manure) (J. S. Singh, Pandey & Tiwari, 1984). The villagers maintain large animal populations, not only for ploughing or for milk, but also for dung which is used to fertilize the soil. If forests were to be the source of

Table XXVII

Water and nutrient losses through run-off and percolation owing to jhuming (based on J. Singh & Ramakrishnan, 1982b)

	Year after jhuming			
	0		50	
	Surface run-off	Percolation	Surface run-off	Percolation
Loss of water (mm)	558	357	313	124
Loss of nutrients (kg ha^{-1})				
N	8.1	14.0	0.5	0.2
P	1.1	0.1	0.5	0.1
K	77.7	21.8	11.0	3.8
Ca	210.0	7.0	11.7	3.7
Mg	15.2	3.5	2.4	0.7

sustained yield of fodder (i.e., when only ground herbage were harvested), about 18 ha of forest would be required per ha of cultivation (U. Pandey & Singh, 1984a, 1984c). The forest area required for firewood is 12 ha of well-wooded forest, provided only wood fall is collected. Against these requirements, the area of the forest of any type available, per ha of cultivation is 1.66 ha and that of well-stocked forest is merely 0.84 ha (J. S. Singh, Pandey & Tiwari, 1984). Thus the exploitation has already far exceeded the carrying capacity of forests. The protein-rich broadleaf species, such as *Quercus* spp., *Bauhinia* spp., *Ficus* spp., *Mallotus philippensis* (with more than 12% protein in leaves) have been the worst sufferers. Oaks bear also the pressure of the demand for firewood and agricultural tools.

Further, in order to promote the growth of grasses, the villagers use surface fire frequently, particularly in the chir pine forests. Oak forests also suffer a great deal from fire spreading from the pine forests. One of the major consequences of fire is the expansion of chir pine at the expense of broadleaf species.

C. COMMERCIAL EXPLOITATION

Table XXVIII contains a chronological summary of the major phases of commercial exploitation of Himalayan forests, the economic activities which necessitated the exploitation of particular timber species, forest management practices and the impact of these on forest structure. The following account is based on the Madras group (1983a, 1983b), A. S.

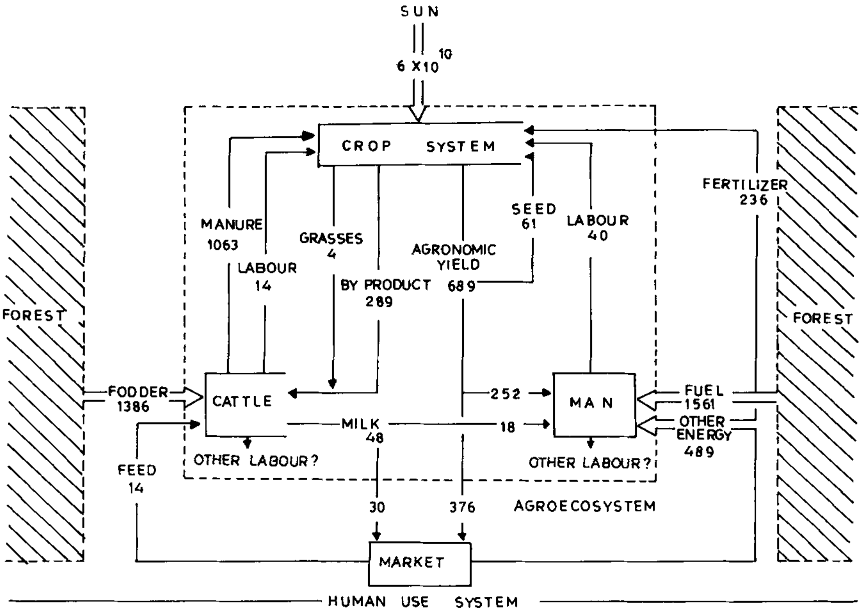

Fig. 22. Average energy flow through the human use system for central Himalayan villages. All values are $\times 10^5$ kJ yr^{-1} per ha of cultivated land. Solar radiation is in 6×10^{10} kJ yr^{-1} ha^{-1}. Of the total manure shown, about 26% comes from live stock. "Other energy" represents imported food from the market (based on U. Pandey & Singh, 1984a, and J. S. Singh, Pandey & Tiwari, 1984).

Rawat (1981, 1985), J. S. Singh, Pandey & Tiwari (1984), Stebbing (1922, 1923, 1926), Tucker (1983), Forest Working Plans, and personal observations. Certain points are evident:

(1) The chronology of exploitation of a timber species was largely influenced by accessibility. However, the demand arising from the prevalent economic activities often proved to be an ascendant force. For example, sal (*Shorea robusta*), a species of the submontane zone, was the first major species to be commercially exploited for construction activities. The demand for railway sleepers from the 1860's to the 1890's resulted in the exploitation of deodar (*Cedrus deodara*), occurring in remote areas above 2000 m, since by that time the stock of sal (*Shorea robusta*) growing in the submontane zone had become inadequate to meet the demand.

(2) Most of the commercial exploitation in the last one and one-half century centered upon three species, viz., sal, deodar, and chir pine. These species make either pure forests or forests in which they share predominance. Out of these, chir pine is an early successional species and the other two are late successionals.

(3) All the above three species were overexploited at one time or the

Table XXVIII

A chronological summary of major events in forest exploitation and related socio-economic and technological conditions in the central Himalaya

Phases	Relevant technologies and resultant economic activities	Technologies for use of forest resources and social aspects	Species exploitation and forest management	Effect on forest resources
Pre-British period: Before 1916 in Kumaun division; before 1809 in parts of Punjab	Age-old agriculture based on forest resources; house construction; iron smelting, charcoaling, mining, etc., at subsistence level.	Technologies of cottage industries-size. Normal subsistence economy, broken occasionally under the military pressure of Gurkhas and Rohillas.	Oak and other broadleaf species for fodder, fuel, agricultural tools, house construction etc., chir pine for charcoaling. Theoretically the king owned forests, in practice villagers exploited in order to maintain subsistence economy; no demarcation of ownership; king's use minimal.	No marked effect, plenty of resources available for subsistence economy.
British Colonial system: Pre-railway era till around 1860	Plains: Expansion of agriculture due to construction of canal networks and cultivation of cash crops even for export; expansion of cities and creation of urban markets. Hills: Introduction of localized tea gardens, and expansion of agriculture in central and outer Hima-	Down-river transportation, British system of charcoaling for smelting iron, copper, etc. Villagers motivated to plough more waste-lands and forests and depopulated villages rehabilitated; kings used forests as source of rewards for courtiers and army personnel.	Heavy exploitation of sal and initiation of deodar exploitation by British contractors. Uncontrolled and unclassified felling for timber, transportation to plains, forest resources thought inexhaustible: therefore, no preservation.	Sal and other broadleaf species exploited at large scale during 1840–1850, and regeneration weakened.

Table XXVIII
Continued

Phases	Relevant technologies and resultant economic activities	Technologies for use of forest resources and social aspects	Species exploitation and forest management	Effect on forest resources
	laya. Mining mostly in Siwaliks; import of iron processed from England with opening of Suez Canal in 1869 destroyed iron smelting in hills.			
Railway building era, mid 1860's–1890's	Use of steam engines; building of railway lines, construction of coaches, improvements of road network; limited expansion of tea gardens in western Himalaya but very extensively in eastern Himalaya.	Creosoting system designed for the use of softwood conifer timber for railway sleepers, but proved unusable. Few contractors became wealthy because of timber trade. Skilled (e.g., sawyers of Punjab foothills) and unskilled labor forces developed; two-way shift in labor forces; outside labor included Nepalese, Beharies, and east Uttar Pradesh.	Sal, deodar, mostly for railway sleepers. First Inspector General of forests appointed in 1865 and controls on forest resources started; variety of harvesting and marketing arrangements developed with private contractors, division of forests from management stand point; forest boundaries, compartments, etc., marked; disputes negotiated.	Deodar overexploited and regeneration weakened.

Table XXVIII
Continued

Phases	Relevant technologies and resultant economic activities	Technologies for use of forest resources and social aspects	Species exploitation and forest management	Effect on forest resources
Beginning of 20th century through 1st World War up to 1920	Gun powder, improved communication, energy concentration and spurt in military demand.	Improved technology for the use of chir-pine resin, development of technologies at the Forest Research Institute for better poles for gun carriages, stock for army rifles, parts for aeroplanes, etc. Large scale army recruitment; immediately after the war relation between hill people and forest department worsened; noncooperation movement against restrictive forest laws; issue of forest politicized.	Chir pine and several other species, even those found rather infrequently, establishment of reserves completed; uncontrolled felling of any accessible tree species under the pressure of war.	Forests available to villagers become inadequate for their subsistence, large scale deliberate burning of forests by the people. Further deterioration in the forest stock.
Between two World Wars	Improved road network, growth in sugar industries; improvement in war technologies—use of aeroplanes; greater concentration of energy in a few countries.	None significant except for plywood. More politicized relations between the Forest Department and the people; army recruitment, more outmigration.	Increased use of chir pine, overexploitation of any species to meet the military demand. Controlled burning in chir pine at larger scale.	Further deterioration in the forest stock.

Table XXVIII

Continued

Phases	Relevant technologies and resultant economic activities	Technologies for use of forest resources and social aspects	Species exploitation and forest management	Effect on forest resources
Post-independence—until 1960's	Expansion of construction works due to rapid urbanization; large sized hydroelectric projects; transformation of Tarai into agricultural land and subsequent expansion of human settlements across Tarai into Bhabar belt; enormous growth in road network in hills and tourism activity; military establishment up to borders.	None significant. Further increase in outmigrants to be settled in Bhabar, women very hardpressed because of scarcity of fodder and fuel; use of government aid without any perceptible improvement; mushroom growth of nongovernment organizations with or without vested interests.	All the materials available, including *Lantana camara*, an obnoxious weed, for fuel. Beginning of the introduction of exotic species; partial replacement of sal by teak and *Eucalyptus*; emphasis on control of soil erosion; Van-Mahotsav,[a] forest cooperatives for selling and utilization.	Transformation of some originally oak forests into chir pine forests, degradation of some reserved forests into shrubs and grasslands; even high mountain subalpine vegetation disturbed; good forest cover reduced to 4.4% of the total area.

Table XXVIII
Continued

Phases	Relevant technologies and resultant economic activities	Technologies for use of forest resources and social aspects	Species exploitation and forest management	Effect on forest resources
Present—1970's and thereafter	As above.	Forest problems became matter of concern for ecologists, social workers, politicians, and administrators; Chipko movement.[b] Emergence of the centers of study on forest management and forest ecology beyond the control of Forest Department; establishment of Central Department of Environment; beginning of physical assaults upon foresters by the people.	Initiation of social forestry, control on Forest Department in the management of forests; blanket-ban on felling of trees above about 1300 m; beginning of the introduction of exotic pines; harvest of first plantation of *Eucalyptus* spp., replacement of contractor system for the tree cutting by the corporation system; ban on oak felling.	As above.

[a] Ceremonial tree plantation organized by the State Forest Department.
[b] Explained in text on page 179.

other. The sal was largely overexploited during the pre-railway era when organized forestry had not been established. It was overexploited further under the pressure of the early railway era and the military demand from the two world wars. Deodar's overexploitation occurred when sal became inadequate to meet the demand for railway sleepers. Chir pine was not exploited until the improved technology for resin processing was made available in the beginning of the twentieth century. Thereafter, this species too could not escape overexploitation, particularly during the post-independence period.

(4) Since the regeneration of sal and deodar could not be adequately revived by the silvicultural practices evolved by organized forestry, inasmuch as they were late successional species, it was easier to regenerate the early successional species, chir pine.

(5) The objective of establishing reserved forests, which would ensure a regular and long-term supply of commercial timber and which would become the prominent forest cover of the hills, could not be achieved. For, not only were the multistratal old-growth forests, particularly of oaks, transformed into simpler forests, particularly of chir pine, but several reserves even degenerated into shrub and grassland as time elapsed.

(6) The level of the rise in the revenue of the State Forest Department indicates that the forests were overexploited also during post-independence.

(7) It was not possible to estimate the rate at which village forests (all the forests which villagers could use) became inadequate to meet the demand of subsistence economy of the villagers. It appears that they became inadequate by the beginning of the twentieth century, when most of the forests in the hills were being categorized as "reserved." This led to a keen and perpetual struggle between the people and the Forest Department. Politicized or well-meaning movements against the restrictions on the use of forest resources were launched by the people in different parts of the central Himalaya, the latest being the "Chipko Andolan" (women hugging the trees in order to save them from commercial felling). Chipko Andolan is incidentally the first ecological movement originating at grass-root level against deforestation. In the forests available to villagers no silvicultural practices were used before independence and, after independence, only a few attempts, albeit unsuccessful, were made to revive them.

(8) There is evidence to indicate that a number of broadleaf species, particularly oaks (*Quercus* spp.), which supported the subsistence economy of the villagers, were disfavored under the organized forestry and commercial species, particularly pine and deodar, were promoted through protection and plantation. Instances are there to indicate that activities, such as lopping and girdling of oaks, were allowed even in reserved forests

so that the conifers would come to preponderate in originally oak forests (Guha, 1983). In order to get a purer crop of chir pine, saplings of oaks were removed from time to time (Champion & Seth, 1968b). The Forest Research Institute, Dehradun, in the beginning was mainly concerned with improving the products of commercial uses. If the research papers published by the personnel of the Forest Department on sylviculture were in any way indicative of the policy, it is apparent that most of the emphasis was on the revival of sal and deodar in the earlier phase and that of spruce and fir (species of higher elevations commercially exploited after independence) later on.

Introduced in the 1840's, tea plantation expanded rapidly in the eastern Himalaya to become the greatest destroyer of the forests after the shifting cultivation in the region. In comparison, the area under tea bushes was far less in the central Himalaya. Nevertheless, no other plantation crop even approximated that extent (6880 ha in 1911) in this region (Tucker, 1983).

The forests have also been destroyed because of the cottage industry of iron smelting (involving firewood) during the nineteenth century, particularly in the central and western Himalayan regions. Activities related to limestone mining and magnesite extraction, particularly during the post-independence era, and the recent build-up of an extensive road network, are some of the factors which have directly led to the destruction of forest habitats.

Some of the major consequences of the afore-cited activities on the forests, as exemplified by the case of the central Himalayan region, are given below:

1. The forested area is only about 28.7%, and good quality forest (>60% crown cover) accounts for only about 4.4% of the geographical area, while the medium quality (30–60% crown cover) and poor quality (<30%) forests account for, respectively, 25% and 10.5% of the area (J. S. Singh, Pandey & Tiwari, 1984). The Himalayan forests have become a net source of carbon for the atmosphere, releasing about 21×10^{12} g C annually (J. S. Singh et al., 1985).
2. As discussed earlier, the forms of density-diameter distribution curves reflect the prevalence of even-aged forests due to short felling cycles, overexploitation of old-growth forests in the past and of young trees in the present, the preponderance of early-successional forests, and replacement of oaks by pine.
3. Weeds, such as *Lantana camara,* have spread over large areas, forming pure stands on the forest edges and contributing substantially to the ground flora of some forests.
4. Several wild animals have become locally extinct and are on the verge of extinction from the area, e.g., red giant flying squirrel of oak forest (*Pataurista petusista*), the caracal (*Felis caracal schmitzi*), leopard

(*Panthera pardus fusca*), the smooth Indian otter (*Lutra perspicillata*), the Himalayan black bear (*Selenarctos thibetanus lenigar*), the sambar (*Cervus unicolor niger*), the barking deer (*Montiacus muntia vaginalis*), and the musk deer (*Moschus moschiferus*) (Khajuria, 1980).

5. Original forests are being replaced by exotic species in order to meet commercial demands (*Eucalyptus* spp., *Populus* spp., exotic pines, such as *Pinus patula, P. greggii, Cryptomeria japonica*), or because of faulty management and hasty decisions, such as the replacement of sal by teak (*Tectona grandis*).

VIII. Acknowledgments

We thank Professors Vishnu-Mittre (Birbal Sahani Institute of Palaeobotany), P. S. Ramakrishnan (North-Eastern Hill University), V. M. Meher-Homji (Institut Français) and K. P. Singh (Banaras Hindu University) for reviewing portions of the manuscript. Prof. Meher-Homji has kindly translated the summary into French. Thanks are also due to P. B. Rao, J. C. Tewari, P. K. Ralhan, Uma Pandey, N. P. Melkania, Y. S. Rawat, R. K. Khanna, and V. P. Upadhyay for able assistance. The preparation of the manuscript has been supported by the Department of Environment, and portions of the research reviewed were supported by the Department of Science and Technology, New Delhi; the Indian Space Research Organisation, Bangalore; and the University Grant Commission, New Delhi.

IX. Literature Cited

Ahlgren, I. F. & C. E. Ahlgren. 1965. Effects of prescribed burning on soil microorganisms in a Minnesota jackpine forest. Ecology **46**: 304–310.

Anonymous. 1977. Himalaya: Ecologie-ethnologie. Editions du Centre National de la Recherche Scientifique, Paris.

Auden, J. B. 1949. Dykes in western India. A study of their relationship with the Deccan Traps. Trans. Natl. Inst. Sci. India **3**: 123–157.

Awasthi, N. 1974. Neogene angiospermous woods. Pages 341–358 *in* K. R. Surange, R. N. Lakhanpal & D. C. Bharadwaj (eds.), Aspects and appraisal of Indian palaeobotany. Birbal Sahni Institute of Palaeobotany, Lucknow.

———. 1982. Tertiary plant megafossils from the Himalaya—A review. Palaeobotanist **30**: 254–267.

Bandhu, D. 1971. A study of the productive structure of tropical dry deciduous forest at Varanasi. Ph.D. Thesis. Banaras Hindu University, Varanasi.

———. 1973. Chakia Project. Tropical deciduous forest ecosystem. Pages 39–62 *in* D. E. Reichle, R. V. O'Neill, J. S. Olson & L. Kern (eds.), Modelling forest ecosystems. Report of International Biological Programme/P.T. Section, Oak Ridge National Laboratory. Oak Ridge, Tennessee.

Bartholomew, W. V., J. Meyer & H. Landelout. 1953. Mineral nutrient immobilization under forest and grass fallow in the Yangambi (Belgian Congo) region. Publications de l'Institut National pour l'Étude Agronomique de Congo Belge, Série Scientifique **57**: 1–27.

Bartos, D. L. & R. S. Johnston. 1978. Biomass and nutrient content of Quaking Aspen at two sites in the Western United States. Forestry **24**: 273–280.

Blasco, F. 1970. Aspects of the flora, and ecology of Savannas of the South Indian Hills. J. Bombay Nat. Hist. Soc. **67**: 522–534.

———. 1971a. Montagnes du Sud l'Inde. Forêts, savanes, l'écologie. Inst. Franç. Pondichéry. Tr. Sect. Sci. Tech. **11**: 1–436.

———. 1971b. Orophytes of South India and Himalayas. J. Indian Bot. Soc. **50**: 377–381.

———. 1977. Relations écologiques et floristiques entre l'Himalaya et les montagnes du Sud de l'Inde. Pages 87–88 *in* Himalaya: Ecologie-ethnologie. Editions du Centre National de la Recherche Scientifique, Paris.

Boojh, R. & P. S. Ramakrishnan. 1981. Phenology of trees in a subtropical evergreen montane forest in north-east India. Geo-Eco-Trop **5**: 189–209.

——— & ———. 1982. Growth strategy of trees related to successional status. I. Architecture and extension growth. Forest Ecol. Managem. **4**: 359–374.

Bor, N. L. 1938. A sketch of the vegetation of the Aka hills, Assam. A synecological study. Indian Forest Rec. (N.S.), Bot. **1**: 103–121.

Bormann, F. H. & G. E. Likens. 1979. Pattern and process in a forested ecosystem. Springer, New York.

Borthakur, D. N., A. Singh, R. P. Awasthi & R. N. Rai. 1980. Shifting cultivation in the North-eastern region. Pages 330–342 *in* Proc. national seminar on resources, development and environment in Himalayan region. Department of Science and Technology, Govt. of India, New Delhi.

Bray, J. R. & J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. **27**: 325–349.

——— **& E. Gorham.** 1964. Litter production in the forests of the world. Advances Ecol. Res. **2**: 101–157.

Burkill, I. H. 1924. The botany of the Abor expedition. A study of forests of Abor hills, Eastern Himalayas. Rec. Bot. Surv. India **10**: 1–420.

Champion, H. G. 1923. The interaction between *Pinus longifolia* (chir) and its habitat in the Kumaun hills. Indian Forester **49**: 342–356.

———. 1936. A preliminary survey of forest types of India and Burma. Indian Forest Rec. (N.S.) **1**: 1–36.

——— **& S. K. Seth.** 1968a. A revised survey of the forest types of India. Manager of Publications, Delhi.

——— & ———. 1968b. General silviculture for India. Manager of Publications, Delhi.

Charles, R. P. 1957. Morphologie dentaire du Tahr et du Bonguetin espèces actuelles et subfossiles des gisements préhistoriques. Mammalia **21**: 136–141.

Chatterjee, D. 1939. Studies on the endemic flora of India and Burma. J. Roy. Asiat. Soc., Bengal **5**: 19–67.

Chaturvedi, O. P. 1983. Biomass structure, productivity and nutrient cycling in *Pinus roxburghii* forest. Ph.D. Thesis. Kumaun University, Nainital.

——— **& J. S. Singh.** 1982. Total biomass and biomasss production of *Pinus roxburghii* trees growing in all aged natural forests. Canad. J. Forest. Res. **12(3)**: 632–640.

——— & ———. 1984. Potential biomass energy from all-aged chir pine forest of Kumaun Himalaya. Biomass **5(2)**: 161–165.

Christensen, O. 1975. Wood litter fall in relation to abscission, environmental factors and the decomposition cycle in a Danish oak forest. Oikos **26**: 187–195.

Clarke, C. B. 1898. On the sub-areas of British India, illustrated by the detailed distribution of the Cyperaceae in that Empire. J. Linn. Soc. (Lond.) Bot. **34**: 1–146.

Connell, J. H. & R. O. Slatyer. 1977. Mechanism of succession in natural communities and their role in community stability and organization. Amer. Naturalist **111**: 1119–1144.

Cottam, G. 1949. The phytosociology of an oak wood in southwestern Wisconsin. Ecology **30**: 271–387.

Cowan, J. M. 1929. The forests of Kalimpong. An ecological account. Records of the Botanical Survey of India. Vol. 12. Botanical Survey of India, Calcutta.

Croizat, L. 1968. The biogeography of India: A note on some of its fundamentals. Rec. Advances Trop. Ecol. **2**: 544–590.

Dabral, B. G., P. Nath & R. Swarup. 1963. Some preliminary investigations on the rainfall interception by leaf litter. Indian Forester **89**: 112–116.

——— **& B. K. Subba Rao.** 1968. Interception studies in chir and teak plantation—New Forest. Indian Forest. **94:** 540–551.

DeAngelis, D. L., R. H. Gardner & H. H. Shugart. 1980. Productivity of forest ecosystems studied during the IBP: The woodlands data set. Pages 567–672 *in* D. E. Reichle (ed.), Dynamic properties of forest ecosystems. Cambridge University Press, Cambridge.

Deb, D. B. 1960. Forest types studied in Manipur. Indian Forest. **86:** 94–111.

Dey, A. K. 1949. The age of the Bengal gap. Symposium on Satpura hypothesis of the distribution of Malayan fauna and flora to Peninsular India. Proc. Natl. Inst. Sci. India **15:** 409–410.

Dhir, R. P. 1967. Pedological characteristics of some soils of the North-western Himalayas. J. Indian Soc. Soil Sci. **15:** 1–15.

Dobremez, J. F. 1972. Carte écologique du Nepal. II. Région Jiri-Thodung 1/50000. Doc. Carte Veg. Alpes **10:** 9–24.

———. 1973. Carte écologique du Nepal. IV. Région Tarai Central. 1/250000. Documents de Cartographie Ecologique **12:** 1–16.

———. 1977. Les Cupulifères Himalayennes Repartition, écologie, signification biogéographique. Pages 89–98 *in* Himalaya: Ecologie-ethnologie. Editions du Centre National de la Recherche Scientifique, France.

——— **& C. Jest.** 1971. Carte écologique de la région Annapurna-Dhaulagiri. Doc. Carte Vég. Alpes **11:** 1–49.

———, **A. Maire & B. Yon.** 1975. Carte écologique de Nepal I. Région Ankhu Khola–Trishuli 1/50,000. Documents de Cartographie Ecologique **15:** 1–20.

——— **& P. R. Shakya.** 1975. Carte écologique du Nepal. IV. Région Birat Nagar–Kangchenjunga 1/250000. Documents de Cartographie Ecologique **26:** 33–48.

Dudgeon, W. & L. A. Kenoyer. 1925. The ecology of Tehri-Garhwal. A contribution to the ecology of western Himalayas. J. Indian Bot. Soc. **4:** 233–285.

Duvigneaud, P. & S. Denaeyer-De Smet. 1970. Biological cycling of minerals in temperate deciduous forests. Pages 199–255 *in* D. E. Reichle (ed.), Analysis of temperate forest ecosystems. Springer-Verlag, New York.

Edwards, P. J. 1977. Studies of mineral cycling in a montane rain forest in New Guinea. II. The production and disappearance of litter. J. Ecol. **65:** 971–992.

Franklin, J. E., T. Maeda, Y. Ohsumi, M. Matsui, H. Yagi & G. M. Hawk. 1979. Subalpine coniferous forests of Central Honshu, Japan. Ecol. Monogr. **49(3):** 311–334.

Ghildyal, B. P. 1980. Soil of the Garhwal and Kumaun Himalaya. Pages 120–137 *in* J. S. Lall & A. D. Moddie (eds.), The Himalaya. Oxford University Press, New Delhi.

Ghosh, R. C. 1956. Ecology of the coniferous forests of West Bengal—A study. Pages 117–118 *in* Proc. IX Silvic. Conf. Part II. Forest Research Institute, Dehradun.

Golley, F. B., J. T. McGinnis, R. G. Clements, G. I. Child & M. J. Duever. 1975. Mineral cycling in a tropical moist forest ecosystem. University of Georgia Press, Athens, Georgia.

Gorrie, R. M. 1933. The Sutlej deodar, its ecology and timber production. Indian Forest Production. Indian Forest Rec. **17:** 1–240.

Greenland, D. J. & J. M. L. Kowal. 1960. Nutrient content of the moist tropical forest of Ghana. Plant Soil **12:** 154–174.

Gresham, C. A. 1982. Litter fall patterns in mature loblolly and longleaf pine stands in coastal South Carolina. Forest Sci. **28:** 223–231.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Amer. Naturalist **111:** 1161–1194.

Grubb, P. J. & P. J. Edwards. 1982. Studies of mineral cycling in a montane rain forest in New Guinea. III. The distribution of mineral elements in the above-ground material. J. Ecol. **70:** 623–648.

Guha, R. 1983. The nature of forestry science. Peoples' Particip. Sci. Techn. Bull. **3(1):** 101–113.

Gupta, A. C. 1963. Annual precipitation and the vegetation of the dry temperate coniferous region of the N.W. Himalayas. J. Indian Bot. Soc. **42:** 313–318.

Gupta, R. K. 1972. Bibliography on "Plant-ecology" in Bhutan, Sikkim and Tibet. Excerpta Bot., Sect. B, Sociol. **12(3):** 226–237.

———. 1981. Bibliography of the Himalayas. Gurgaon Indian Documentation Service, Gurgaon.

——— **& J. S. Singh.** 1962. Succession of vegetation types in the Tons Valley of Garhwal Himalaya. Indian Forester **88:** 289–296.

Heath, G. W., M. K. Arnold & C. A. Edwards. 1966. Studies in leaf litter breakdown. I. Breakdown rates among leaves of different species. Pedobiologia **6:** 1–12.

Hill, S. A. 1976. Meteorology of North-west Himalayas. Indian Meteorol. Mem. **1(6):** 376–419.

Hingston, F. J., G. M. Dimmock & A. G. Turton. 1980. Nutrient distribution in a Jarrah (*Eucalyptus marginata* Don ex Sm.) ecosystem in South West Australia. Forest. Ecol. Managem. **3:** 183–207.

Hitchcock, J. T. 1977. Buying time. Population, trees, Liebig's "law" and two Himalayan adaptive strategies. Pages 443–452 *in* Himalaya Ecologie-ethnologie. Editions du Centre National de la Recherche Scientifique, Paris.

Hooker, J. D. 1852. On the climate and vegetation of the temperate and cold regions of East Nepal and the Sikkim mountains. J. Hort. Soc. London **7:** 69–131.

———. 1906. A sketch of flora of British India. London.

Hora, S. L. 1949. Satpura hypothesis of the distribution of the Malayan fauna and flora to Peninsular India. Proc. Natl. Inst. Sci. India **15:** 309–313.

———. 1950. Satpura hypothesis as aspect of Indian biogeography. Curr. Sci. **19:** 364–370.

Horn, H. S. 1974. The ecology of secondary succession. Annual Rev. Ecol. Syst. **5:** 25–37.

Jain, S. K. & A. R. K. Sastry. 1980. Plant resources in the Himalayas. Pages 98–107 *in* Proc. national seminar on resources, development and environment in the Himalayan region. Department of Science and Technology Govt. of India, New Delhi.

Jenny, H., S. P. Gessels & F. T. Bingham. 1949. Comparative study of decomposition rates of organic matter in temperate and tropical regions. Soil Sci. **68:** 419–432.

Johnson, F. L. & P. G. Risser. 1974. Biomass, annual net primary productivity and dynamics of six mineral elements in a postoak-blackjack oak forest. Ecology **55:** 1246–1258.

Jokela, E. J., C. A. Shannon & E. H. White. 1981. Biomass and nutrient equations for mature *Betula papyrifera* Marsh. Canad. J. Forest. Res. **2:** 298–304.

Jordan, C. & P. G. Murphy. 1978. A latitudinal gradient of wood and litter production. Amer. Midl. Naturalist **99:** 415–434.

Jordan, C. F. 1977. Distribution of elements in a tropical montane rain forest. Trop. Ecol. **18:** 124–130.

Kanai, H. 1963. Phytogeographical observations on the Japano-Himalayan elements. J. Fac. Sci. Univ. Tokyo. Ser. III Bot. **8:** 305–339.

———. 1966. Phytogeography of eastern Himalaya. Pages 13–38 *in* Flora of eastern Himalaya. University of Tokyo.

Kar, N. R. 1972. Some aspects of the Pleistocene geomorphology of the Himalaya. Geol. Surv. India Misc. Publ. **15:** 53–60.

Kärenlampi, I. L. 1971. Weight loss of leaf litter on forest soil surface in relation to weather at Kevo Station, Finnish Lapland. Rep. Kevo. Subarctic Res. Station **8:** 101–103.

Kartawinata, K. 1978. The "Kerangas" heath forest in Indonesia. Pages 145–153 *in* J. S. Singh & B. Gopal (eds.), Glimpses of ecology. Professor R. Misra Commemoration Volume. International Scientific Publications, Jaipur.

Kaul, O. N. & P. B. L. Srivastava. 1967. Nutrient uptake of fir (*Abies pindrow*) and spruce (*Picea smithiana*). Indian Forest **93:** 249–257.

Kaul, R. N. & B. N. Ganguli. 1961. Studies on the introduction of *Eucalyptus* in the arid zone of India. Pages 626–637 *in* Proc. X Silv. Conf. Forest Research Institute, Dehradun.

Kaul, V. & Y. K. Sarin. 1976. Life-form classification and the biological spectrum of the flora of Bhaderwah. Trop. Ecol. **17:** 132–139.

Kaushik, S. D. 1962. Climatic zones and their related socioeconomy in the Garhwal Himalaya. Geogr. Rev. India **24:** 22–41.

Kenoyer, L. A. 1921. Forest formations and successions in the Sat Tal Valley, Kumaun Himalayas. J. Indian Bot. Soc. **2:** 236–258.

Khajuria, H. 1980. The wild mammals of the western Himalayas. Pages 216–229 *in* Proc. national seminar on resources, development and environment in the Himalayan region. Department of Science and Technology, Govt. of India, New Delhi.

Killingbeck, K. T. & M. K. Wali. 1978. Analysis of a North Dakota gallery forest: Nutrient, trace element and productivity relations. Oikos **30:** 29–60.

Lakhanpal, R. N. 1970. Tertiary floras of India and their bearing on the historical geology of the region. Taxon **19(5):** 675–694.

Legris, P. & V. M. Meher-Homji. 1968. Floristic elements in the vegetation of India. Rec. Advances Trop. Ecol. **2:** 536–543.

Lieth, H. 1973. Primary production: Terrestrial ecosystems. Human Ecol. **1:** 303–322.

———. 1975. Primary production of the major vegetation units of the world. Pages 203–215 *in* H. Lieth & R. H. Whittaker (eds.), Primary productivity of the biosphere. Springer-Verlag, New York.

Longman, K. A. & K. K. Jenik. 1974. Tropical forest and its environment. Longman, London and New York.

Loucks, O. L. 1970. Evolution of diversity, efficiency, and community stability. Amer. Zool. **10:** 17–25.

Madgwick, H. A. I., P. Beets & S. Gallagher. 1981. Dry matter accumulation, nutrient and energy content of the aboveground portion of 4-year old stands of *Eucalyptus nitens* and *E. fastigata.* New Zealand J. Forest Sci. **11:** 53–59.

Madras Group. 1983a. The story of scientific forestry in India: Some highlights. People's Particip. Sci. Techn. Bull. **3(1):** 31–67.

———. 1983b. The vision of modern forestry: What it is doing to our forests. People's Particip. Sci. Techn. Bull. **3(1):** 68–100.

Mani, M. S. (ed.). 1974. Ecology and biogeography in India. Dr. W. Junk, The Hague.

Medlicott, H. B. & W. T. Blandford. 1879. A manual of geology of India, Calcutta.

Meher-Homji, V. M. 1970. Some phytogeographic aspects of Rajasthan. Vegetatio **21:** 299–320.

———. 1972. Himalayan plants on South Indian hills: Role of Pleistocene glaciation vs. long distance dispersal. Sci. & Cult. **38:** 8–12.

———. 1974. Disjunct distributions in plant kingdom. Sci. & Cult. **40:** 217–227.

——— **& K. C. Misra.** 1973. Phytogeography of the Indian sub-continent. Pages 9–89 *in* R. Misra, B. Gopal & J. S. Singh (eds.), Progress of plant ecology in India. Today and Tomorrow Publ., New Delhi.

Mehra, M. S., U. Pandey & J. S. Singh. 1983. Restitution of reproductive biomass of overstorey tree species in certain forests of Kumaun Himalaya. Trop. Pl. Sci. Res. **1(2):** 175–180.

———**, P. C. Pathak & J. S. Singh.** 1985. Nutrient movement in litter fall and precipitation components for Central Himalayan forests. Ann. Bot. **55:** 153–170.

——— **& J. S. Singh.** 1985. Pattern of wood litter fall in five forests located along an altitudinal gradient in central Himalya. Vegetatio **63:** 3–11.

Mellinger, M. V. & S. J. McNaughton. 1975. Structure and function of successional vascular plant communities in Central New York. Ecol. Monogr. **45:** 161–162.

Meusel, H. 1971. Mediterranean elements in the flora and vegetation of the west Himalaya. Pages 53–72 *in* P. H. Davis, P. C. Harper & I. C. Hedge (eds.), Plant life of Southwest Asia. Bot. Soc. Edinburgh.

Mishra, B. K. & P. S. Ramakrishnan. 1981. The economic yield and energy efficiency of hill agro-ecosystems at higher elevations of Meghalaya in North-Eastern India. Oecol. Applic. **2:** 369–389.

——— **&** ———. 1982. Energy flow through a village ecosystem with slash and burn agriculture in north-eastern India. Agricultural Systems **9:** 57–72.

——— **&** ———. 1983a. Secondary succession subsequent to slash and burn agriculture at higher elevations of north-east India. Oecol. Applic. **4:** 95–107.

——— **&** ———. 1983b. Secondary succession subsequent to slash and burn agriculture at higher elevations of north-east India. II. Nutrient cycling. Oecol. Applic. **4:** 237–245.

Mohan, N. P. 1933. Ecology of *Pinus longifolia* with particular reference to Kangra and Hoshiarpur forest divisions. Indian Forester **59:** 812–826.

——— **& G. S. Puri.** 1956. Himalayan conifers. V. The succession of forest communities in chir pine (*Pinus roxburghii*) forests of Punjab and Himachal Pradesh. Indian Forester **82:** 356–364.

———, ——— **& A. C. Gupta.** 1956. The Himalayan conifers. IVA. Case study of some soil profiles under some forest communities in the Bashahr Himalayas. Indian Forester **82:** 295–307.

Moral, R. del. 1979. High elevation vegetation of the Enchantment Lakes Basin, Washington. Canad. J. Bot. **57:** 1111–1130.

Mueller-Dombois, D. & H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, New York.

Mukerji, B. K. & N. K. Das. 1940. Studies on Kumaun hill soils. Indian J. Agric. Sci. **10:** 990–1020.

——— **&** ———. 1941. Effect of terracing and cultivation on soil types of Choubattia. Indian J. Agric. Sci. **11:** 914–953.

Muller, R. N. & F. H. Bormann. 1976. Role of *Erythronium americanum* Ker. in energy flow and nutrient dynamics of a northern hardwood forest ecosystem. Science **193:** 1126–1128.

Murthy, R. S. & S. Pandey. 1980. Soil and land use in the Himalayan region. Pages 40–45 *in* Proc. national seminar on resources, development and environment in the Himalayan region. Department of Science and Technology, Govt. of India, New Delhi.

Negi, K. S., Y. S. Rawat & J. S. Singh. 1983. Estimation of biomass and nutrient storage in a Himalayan moist temperate forest. Canad. J. Forest Res. **13:** 1185–1196.

Numata, M. 1965. Ecological study and mountaineering of Mt. Nambur, in eastern Nepal. Univ. of Chiba, Japan.

Nye, P. H. 1958. The relative importance of fallow and soils in storing plant nutrients in Ghana. J. W. African Sci. Assoc. **4:** 31–50.

Odum, E. P. 1969. The strategy of ecosystem development. Science **164:** 262–270.

Osmaston, A. E. 1922. Notes on the forest communities of the Garhwal Himalayas. J. Ecol. **10:** 129–167.

Ovington, J. D., D. Heitkamp & D. Lawrence. 1963. Plant biomass and productivity of prairie-savannah, oak wood and maize field ecosystems. Ecology **44:** 52–63.

——— **& H. A. I. Madgwick.** 1959. The growth and composition of natural stands of birch. Plant Soil **10:** 389–399.

Pande, D. C. 1956. Progress of the sal natural regeneration in Uttar Pradesh under the normal prescriptions of working plans. Pages 91–96 *in* IX Silvic. Conf. Part I. Forest Research Institute, Dehradun.

Pandey, A. N., P. C. Pathak & J. S. Singh. 1983. Water, sediment and nutrient movement in certain forested and non-forested sites in Kumaun Himalaya. Forest Ecol. Managem. **7:** 19–29.

——— **& J. S. Singh.** 1985. Mechanism of ecosystem recovery: A case study from Kumaun Himalaya. Reclam. Reveg. Res. **3:** 271–292.

Pandey, U. & J. S. Singh. 1981a. A quantitative study of the forest floor, litter fall and nutrient return in an oak-conifer forest in Himalaya. I. Composition and dynamics of forest floor. Oecol. Generalis **2:** 49–61.

——— **&** ———. 1981b. A quantitative study of the forest floor, litter fall and nutrient return in an oak-conifer forest in Himalaya. II. Pattern of litter fall and nutrient return. Oecol. Generalis **2:** 83–99.

——— **&** ———. 1982. Leaf litter decomposition in an oak-conifer forest in Himalaya: The effects of climate and chemical composition. Forestry **55:** 47–59.

——— **&** ———. 1984a. Energy flow relationships between agro- and forest-ecosystems in Central Himalaya. Environ. Conserv. **10:** 343–345.

——— **&** ———. 1984b. Nutrient changes and release during decomposition of leaf litter in an Himalayan oak-conifer forest. Canad. J. Bot. **62(9):** 1824–1831.

——— **&** ———. 1984c. Energetics of hill agroecosystems: A case study from Central Himalaya. Agric. Syst. **13:** 83–96.

Pathak, P. C. 1983. Vegetational hydrology and its impact on nutrient cycling in selected forest ecosystems of Kumaun Himalaya. Ph.D. Thesis. Kumaun University, Nainital.

———, **A. N. Pandey & J. S. Singh.** 1983. Partitioning of rainfall by certain forest stands in Kumaun Himalaya. Trop. Pl. Sci. Res. **1(2):** 123–126.

———, ——— & ———. 1984. Overland flow, sediment output and nutrient loss from certain forested sites in the central Himalaya, India. J. Hydrol. **71:** 239–251.

———, ——— & ———. 1985. Apportionment of rainfall in Central Himalayan forest (India). J. Hydrol. **76:** 319–332.

——— **& J. S. Singh.** 1984. Nutrients in precipitation components for the pine and oak forests in Kumaun Himalaya. Tellus **36:** 44–49.

Patriat, P. & J. Achache. 1984. India-Eurasia collision chronology has implications for crustal shortening and driving mechanism of plates. Nature **311:** 615–621.

Prakash, U. 1965. A survey of the fossil dicotyledonous woods from India and the far east. J. Paleontol. **39:** 815–827.

———. 1972. Palaeoenvironmental analysis of Indian Tertiary floras. Geophytology **2(2):** 178–205.

———. 1975. Fossil woods from the Lower Siwalik beds of Himachal Pradesh. Palaeobotanist **22:** 192–210.

———. 1979. Some more fossil woods from the Lower Siwalik beds of Himachal Pradesh, India. Himalayan Geol. **8:** 61–81.

Proctor, J., J. M. Anderson, P. Chal & H. W. Vallack. 1983. Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak II. Litter fall, litter standing crop and preliminary observations on herbivory. J. Ecol. **71:** 261–283.

Puri, G. S. 1960a. Indian forest ecology. Vol. I. Oxford Book and Stationery Co., New Delhi.

———. 1960b. Indian forest ecology. Vol. II. Oxford Book and Stationery Co., New Delhi.

———, **V. M. Meher-Homji, R. K. Gupta & S. Puri.** 1983. Forest ecology, phytogeography and forest conservation. Oxford Publ. Co., New Delhi.

Raina, B. N., N. B. Hukku & R. V. Chalapati Rao. 1980. Geological features of the Himalayan region, with special reference to their impact on environmental appreciation and environmental management. Pages 1–19 *in* Proc. national seminar on resources, development and environment in the Himalayan region. Department of Science and Technology, Govt. of India, New Delhi.

Ralhan, P. K., R. K. Khanna, S. P. Singh & J. S. Singh. 1985a. Phenological characteristics of the tree layer of Kumaun Himalayan forests. Vegetatio **60:** 91–101.

———, ———, ——— & ———. 1985b. Certain phenological characters of the shrub layer of Kumaun Himalayan forests. Vegetatio **63:** 113–120.

———, **A. K. Saxena & J. S. Singh.** 1982. Analysis of forest vegetation at and around Nainital in Kumaun Himalaya. Proc. Indian Natl. Sci. Acad. **48B:** 122–138.

Ramakrishnan, P. S. & O. P. Toky. 1981. Soil nutrient status of hill agro-ecosystems and recovery pattern after slash and burn agriculture (jhum) in north-eastern India. Plant Soil **60:** 41–64.

———, ———, **B. K. Mishra & K. G. Saxena.** 1981. Slash and burn agriculture in north-east India. Pages 570–587 *in* H. A. Mooney, T. M. Bonnicksen, N. L. Christensen, J. E. Lotan & W. A. Reiners (eds.), Fire regimes and ecosystem properties. USDA Forest Service General Technical Report WO-26.

Rao, P. B. 1984. Regeneration of some trees of Western Kumaun Himalaya. Ph.D. Thesis. Kumaun University, Nainital.

——— **& S. P. Singh.** 1985. Population dynamics of foothill sal (*Shorea robusta* Gaertn. f.) forest in Kumaun Himalaya. Œcol. Pl. **6:** 161–166.

Rao, Y. P. 1980. The Himalayas—Their climate. Pages 20–39 *in* Proc. national seminar on resources, development and environment in the Himalayan region. Department of Science and Technology, Govt. of India, New Delhi.

Rapp, M. 1969. Production de litière et apport au sol d'éléments minéraux dans deux ecosystems méditerranéens: La forêt de *Quercus ilex* L. et la garrigue de *Quercus coccifera* L. Oecol. Pl. **4(4):** 377–410.

Raunkiaer, C. 1934. The life forms of plants and statistical plant geography. Clarendon Press, Oxford.

Rawat, A. S. 1981. Forest management in Garhwal during the British rule. Pages 273–

285 *in* J. S. Singh, S. P. Singh & C. Shastri (eds.), Science and rural development in mountains. Gyanodaya Prakashan, Nainital, India.

———. 1985. Forest movement in U. P. Himalayas: 1906–1947. Pages 248–259 *in* J. S. Singh (ed.), Environmental regeneration in the Himalaya: Concepts and strategies. Central Himalayan Environment Association, Nainital, India.

Rawat, Y. S. 1983. Plant biomass, net primary production and nutrient cycling in oak forests. Ph.D. Thesis. Kumaun University, Nainital.

———**, U. Pandey, J. S. Singh & S. P. Singh.** 1983. The U. P. Himalaya: Ecological perspectives. Pages 47–64 *in* O. P. Singh (ed.), The Himalaya: Climate and geography. Rajesh Publ., New Delhi.

Raychaudhri, S. P., R. R. Agarwal, N. R. Dutta Vishwas, S. P. Gupta & P. K. Thomas. 1963. Soils of India. Indian Council of Agricultural Research, New Delhi.

Razi, B. A. 1955. Some observations on plants of South Indian hilltops and their distribution. Proc. Natl. Inst. Sci. India **21B:** 79–89.

Reiners, W. A. 1972. Structure and energetics of three Minnesota forests. Ecol. Monogr. **42:** 71–94.

Rice, E. L. 1974. Allelopathy. Academic Press, New York.

Rochow, J. J. 1972. A vegetational description of a mid Missouri forest using gradient analysis techniques. Amer. Midl. Naturalist **87(2):** 377–396.

Rodin, L. E. & N. P. Bazilevich. 1967. Production and mineral cycling in terrestrial vegetation (Engl. transl., G. E. Fogg). Oliver and Boyd, Edinburgh and London.

Roy Chowdhury, M. K. 1973. Status of recent work of the Geological Survey of India in the Himalaya and the programme of work in the field of geodynamics. Pages 13–24 *in* Seminar on geodynamics of the Himalayan region. Natl. Geophys. Res. Inst., Hyderabad.

Saxena, A. K. 1979. Ecology of vegetation complex of northwestern catchment of river Gola. Ph.D. Thesis. Kumaun University, Nainital.

———**, P. Pandey & J. S. Singh.** 1982. Biological spectrum and other structural-functional attributes of the vegetation of Kumaun Himalaya. Vegetatio **49:** 111–119.

———**, U. Pandey & J. S. Singh.** 1978. On the ecology of oak forests in Nainital hills, Kumaun Himalaya. Pages 167–180 *in* J. S. Singh & B. Gopal (eds.), Glimpses of ecology: Professor R. Misra commemoration volume. International Scientific Publishers, Jaipur.

——— **& J. S. Singh.** 1982a. A phytosociological analysis of woody species in forest communities of a part of Kumaun Himalaya. Vegetatio **50:** 3–22.

——— **&** ———. 1982b. Quantitative profile structure of certain forests in the Kumaun Himalaya. Proc. Indian Acad. Sci. B **91:** 529–549.

——— **&** ———. 1984. Tree population structure of certain Himalayan forest associations and implications concerning future composition. Vegetatio **58:** 61–69.

———**, S. P. Singh & J. S. Singh.** 1984. Population structure of forests of Kumaun Himalaya: Implications for management. J. Environ. Managem. **19:** 307–324.

Schweinfurth, U. 1957. Die horizontale und vertikale Verbreitung der Vegetation in Himalaya. Bonner Geogr. Abh. **20:** 1–372.

———. 1968. Vegetation of the Himalaya. Pages 110–136 *in* Mountains and rivers of India, 21st Intern. Geogr. Congr. New Delhi.

Shanks, R. E. & J. S. Olson. 1961. First year breakdown of leaf litter in Southern Appalachian forests. Science **134:** 194–195.

Sharma, A. P., J. S. Bisht & J. S. Singh. 1984. Microarthropods associated with certain litter species in Kumaun Himalaya. Pedobiologia **27:** 229–236.

Sharma, E. & R. S. Ambasht. 1984. Seasonal variation in nitrogen fixation by different ages of root nodules of *Alnus nepalensis* plantations in the eastern Himalayas. J. Appl. Ecol. **21:** 265–270.

Sharma, V. K. 1971. Ecology of *Shorea robusta* Gaertn. and *Buchanania lanzan* Spreng. at Varanasi forests. Ph.D. Thesis. Banaras Hindu University, Varanasi.

Shelton, M. G., L. E. Nelson, G. L. Switzer & B. G. Blackmon. 1981. The concentration of nutrients in tissues of plantations-grown Eastern Cottonwood (*Populus deltoides* Bart.). Mississipi Agric. Forest. Exptl. Station Tech. Bull. 106, Mississipi State Univ., Mississippi.

Shrestha, T. B. 1982. Ecology and vegetation of north-west Nepal (Karnali Region). Royal Nepal Academy, Kathmandu.

Shukla, R. P. & P. S. Ramakrishnan. 1982. Phenology of trees in a subtropical humid forest in northeastern India. Vegetatio **49:** 103–109.

Singh, H. P. 1982. Tertiary palynology of the Himalaya. A review. Palaeobotanist **30:** 268–278.

Singh, J. & P. S. Ramakrishnan. 1981. Biomass and nutrient movement through litter in *Shorea robusta* Gaertn. plantations in Meghalaya. Proc. Indian. Natl. Sci. Acad. B. **47:** 852–860.

——— & ———. 1982a. Structure and function of a sub-tropical humid forest of Meghalaya. I. Vegetation, biomass and its nutrients. Proc. Indian Acad. Sci. B **91:** 241–253.

——— & ———. 1982b. Structure and function of a sub-tropical humid forest of Meghalaya III. Nutrient flow through water. Proc. Indian Acad. Sci. B **91:** 269–280.

Singh, J. S. & O. P. Chaturvedi. 1982. Photosynthetic pigments on plant bearing surfaces in the Himalaya. Photosynthetica **16(1):** 101–114.

——— **& O. P. Goel (eds.).** 1983. Integrated study of natural resources and environment of parts of Kumaun Himalaya through remote sensing. Final report submitted to the ISRO, Bangalore, Kumaun University, Nainital.

——— **& S. R. Gupta.** 1977. Plant decomposition and soil respiration in terrestrial ecosystems. Bot. Rev. **43:** 449–528.

———**, A. N. Pandey & P. C. Pathak.** 1983. A hypothesis to account for the major pathway of soil loss from Himalaya. Environ. Conserv. **10:** 343–345.

———**, U. Pandey & A. K. Tiwari.** 1984. Man and forests: A central Himalayan case study. Ambio **13(2):** 80–87.

———**, Y. S. Rawat & O. P. Chaturvedi.** 1984. Replacement of oak forest with pine in the Himalaya affects the nitrogen cycle. Nature **311:** 54–56.

——— **& S. P. Singh.** 1984a. An integrated ecological study of eastern Kumaun Himalaya, with emphasis on natural resources. Vol. 1. Studies with regional perspectives. Final Report (HCS/DST/187/76). Kumaun University, Nainital.

——— & ———. 1984b. An integrated ecological study of eastern Kumaun Himalaya, with emphasis on natural resources. Vol. 2. Site specific studies. Final Report (HCS/DST/187/76). Kumaun University, Nainital.

——— & ——— **(eds.).** 1984c. An integrated ecological study of eastern Kumaun Himalaya, with emphasis on natural resources. Vol. 3. Synthesis and summary. Final Report (HCS/DST/187/76). Kumaun University, Nainital.

———, ———**, A. K. Saxena & Y. S. Rawat.** 1984. India's Silent Valley and its threatened rain-forest ecosystems. Environ. Conserv. **11:** 223–233.

———**, A. K. Tiwari & A. K. Saxena.** 1985. Himalayan forests: A net source of carbon to the atmosphere. Environ. Conserv. **12:** 67–69.

Singh, K. P. & R. Misra. 1978. Structure and functioning of natural, modified and silvicultural ecosystems of eastern Uttar Pradesh. Final Technical Report MAB Project I, Banaras Hindu University, Varanasi.

Singh, Rajendra P. 1979. Primary production and energy dynamics of tropical dry deciduous forest in Chandraprabha region, Varanasi. Ph.D. Thesis. Banaras Hindu University, Varanasi.

Singh, Ram P. 1974. A study of primary productivity and nutrient cycling in Chakia forest, Varanasi. Ph.D. Thesis. Banaras Hindu University, Varanasi.

Singh, S. 1929. The effect of climate on the conifers in Kashmir. Indian Forester **55:** 189–203.

Singh, S. P., R. K. Khanna & J. S. Singh. 1985. Accumulation in wood: A nutrient-conserving strategy of tropical forests. Environ. Conserv. **12:** 170–173.

———**, P. K. Ralhan & J. C. Tewari.** 1985. Stability of Himalayan climax oak forests in view of resilience hypothesis. Environ. Conserv. **12:** 73–75.

——— **& J. S. Singh.** 1985. Structure and function of forest ecosystems of Central Himalaya: Implications for management. Pages 85–113 *in* J. S. Singh (ed.), Environmental regeneration in Himalaya: Concepts and strategies. Central Himalayan Environment Association, Nainital, India.

Smith, W. H., F. H. Bormann & G. E. Likens. 1968. Response of chemoautotrophic nitrifiers to forest cutting. Soil Sci. **106:** 471–473.

Spate, O. H. K. 1967. India and Pakistan: A general and regional geography. Methuen & Co., London.

Stainton, J. D. A. 1977. Some problems of Himalayan plant distribution. Pages 99–102 *in* Himalaya: Ecologie-ethnologie. Editions du Centre National de la Recherche Scientifique, Paris.

Stark, N. 1971. Nutrient cycling II: Nutrient distribution in Amazonian vegetation. Trop. Ecol. **12:** 176–201.

Stebbing, E. P. 1922. The forests of India. Vol. I. A. J. Reprinters Agency, New Delhi.

———. 1923. The forests of India. Vol. II. A. J. Reprinters Agency, New Delhi.

———. 1926. The forests of India. Vol. III. A. J. Reprinters Agency, New Delhi.

Subba Rao, B. K., B. G. Dabral & S. K. Pande. 1972. Litter production in forest plantation of chir (*Pinus roxburghii*), teak (*Tectona grandis*) and sal (*Shorea robusta*) at New Forest, Dehra Dun. Pages 235–243 *in* P. M. Golley & F. B. Golley (eds.), Tropical ecology with an emphasis on organic production. University of Georgia, Athens.

Tanner, E. V. J. 1981. The decomposition of leaf litter in Jamaican montane forests. J. Ecol. **69:** 263–275.

Tewari, J. C. 1982. Vegetational analysis along altitudinal gradients around Nainital. Ph.D. Thesis. Kumaun University, Nainital.

——— **& J. S. Singh.** 1983. Application of aerial photo-analysis for assessment of vegetation in Kumaun Himalaya. I. Ranibagh to Nainapeak-Kilbari. Proc. Indian Natl. Sci. Acad. B **49:** 336–347.

——— **& S. P. Singh.** 1981. Vegetation analysis of a forest lying in transitional zone between lower and upper Himalayan moist temperate forests. Pages 104–119 *in* G. S. Paliwal (ed.), The vegetational wealth of Himalaya. Puja Publishers, New Delhi.

——— **&** ———. 1985. Analysis of woody vegetation in a mixed oak forest of Kumaun Himalaya. Proc. Indian Natl. Sci. Acad. **51B:** 332–347.

Tewary, C. K., U. Pandey & J. S. Singh. 1982. Soil and litter respiration rates in different microhabitats of a mixed oak conifer forest and their control by edaphic conditions and substrate quality. Plant Soil **65:** 233–238.

Thomas, W. A. 1968. Decomposition of loblolly pine needles with and without the addition of dogwood leaves. Ecology **49:** 568–571.

Thompson, T. 1852. Sketch of the climate and vegetation of the Himalaya. J. Hort. Soc. London **6:** 245–258.

Thornthwaite, C. W. 1931. The climates of North America; according to a new classification. Geogr. Rev. (New York) **21:** 633–655.

Tiwari, A. K., A. K. Saxena & J. S. Singh. 1985. Inventory of forest biomass for Indian Central Himalaya. Pages 236–247 *in* J. S. Singh (ed.), Environmental regeneration in the Himalaya: Concepts and strategies. Central Himalayan Environment Association, Nainital, India.

——— **& J. S. Singh.** 1984. Mapping forest biomass in India through aerial photographs and nondestructive field sampling. Appl. Geogr. **4:** 151–165.

———**, J. C. Tewari & J. S. Singh.** 1983. Application of aerial photo-analysis for assessment of vegetation in Kumaun Himalaya. II. Kathgodam to Okhal Kanda. Proc. Indian Natl. Sci. Acad. B **49:** 421–435.

Toky, O. P. & P. S. Ramakrishnan. 1981a. Run-off and infiltration losses related to shifting agriculture (jhum) in north eastern India. Environ. Conserv. **8:** 313–321.

——— **&** ———. 1981b. Cropping and yields in agricultural systems of north-eastern India. Agro-Ecosystems **70:** 11–25.

——— **&** ———. 1982. A comparative study of the energy budget of hill agroecosystems with emphasis on the slash and burn system (Jhum) at lower elevations of North-eastern India. Agric. Syst. **9:** 143–154.

——— **&** ———. 1983a. Secondary succession following slash and burn agriculture in north-eastern India. I. Biomass, litter fall and productivity. J. Ecol. **71:** 735–745.

——— **&** ———. 1983b. Secondary succession following slash and burn agriculture in north-eastern India. II. Nutrient cycling. J. Ecol. **71:** 747–757.

Tripathi, C. & P. R. Chandra. 1972. Fossils from the Karewas near Nichanoma, Kashmir. Geol. Surv. India Misc. Publ. **15:** 261–264.

Troll, C. 1939. Das Pflanzenkeid des Nanga Parbat. Begleitwarte zur Vegetations-Karte der Nanga-Parbat-Gruppe (NW-Himalaya) 1: 50,000. Wiss. Veröff. Deutsch. Mus. Länderk., N.F. **7:** 151–180.

Troup, R. S. 1921. The silviculture of Indian trees. Vols. I–III. Clarendon Press, Oxford.

Tucker, R. P. 1983. The British Colonial system and the forests of the Western Himalaya. Pages 1815–1914 *in* R. P. Tucker & J. F. Richards (eds.), Global deforestation and the nineteenth-century world economy. Duke Press Policy Studies, Durham, North Carolina.

UNESCO. 1973. International classification and mapping of vegetation, ecology, and conservation. **6:** 1–93. UNESCO, Paris.

Upadhyay, V. P., U. Pandey & J. S. Singh. 1985. Effect of habitat on decomposition of standard leaf-litter species. Biol. Fert. Soils **1:** 201–207.

——— **& J. S. Singh.** 1985a. Nitrogen dynamics of decomposing hardwood leaf litter in a Central Himalayan forest. Soil Biol. Biochem. **17:** 827–830.

——— & ———. 1985b. Decomposition of woody branch litter on an altitudinal transect in the Himalaya. Vegetatio **64:** 49–54.

Upreti, N. 1982. A study on phytosociology and state of regeneration of oak forests at Nainital. Ph.D. Thesis. Kumaun University, Nainital.

———, **J. C. Tewari & S. P. Singh.** 1985. The oak forests of the Kumaun Himalaya (India): Composition, diversity and regeneration. Mountain Res. Developm. **5:** 163–174.

Valdiya, K. S. 1970. Simla slates: The Precambrian flysch of the lesser Himalaya, its turbidites, sedimentary structures and paleocurrents. Bull. Geol. Soc. Amer. **81:** 451–467.

——— **& S. B. Bhatia (eds.).** 1980. Stratigraphy and correlations of lesser Himalayan formations. Hindustan Publishing Corp. (India), Delhi.

Vishnu-Mittre. 1965. Floristic and ecological reconsiderations of the Pleistocene plant impressions from Kashmir. Palaeobotanist **13:** 308–327.

———. 1966. Some aspects of pollen analytical investigations in the Kashmir valley. Palaeobotanist **15:** 157–175.

———. 1972. The glacial succession in the Kashmir valley. A summary and discussion of recent research. Geol. Surv. India Misc. Publ. **15:** 89–96.

———. 1974. Late Quaternary palaeobotany and palynology in India. Pages 16–51 *in* Vishnu-Mittre (ed.), An appraisement in Late Quaternary vegetational development in extra-European areas. Birbal Sahni Institute of Palaeobotany, Lucknow.

———. 1979. Palaeobotanical evidence of the environment of early Man in Northwestern and Western India. Grana **18:** 167–181.

———. 1984. Quaternary palaeobotany/palynology in the Himalaya: An overview. Palaeobotanist **32:** 158–187.

———. 1984. Floristic changes in the Himalaya (southern slopes) and Siwaliks from the Mid-Tertiary to Recent times. Pages 483–503 *in* R. O. Whyte (ed.), The evolution of the east Asian environment. Vol. II. Palaeobotany, palaeozoology and palaeoanthropology. Centre of Asian Studies, University of Hong Kong.

———, **C. Sharma, A. K. Saxena, K. Prasad, A. Bhattcharya & M. S. Chauhan.** 1984. Pollen stratigraphy of India. Puratattua, Bull. Indian Archaeol. Soc. **13/14:** 115–122.

Vogt, K. A., C. C. Grier, C. E. Meier & M. R. Keyes. 1983. Organic matter and nutrient dynamics in forest floors of young and mature *Abies amabilis* stands by fine root input. Ecol. Monogr. **53:** 139–157.

Wadia, D. N. 1936. Structure of the Himalaya and of the North Indian Fore Land. Pages 38–49 *in* Proc. Indian Sci. Congr. Vol. 25, Pt. 2. Calcutta.

———. 1937. Recent geological changes in northern India and their effect upon the drainage of the Indo-Gangetic basin. Sci. & Cult. **2:** 384–387.

———. 1963. Problems of Himalayan Geology. Sci. & Cult. **29:** 20–23.

Whittaker, R. H. 1966. Forest dimensions and production in the Great Smoky Mountains. Ecology **47:** 103–121.

———. 1970. The biochemical ecology of higher plants. Pages 43–70 *in* E. Sondheimer & J. B. Simeone (eds.), Chemical ecology. Academic Press, New York.

———. 1973. Climax concepts and recognition. Handb. Veg. Sci. **8:** 137–154.

———. 1975. Community and ecosystems, 2nd ed. Macmillan, New York.

———, **G. E. Likens, F. H. Bormann, J. S. Eaton & T. G. Siccama.** 1969. The Hubbard Brook ecosystem study: Forest nutrient cycling and element behavior. Ecology **60(1):** 203–220.

——— **& G. M. Woodwell.** 1969. Structure, production and diversity of the oak-pine forest at Brookhaven, New York. J. Appl. Ecol. **57:** 155–174.

Wiegert, R. G. 1970. Effects of ionizing radiation on leaf fall, decomposition, microarthropods of a montane rain forest. Pages H.89–H.100 *in* H. T. Odum & R. F. Pigeon (eds.), A tropical rain forest—A study of irradiation and ecology at El Verde, Puerto Rico. USAEL, Oak Ridge, Tennessee.

Wikum, D. A. & M. K. Wali. 1974. Analysis of a North Dakota gallery forest. Vegetation in relation to topographic and soil gradients. Ecol. Monogr. **44:** 441–464.

Witkamp, M. 1966. Decomposition of leaf litter in relation to environmental conditions, microflora and microbial respiration. Ecology **47:** 194–201.

——— **& J. S. Olson.** 1963. Breakdown of confined and non-confined oak litter. Oikos **14:** 138–147.

Woodwell, G. M., R. H. Whittaker & R. A. Houghton. 1975. Nutrient concentration in plants in the Brookhaven oak-pine forest. Ecology **56:** 318–332.

Zangerl, A. R. & F. A. Bazzaz. 1983. Responses of an early and late successional species of *Polygonum* to variations in resource availability. Oecologia (Berlin) **56:** 397–404.

Zutshi, D. P. & K. K. Vass. 1978. Limnological studies on Dal Lake—Chemical features. Indian J. Ecol. **5:** 90–97.