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Ecology of Himalayan Alder (*Alnus nepalensis* D. Don)

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Himalayan alder (*Alnus nepalensis*) is a common native species widely used in forestry and agroforestry in the eastern Himalaya. It naturally regenerates in freshly exposed landslide-affected soils, degraded and disturbed sites. It grows between 1000 and 2500m elevational range. It is an actinorhizal plant bearing root-nodules that are capable of fixing atmospheric nitrogen. There has been a growing concern about ecological and economical values of the Himalayan alder which has resulted in far more interest in the management of this species. Taxonomy and distribution of the species and its symbiotic association with *Frankia* are presented in this review. Root-nodule is the site where *Frankia* endophytes are housed by the host alder and therefore its production and turnover are very important and covered in details. Altitudinal, seasonal and diurnal variations in nitrogenase activity, nitrogen accretion, biomass, net primary productivity and nutrient cycling of *Alnus nepalensis* feature in greater details in this review for either naturally regenerated landslide-affected sites or nursery seedlings or an age series of plantations and/or *Alnus* in cardamom-based agroforestry systems. Role of *Alnus* in shifting cultivation in north-eastern India has been dealt. *In vitro* culture of *Frankia* strains and their nitrogen-fixing potential are also presented. Above specific information on some aspects of biology and ecology of *A. nepalensis* is summarized in this review which could be of some use in its management.

Key Words: **Taxonomy, *Frankia*-symbiosis, Root-nodule turnover, Nitrogenase activity, Nitrogen accretion, Productivity, Energetics, Nutrient cycling**

Introduction

Himalayan alder (*Alnus nepalensis*), also called Nepalese alder, is the most common tree species in the eastern Himalaya. It regenerates naturally on the landslide-affected freshly exposed and degraded sites. It is grown in forestry, agroforestry, shifting cultivation in north-eastern India, and as nurse tree in *Cinchona* (medicinal plant) plantations. It is planted in perennial landslides to check erosion and control land-slips. It is being widely used recently in reclamation of degraded habitats in eastern and central Himalaya. It is relatively short-lived and intolerant pioneer with rapid juvenile growth that has the capability to fix atmospheric nitrogen. It has tolerance to wet soil conditions and has high water-use efficiency (Nautiyal & Purohit 1987). The species is favoured by disturbance and often increases after harvesting and burning as evident in shifting cultivation. Commercial value of the Himalayan alder has traditionally been lower than many of the native and exotic species in the region, and most of these high-valued species have become less in number recently and therefore alder prices have gone up. Himalayan alder is cultivated widely as shade tree in private large cardamom (cash crop) based agroforestry in the Sikkim Himalayan region.

The altitudinal range of the Himalayan alder is sympatric with the agroclimatic range of large cardamom farming. It provides fuelwood for both cardamom-curing and domestic use. Trees attaining more than 25-30 years age provide timber. Its value has increased substantially in recent years and interest in the management of this species has increased accordingly, which in turn has led to an increased need for detailed information and more understanding on the ecology of the species. Information available on some aspects of biology and ecology of the Himalayan alder is summarized in this review.

Taxonomy and Distribution

Himalayan alder (genus *Alnus*) is a member of the family Betulaceae of the order Fagales. Other common Himalayan genus in this family is the birch (*Betula*). The presence of male catkins (compact aggregates of staminate flowers) is the most conspicuous feature of these two genera. The seed-bearing catkins in *Alnus* and *Betula* are similar when immature, but the *Betula* catkin disintegrates as seeds are dispersed, while the *Alnus* catkin remains intact and attached to the plant during seed dispersal and even after dispersal is completed. *Alnus* and *Betula* have been shown on the basis of anatomical features to be the most primitive members of the family Betulaceae, having formed a distinct line before other members, such as *Corylus, Ostrya, Ostryopsis* and *Carpinus,* diverged and evolved to form another complex (Ager & Stettler 1994).

The geographic origin of the genus *Alnus* is uncertain although the best available evidence points to the Asian land mass, either southwest, east, or west Gondwanaland before Africa and South America separated. Furlow (1979) proposed that the major divisions of the genus evolved in distinct regions of Asia before their migration to other parts of the world. About 35 species of *Alnus* are reported and most of them are distributed in the temperate climates and high latitude countries.

Two species of alders are found in the Himalaya viz., *Alnus nepalensis* (Himalayan alder) in the eastern Himalaya and *Alnus nitida* in the north-western Himalaya; while both of these species grow in the central and western Himalaya. *Alnus nepalensis* grows between 1000 m and 2500 m elevation belt most predominantly in the eastern Himalaya which encompasses eastern Nepal, Sikkim, Darjeeling, Bhutan, Arunachal Pradesh, Nagaland and also in the Khasi hills of Meghalaya. It is a pioneer species on freshly exposed landslide soils. It grows on sandy eroded soils, denuded habitats, rocky slopes, landslide-affected slopes, steep stream sides and in natural areas. It has been a common species in natural forests and recently has also become an important species of plantation forests in the Sikkim Himalaya. It has been considered as a useful species in social forestry and agroforestry in the region. It is also used as a chief shade tree in large cardamom (*Amomum subulatum*) based traditional agroforestry systems in the region. Shifting agriculture or jhum is the major economic activity in the north-eastern India. Management of fallow species in jhum system between two cultivations has become an important issue for sustaining this traditional practice. *A. nepalensis* has been an important fallow species in the jhum system that is traditionally valued and conserved by jhum farmers (Ramakrishnan 1994).

Actinorhizal (*Frankia*) Associations

Many angiospermic plants other than legumes also possess N_2-fixing root nodules (Akkermans & Van Dijk 1981). The actinomycetous endophyte of such nodules belongs to the genus *Frankia* (Becking 1970). These root nodules were often described as "non-leguminous root nodules" but recently more specific terms such as *Alnus*-type nodules, actinomycete symbiosis or actinorhizas were given (Fessenden 1979). *Frankia* symbioses have been recorded in more than 200 plant species belonging to 24 genera within the angiospermeae (Dixon & Wheeler 1986). *Alnus* is the most prominent actinorhizal genus in the Himalaya, other actinorhizal genera are *Elaeagnus, Myrica, Hippophae* and *Coriaria.*

There had been a long persistent international effort on isolation of *Frankia* from the host nodule. The first successful isolation of *Frankia* in axenic culture followed by demonstration of nodulation of its original host (*Comptonia peregrina*) was made by Callaham et al. (1978). Since then hundreds of *Frankia* isolates have been obtained from root nodules of different *Alnus* spp (Baker 1989) and other actinorhizal plants (Racette & Torrey 1988, Favre-Raynaud et al. 1990). Pradhan (1993) isolated three

Frankia strains viz., AnF_1, AnF_2 and AnF_3 from *A. nepalensis* and these were classified into different strains on the basis of morphological, physiological and host nodulation characteristics. All these *Frankia* strains showed cushion-like branched septate hyphae ranging from 0.5–1.2 µm in diameter. Vesicles were produced by all these three isolates especially in nitrogen-free medium.

Frankia is the partner responsible for nitrogen fixation in this symbiosis. The characteristic morphology of symbiotic *Frankia* in different seasons have significant ecological implications. The dominance of *Frankia* vesicles in nodule cortical cells in *A. nepalensis* during rainy season coincided with the higher rate of nitrogenase activity indicating that the vesicles are the sites of enzyme activity (Pradhan 1993). Schwintzer et al. (1982) have also shown that *Frankia* vesicles are the sites of nitrogenase activity. The cells in basal and middle zone of nodular tissue in *A. nepalensis* harboured abundant *Frankia* sporangia during mid winter that indicates termination of active growth and nitrogen fixation. Sporulation of the endophyte corroborates with the maintenance of *Frankia* population in soil by its dispersal after nodule decay, to tide over the hostile environmental conditions in winter and then infect new root sites in the following growing season (Akkermans & Van Dijk 1981). *Frankia* strains isolated from soil supporting *A. nepalensis* exhibited a branched, septate and cushion-shaped hyphae, electron dense vesicles borne on short stalk and multi-locular sporangia that resembled those obtained from root nodules (Pradhan 1993). Vesicular-arbuscular mycorrhizal (VAM) fungi association of *A. nepalensis* roots and nutrient mobilization by VAM has also been recorded by Pradhan (1993).

Root Nodule Production and Turnover

Root nodules in the field are normally classified into two distinct categories i.e., active and inactive. Sharma and Ambasht (1986) classified them on the basis of colour and were initially confirmed by N_2-fixing potential. They further classified active nodules in *A. nepalensis* into three age-classes; young, medium and old; and the age in the field was determined by colour — young being pale yellow, medium-aged as dull yellow and old as yellowish-brown. The inactive nodules were dark brown. Akkermans (1971) followed a different method of estimation of perennial nodule age by counting the number of annual rings in the xylem of the subtending roots.

The active root nodule biomass in *A. nepalensis* increased markedly in the growing season from April onwards to a peak in October, followed by a decrease in winter in all stands of an age series of plantations (7-, 17-, 30-, 46- and 56-year-old). The highest active nodule biomass (307 kg/ha) was obtained towards the end of the growing season in the youngest stand. The active and inactive nodule biomass build-ups in different seasons were inversely related. The biomass contribution of the three age-classes of active nodules varied with season. The medium-aged nodules showed little fluctuation, but there were wide variations in contributions of young (8 to 55%) and old (13 to 73%) nodules. The highest contributions of young nodule biomass (55±14%) was obtained in peak growing season (July) and old nodule biomass (73±15%) in winter (January) season (Sharma & Ambasht 1986). Annual root nodule production was highest (492 kg/ha) in the 7-year stand and lowest (244 kg/ha) in the 56-year stand. The proportion of annual production of active and inactive nodules was almost equal in young stand, but the annual production of inactive nodule was lower than active nodule in the older stands. The annual formation and production of new nodules was ≃ 40% of total nodule production in *A. nepalensis* (Sharma & Ambasht 1986). Zavitkovski and Newton (1968) estimated nodule biomasses of 117 kg/ha in 7-year and 244 kg/ha in 30-year-old pure *A. rubra* stands. Akkermans and Van Dijk (1976) recorded an average nodule biomass of 454 kg/ha in a 20-year-old *A. glutinosa* stand and Binkley (1981) reported 390 and 110 kg/ha in *A. rubra* and *A. sinuata* stands, respectively. Sharma (1995) estimated 201 kg/ha active root nodule biomass in *A. nepalensis* grown as shade tree in a large cardamom-based agroforestry system in Sikkim. Akkermans and Van Dijk (1976) reported healthy nodule biomass of 454 kg/ha (77% of the total) and 136 kg/ha (23%) of necrotic nodules; these values are slightly greater than the highest active and inactive nodules in *A. nepalensis* as reported by Sharma and Ambasht (1986). The nodule biomass and its annual production were highest in the youngest plantation stand and it decreased with the increase in plantation age. However, turnover time, which is the time required to produce a quantity equal to maximum biomass, was longest in 7-year stand (11 months) and approximately equal in all the other older (17-, 30-, 46- and 56-year-old) stands in *A. nepalensis* (Sharma & Ambasht 1986).

In the course of extensive field work on the 7-year-old stands of *A. nepalensis*, only a few nodules were found to exceed the 30 mm size and 82% of the nodules were 1-3 years old. Young nodules within a year changed to 40% and 60% of active old and inactive nodules, respectively. The medium and old nodules regressed to totally inactive nodules within one year. By the end of growing season, young and medium-aged nodules showed 60-70% transition to older age-classes, whereas the old nodules did not show any change. Inactive nodule formation occurred mostly in the winter season. The annual total nodule production included 51-58% of active nodules and 42-49% of inactive nodules (Sharma 1985, Sharma & Ambasht 1986). The increase in inactive nodule biomass was mostly through transition of 1 to 2 year-old active nodules. Annual root nodule production was higher than the actual total nodule biomass at a time per unit area in all the stands of an age series of plantations. Sharma and Ambasht (1986) suggested that the nodule formation, growth, age-class-transition and decay were continual processes with not much difference in nodule biomass accumulation. They reported that the percentage of nodule age-class-transition and transition to inactive nodule in *A. nepalensis* were functions of the season, nodule age and their N_2-fixing potential. Schwintzer et al. (1982) reported that 88% of the field nodules of *Myrica gale* (another actinorhizal species) were 1-3 years old, which is comparable to 82% for *A. nepalensis* (Sharma & Ambasht 1986).

Sharma (1988) estimated the root nodule biomass of naturally regenerated seedlings of *A. nepalensis* at 10 different landslide-affected elevated (1000-2500 m) sites in the Kalimpong forest division of Darjeeling. Natural regeneration was vigorous at altitudes between 1380 and 1980 m and the root nodule biomass per seedling was about three times higher at 1675 m elevation than at 1070 and 2450 m. Root nodule dry weight per unit area in 1-year-old seedlings was also higher in the middle elevation zone with the highest value of 61.5 kg/ha occurring at 1675 m altitude.

Nitrogen Fixation and Accretion

Fixation

Sharma (1988) estimated the nitrogenase activity by acetylene reduction technique and assumed that rates of acetylene reduction reflect the enzyme activities. Figure 1 shows the change of these activities with altitude between 1000 and 2500 m in naturally regenerated *A. nepalensis* seedlings of landslide-affected sites. Measurements made in peak growing month (July) showed that the activity ranged from 5 to 19 μmol C_2H_4/g nodule dry weight/hr. Although there was considerable variation in the values from any one site, it is clear from figure 1, that activity is highest in the middle zone where the natural regeneration of *A. nepalensis* is most vigorous. The rate of acetylene reduction was significantly related to both the mean soil temperature and the root nodule moisture ($R^2 = 0.62$, d.f. = 9, $P < 0.05$; $F_{2,9} = 7.37$, $P < 0.025$). This shows that the nitrogenase activity is largely dependent on the soil temperature and the root nodule moisture in *A. nepalensis* (Sharma 1988). Light flux can also effect nitrogenase activity (Wheeler 1969) but all the sites studied by Sharma (1988) are at much the same latitude and longitude, so there could be only a little difference in illumination at the different elevation sites.

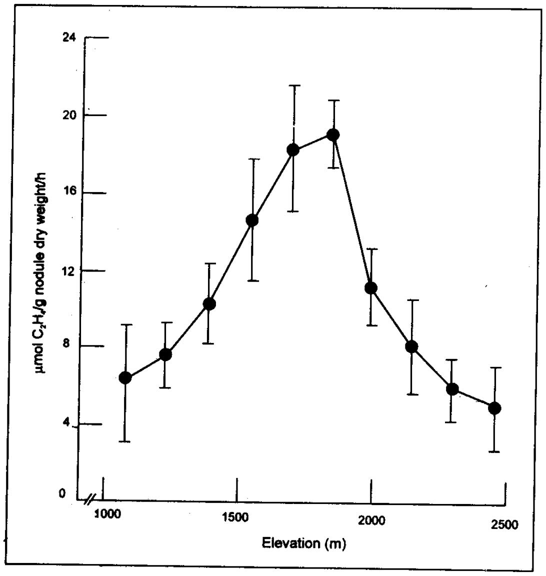

Figure 1. Altitudinal variation in nitrogenase activity of *A. nepalensis* seedling root nodules at 10 sites at different elevations in July 1982. These seedlings were naturally regenerated on landslide-affected slopes. Values are means ± SE; $n = 5$ (*after Sharma 1988*)

Seasonal variation in nitrogenase activity in *A. nepalensis* root nodules at three different elevations was quite clear (table 1). Activity was highest in the rainy season (July) and lowest in winter (December). It was higher in October than in April because October is the month of higher growth rate just after the rainy season; whereas April is the month when growth starts with the sprouting of new leaves after 4 months of winter even though some old leaves are retained. More readily available moisture and slightly higher soil temperature in October may contribute to the higher activity compared to April. These findings are consistent with those from studies on an age series of *A. nepalensis* plantations in the same forest division (Sharma & Ambasht 1984). The high nitrogenase activity in July correlates with high temperature, adequate soil moisture, and high growth rate. The optimum temperature for acetylene reduction is between 20 and 25°C in most actinorhizal plants —*A. glutinosa* (Akkermans 1971, Wheeler 1971), *A. nepalensis* (Sharma & Ambasht 1984), *A. viridis* (Benecke 1970) and *Purshia tridentata* (Dalton & Zobel 1977). Analysis of variance showed significant ($P<0.005$) variation in rate of acetylene reduction between seasons (table 1). The variation with the altitude of the three selected sites was also apparent in all seasons. Activity was remarkably high at 1830 m altitude in July, being eight times higher than it was in December (table 1).

Table 1. *Seasonal variation in nitrogenase activity (acetylene reduction) of* ***A. nepalensis*** *root nodules at three different elevations of landslide-affected sites (after Sharma 1988)*

Elevation	µmol C_2H_4/g nodule dry weight/hour			
(m)	July 1982	Oct. 1982	Dec. 1982	April 1983
1220	7.65±1.10	6.24±0.63	1.14±0.16	4.16±0.65
1830	18.43±2.12	11.72±1.43	2.25±0.18	6.32±0.84
2450	5.38±0.88	5.12±0.76	0.78±0.11	2.42±0.38

ANOVA: Elevation $F_{2,88} = 866$, $P<0.005$; Season $F_{3,88} = 944$, $P<0.005$; Elevation × Season interaction $F_{6,88} = 149$, $P<0.005$. The difference between a specific pair of means between altitude is significant at 5% level. Values are means±SE; $n = 9$.

A. nepalensis at the 1830 m elevation site in the rainy season (July) was most active in terms of nitrogenase activity and thus Sharma (1988) selected this site for a study of diurnal variation. He conducted the experiment between 05.00 and 20.00 hours in July, 1983. A marked diurnal variation in the rate of acetylene reduction was recorded (figure 2). There was no activity during predawn hours, activity being first recorded shortly after sunrise. It increased sharply to reach a midday maximum at 13.00-14.00 hours, the maximum being possibly due to high irradiance and high temperature at this time. Activity was fairly high in the afternoon and declined sharply in the evening. The nitrogenase activity in young plants of *A. glutinosa* and *Myrica gale* growing in a glasshouse under natural illumination, but at nearly constant temperature, was also maximal at about midday (Wheeler 1969). The diurnal fluctuation in 1-year-old *A. nepalensis* seedlings (Sharma 1988) was greater than in young plants of *A. glutinosa* (Wheeler 1969) probably because in *A. nepalensis* study both irradiance and temperature were dynamic. High irradiance leads to rapid transport of photosynthate to the nodules and hence high nitrogenase activity, this falls when carbohydrate levels in the nodules are depleted in darkness (Wheeler 1971).

The ecological amplitude of *A. nepalensis* is narrow (1000-2500 m) altitudinally but fairly wide in relation to environmental conditions as there is a large change in environmental conditions with increasing altitude. Nitrogenase activity is high

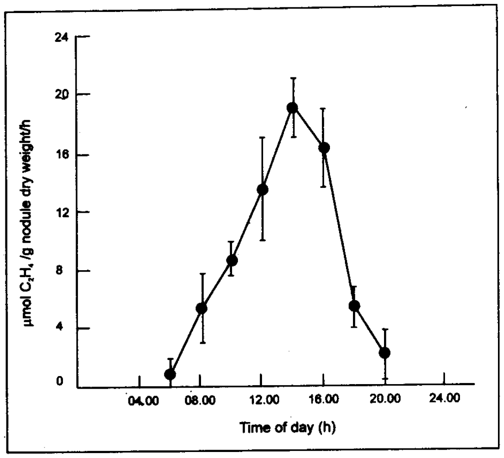

Figure 2. Diurnal variation in nitrogenase activity of naturally regenerated *A. nepalensis* seedling root nodules at the 1830 m elevation landslide-affected site in July 1983. Values are means ± SE; $n = 5$ (*after Sharma 1988*)

between 1500 and 2000 m altitude and outside this range *A. nepalensis* does not perform well.

Sharma and Ambasht (1984) made a detailed study on nitrogenase activity which ranged between 3 and 25 µmol C_2H_4/g nodule dry weight/hr in an age series of *A. nepalensis* plantation stands (7-, 17-, 30-, 46- and 56-year-old). They reported that the seasonal variation in nitrogenase activity was quite distinct with the highest activity in growing season and lowest in winter, and the analysis of variance showed both season and nodule age to be highly significant at all the plantation ages. There was significant interaction between age-class of nodules and age of plantations (Sharma & Ambasht 1984), but nodule biomass in a hectare area was much greater in the younger plantations (Sharma & Ambasht 1986). Nitrogenase activity was highest in the young age-class, fairly high in the medium and very low in the old nodules with similar trend of seasonal fluctuations in all the stands of an age series of plantations (Sharma & Ambasht 1984). Therefore, the difference in the amounts of active root nodule biomass and age of the nodules in the stand actually caused the difference in total nitrogen fixation in a stand. Nodule nitrogen content when treated as independent variable against nitrogenase activity as dependent variable gave a highly significant ($P<0.001$) negative correlation in all the months (Sharma & Ambasht 1984), consistent with Skeffington's hypothesis, which predicts higher nodule activity coupled with lower nodule nitrogen.

Sharma (1995) estimated nitrogenase activity in *A. nepalensis* (shade tree) in a large cardamom-based agroforestry system in Sikkim. She reported an activity rate of 15 µmol C_2H_4/g nodule dry weight/hr in the growing season. These *A. nepalensis* not only serve as shade trees but fix atmospheric nitrogen and help in biological maintenance of soil fertility in such cash-crop based agroforestry systems.

Pradhan (1993) estimated *in vitro* nitrogenase activity in *Frankia* isolates (from *A. nepalensis* host) grown in Defined Proportionate Minimal Medium (DPM) supplemented either with sodium propionate (carbon source) or ammonium chloride (nitrogen source). The activity was recorded with both the supplements showing the higher activity right from the beginning in propionate while in ammonium chloride it increased with the lapse in time. In propionate-supplemented medium the activity in different *Frankia* strains ranged from 17 to 28 nmol C_2H_4/5 ml suspension/hr, while in ammonium chloride the value ranged from 2 to 21 nmol C_2H_4/5 ml suspension/hr.

Accretion

Nitrogen accretion through biological fixation has been made directly by estimating acetylene reduction and then using $C_2H_2 : N_2$ conversion factor of 2.4 : 1 for *A. nepalensis* by Sharma and Ambasht (1988). The above ratio was based on reports for *Alnus*, the only actinorhizal plant for which this factor has been calculated (Hardy et al. 1973). The theoretical ratio from electron requirement is three, and eventually the ratio 3 does not exactly stand true in all cases and varies usually between 2.4 to 3.0 depending upon species, distribution, environmental constraints etc. Sharma and Ambasht (1988) performed nitrogen accretion studies in an age series of *A. nepalensis* plantation stands (7-, 17-, 30-, 46- and 56-year-old). Seasonal nitrogen accretion in all these plantation stands showed two distinct phases - high accretion in the growth period between June and November (95-98% of total annual accretion) and very low in the severe winter with dormant growth period between December and April (2-5%). Highest accretion was observed in the months of September, October and November in all the stands excepting the 7-year-old stand (table 2). The 7-year stand had the highest accretion between the months of June and August. The nitrogen fixation rate was high in the period between June and August but the total accretion was less in this period in four of the older stands (17-, 30-, 46- and 56-years) because the active nodule biomass was much higher in the same plantation stands at the late growing season i.e. October-November (Sharma & Ambasht 1986). Annual accretion of nitrogen was highest (117 kg/ha/year) in the 7-year stand and lowest (29 kg/ha/year) in the 56-year stand (table 2). Sharma (1995) estimated 65 kg/ha/year nitrogen accretion by *A. nepalensis* in a large cardamom based agroforestry system. In this stand *Alnus* tree age was 7-8 years at the time of nitrogen accretion estimation.

Average annual accretion of nitrogen in alder ecosystems based on acetylene reduction assay was highest (130 kg/ha/year) in *A. rubra* as reported by Binkley (1981). The lowest accretion value of 20 kg/ha/year was recorded in a 15- to 20-year old *A. sinuata* and *A. crispa* mixed stand (Binkley 1981). Annual nitrogen accretion (117 kg/ha) in the 7-year old *A. nepalensis* plantation is reasonably high. The

Table 2. *Seasonal accretion of nitrogen (kg/ha) in the age series of* A. nepalensis *plantations based on acetylene reduction (after Sharma and Ambasht 1988)*

	Plantation stands (years)				
Months	7	17	30	46	56
June-August 1981	69.23	25.04	21.24	15.63	13.60
Sept.-Nov. 1981	43.34	28.21	21.98	19.88	14.78
Dec. 1981-Feb. 1982	3.13	2.05	1.21	0.68	0.39
March-May 1982	1.59	0.83	0.72	0.45	0.28
Total annual accretion	117.29	56.13	45.15	36.64	29.05

30-year-old *A. incana* (Johnsrud 1978) and *A. nepalensis* stands had 43 and 45 kg/ha/year nitrogen accretion, respectively, which is very similar although these stands are from two different geographical regions viz., Europe and the Himalaya. Nitrogen accretion of 58 kg/ha/year in a 5- to 20-year-old *A. glutinosa* stand (Akkermans & Van Dijk 1976), is comparable to 56 kg/ha/year of 17-year *A. nepalensis* stand. The nitrogen build-up strategy and N_2-fixation in alders are counterbalanced to a considerable extent, irrespective of their distribution, species to species difference, nodule age, plantation age and microclimate regulation.

Annual total nitrogen uptake (from soil and N_2-fixation) in the 7-year stand was reported to be 1.3 times that of the 56-year *A. nepalensis* stand (Sharma & Ambasht 1988). Nitrogen accretion through biological fixation reduced sharply with the stand age. The contribution of biological N_2-fixation in total nitrogen uptake were 33%, 19%, 15%, 13% and 11% in 7-, 17-, 30-, 46- and 56-year-old plantations, respectively, and decrease in nitrogen demand was accompanied with decrease in N_2-fixation. Although total nitrogen uptake remained the same in 17-, 30- and 46-year-old plantations, the nitrogen accretion through fixation decreased with plantation age; 56, 45 and 37 kg/ha, respectively.

Energetics

Energy cost in N_2-fixation and nodulation of an age series of *A. nepalensis* plantations were estimated by Sharma and Ambasht (1988). Energy utilized in N_2-fixation and net input in nodulation were 4.01 and 1.97 times higher, respectively, in the 7-year stand than those of 56-year stand because of greater nodule biomass and higher N_2-fixation in younger stands. Net energy input in nodulation for unit N_2-fixation in 56-year stand (15×10^4 kJ/kg N_2-fixation) was much higher than 7-year stand (7×10^4 kJ/kg N_2-fixation). Energy cost per kg N_2-fixation was 9.69×10^4 kJ in 7-year stand and 17.14×10^4 kJ in 56-year stand, and N_2-fixation efficiency decreased to nearly half from 7-year stand to 56-year stand. Like N_2-fixation efficiency, net energy allocation in nodules was also reduced to half. Decrease in nitrogen demand coupled with decrease in accretion through N_2-fixation and uptake remaining nearly the same with stand development is compensated for by low N_2-fixation efficiency and low net energy allocation in nodules in older stands. Thus, the *A. nepalensis* stands supplement substantially their nitrogen requirement through the high energy consumptive process of nodule formation and biological N_2-fixation but as nitrogen demand decreases and soil pool gets enriched with stand age (Sharma et al. 1985), the process slows down both through reduction in nodule biomass production (Sharma & Ambasht 1986) and efficiency.

Biomass, Net Primary Productivity and Energetics

Seedlings

Naturally regenerated *A. nepalensis* seedlings in landslide-affected sites in ten different elevations (range 1000-2500m) showed very high density at 1500-1800m and moderate upto 1200m downwards and 2100m upward elevations. These seedlings were about 1-year-old and shoot height, seedling dry weight, root nodule dry weight and ratio of root nodule dry weight : seedlings density were higher in the middle zone elevation. Natural regeneration of 8-9 seedlings/m^2, shoot height 56-71 cm, seedling dry weight 561-684 g/m^2 and root nodule dry weight 5.38-6.15 g/m^2 were highest values reported in the middle zone elevation of 2-year old landslide affected sites (Sharma 1988).

A. nepalensis seedlings raised in nursery were subjected to growth estimations at 90, 180, 360 and 540 days age. Shoot height, leaf area, root nodule fresh weight, and plant component and total dry weights increased with seedling age (Sharma 1995). Belowground : aboveground dry matter ratio is an important morphological character and it remained very low up to 180 days and then increased thereafter to be more than 0.3. This indicates that *A. nepalensis* showed weaker proportion of roots in the early stages of seedling growth and then slowly developed with age. Leaf litterfall in *A. nepalensis* seedling was not recorded in spite of measurements also made during the peak litterfall months of these species. This is a very interesting physiological behaviour that enables seedling to grow continuously by retaining the assimilating structure. This shows an energy conserving strategy by *A. nepalensis* at early stages of development. High values of leaf area ratio indicate the plant to be highly efficient and it was higher in *A. nepalensis* than another symbiotic N_2-fixer *Albizia stipulata* (legume) at 180 days seedling stage and continued to remain higher. Photosynthesis in green parts of the shoot other than the foliage is usually small and the leaf is regarded as the sole assimilatory organ. Net assimilation rate quantifies the increase in dry matter with reference to the assimilating area (foliage) in a given time interval. Net assimilation rate when compared in *A. nepalensis* and *Albizia stipulata* between 90-360 days of seedling age clearly showed higher values for *A. nepalensis* indicating better growth performance (Sharma & Purohit 1996).

Plantations

Average annual litterfall ranged from 3.2 Mg/ha in the 7-year stand to 5.8 Mg/ha in the 46-year stand (table 3). Temporal distribution of litterfall and decomposition in an age series (7-, 17-, 30-, 46- and 56-years-old) of plantations have been described in greater details by Sharma and Ambasht (1987). The above litterfall values in the Himalaya are within the range reported for *Alnus* species in North America (Zavitkovski & Newton 1971). Forest-floor litter weight increased with stand age from 14 mg/ha in the 7-year stand to 30 mg/ha in the 56-year stand (table 3). Accumulated litter on the forest floor included branches, twigs, bark, catkins and leaves. The equilibrium of litter accumulation could not be firmly established with this data in *A. nepalensis* stands. Bormann and DeBell (1981) reported a forest-floor litter value as high as 39 Mg/ha in a 40-year *A. rubra* stand, and indicated the possibility of reaching equilibrium at about 25 years of age. However, according to Zavitkovski and Newton (1971) equilibrium was reached in a 6-year-old *A. rubra* stand and maintained at about 19 mg/ha litter for several decades.

Table 3. *Litterfall, forest-floor litter and root nodule biomass in an age series of **A. nepalensis** plantations and cardamom agroforestry. Values are means and standard error of each estimate was less than 15%* (data after Sharma 1995, Sharma and Ambasht 1991, Sharma *et al.* 1994)

Stands	Litterfall (kg/ha/year)	Forest-floor litter weight* (kg/ha)	Active root nodule biomass (kg/ha)
Plantation age (years)			
7	3200	14100	307
17	5200	19110	215
30	5662	19000	190
46	5796	24200	175
56	5450	30500	150
Agroforestry systems#			
Alnus-cardamom	7270	6881	201
Forest-cardamom	4574	5280	-

*Includes branches, twigs, bark, catkins and leaves.
#Includes cardamom-crop residue in both litterfall and floor-litter mass.

The total biomass in an age series of *A. nepalensis* plantations increased from 106 Mg/ha in the 7-year stand to 606 Mg/ha in the 56-year stand (table 4). Whittaker and Likens (1975) have given 600 Mg/ha total biomass as the upper limit in temperate deciduous forests. The managed, mature plantation (56-year) showed just about the upper limit of biomass range, and this could be as a result of better growth conditions in temperate zones in mountains of the tropical region. This high biomass accumulation was probably due to: (a) a long growing season with negligible water deficit, (b) freshly weathered soil with moderately high base saturation, and (c) cool nights and low respiration loss during the growing and dormant seasons. The standing biomass of trees and stand density showed a negative relationship, while standing biomass and stand basal area showed a strong positive relationship (Sharma & Ambasht 1991). Lower density in mature *A. nepalensis* plantations resulted from selective thinning at an early age followed by self-thinning, whereas higher basal area in mature plantations was a function of tree age and less dense spacing of trees.

The total net primary production rates of an age series of *A. nepalensis* plantations ranged from 13-25 mg/ha/year, and it decreased with age (table 4), closely matching rates of *A. rubra* found by Zavitkovski and Stevens (1972). Immature stands often have a net primary production rate more than

Table 4. *Biomass (Mg/ha) and net primary productivity (Mg/ha/year) in an age series of A.* ***nepalensis*** *plantations. Values in parentheses are per cent contribution to the total net primary productivity (after Sharma & Ambasht 1991)*

Parameter	Plantation age (years)				
	7	17	30	46	56
Biomass	106	238	350	474	606
Productivity					
Twig & leaf	4.63(18)	5.20(26)	5.66(29)	5.80(35)	5.45(41)
Catkin	0.86 (3)	1.25 (6)	1.51 (8)	1.73(10)	1.90(14)
Branch	3.93(16)	2.62(13)	2.08(11)	1.53 (9)	0.92 (7)
Bole	11.18(45)	8.39(42)	7.01(36)	5.38(32)	3.37(26)
Understorey vegetation	0.92 (4)	0.75 (4)	1.69 (9)	1.33 (8)	1.10 (8)
ANP	21.52(86)	18.21(91)	17.95(93)	15.77(94)	12.74(96)
BNP	3.56(14)	1.88 (9)	1.34 (7)	0.92 (6)	0.50 (4)
TNP	25.08	20.09	19.29	16.69	13.24

ANP = aboveground primary productiveness; *TNP* = total net primary productivity; *BNP* = accumulation of major root biomass (fine root biomass was not estimated)

twice as great as mature stands. This is true in *A. nepalensis* plantations, which showed that the net production rate in the 56-year stand was about half of that in the 7-year stand. Except for the most immature *A. nepalensis* plantation (7-year), the productivity of all other plantations was within the above range and towards the upper limit (table 4). The Miami model prediction of productivity of this warm temperate Himalayan zone was 23 and 19 mg/ha/year using annual precipitation and mean temperature, respectively. These predicted values were within the estimated range of the *A. nepalensis* plantations.

The percentage distribution of net primary production in different components of all the *A. nepalensis* plantations ranged from 18 to 41% in twig & leaf, 3-14% in catkin, 7-16% in branch, 26-45% in bole, 4-9% in understorey vegetation, and 4-14% in belowground parts (table 4). Net primary production in the *A. nepalensis* plantations is high for twig & leaf and bole, and low for branches. The biomass accumulation ratio (biomass/net production) is used in categorizing the production conditions of forest communities (Whittaker 1966). It expresses the amount of biomass accumulated per unit of net production. The biomass accumulation ratios of the intermediate and mature *A. nepalensis* plantations ranged between 18.1 and 45.6. This is close to the 20-50 range for the forests of intermediate and mature age reported by Whittaker (1966). However, the ratio was very low in immature 7-year (4.2) and 17-year (11.8) plantations. Smith (1977) has also reported a low average ratio of 2.86 in immature 8-10 year old *A. rubra* stands. The higher ratio in mature *A. nepalensis* plantations (46- and 56-year) indicates that for a given amount of net primary production, they support a greater total biomass.

The net primary production per unit weight of leaf is the production efficiency. The production efficiency in the *A. nepalensis* plantations ranged between 2.4 and 5.3 Mg/Mg leaf/year. The efficiency was high in immature plantations (7 and 17 year). It varied between 2.4 and 3.3 Mg/Mg leaf/year in intermediate and mature plantations. These values are comparable to 3.3 Mg/Mg leaf/year for a variety of deciduous species in the south-eastern USA (Hedman & Binkley 1988). The production efficiency of *A. nepalensis* showed a highly significant negative logarithmic relationship with plantation age. The efficiency curve tended to flatten with plantation age and the natural logarithm of the plantation age against normal efficiency values presented the best fit (Sharma & Ambasht 1991).

Energy distribution and flow rates in the components of 7-year and 56-year of *A. nepalensis* plantations were estimated by Sharma and Ambasht (1991). They reported net annual energy fixation to be highest (421 x10^6 kJ/ha/year) in the 7-year *A. nepalensis* stand and it declined sharply with the plantation age to be lowest (215 x10^6 kJ/ha/year) in the 56-year stand. Of the total energy build up from the 7-year to 56-year stand, 97% was in the vegetation pool and just 3% in the forest floor litter pool. The heat release value of 121 x10^6 kJ/ha/year in the 56-year stand was 1.46 times higher than that of the 7-year stand (Sharma & Ambasht 1991). Energy conversion efficiency at the autotrophic level is the ratio of energy captured by vegetation to the usable solar radiation reaching an area over a period of time expressed as percentage. It was highest (3.49%) in immature (7-year) stand of *A. nepalensis* and decreased with plantation age. The range of 1.8-4.2% energy conversion efficiency in *A. rubra* stands of Canada (Smith 1977) is closely comparable to the 1.8-3.5% in the *A. nepalensis* stands (Sharma & Ambasht 1991). The relationship between energy conversion efficiency and plantation age was inverse, and the best-fit of the curve was obtained by using the natural logarithmic form of plantation age (Sharma & Ambasht 1991)

The N_2-fixation efficiency decreased by half from the 7-year stand to the 56-year stand of *A. nepalensis*. The energy utilized per unit N_2-fixed increased rapidly at first, then more slowly as the stand aged. The stand continued to use more net energy per unit N_2-fixed even in the 56-year stand (Sharma & Ambasht 1988).

The production efficiency and energy conversion efficiency of the age series of *A. nepalensis* plantations showed an exponential relationship (figure 3). Both production and energy conversion efficiencies were high in the immature 7-year stand and decreased with stand age to the lowest values in the 56-year stand. The relationships of energy efficiency in N_2-fixation with energy conversion efficiency and production efficiency of the plantations also showed exponential functions (figures 4 & 5). These exponential equations predict that stand energy efficiency in N_2-fixation should level off with the energy conversion and production efficiencies. In fact, each of the efficiencies is dependent on plantation age (Sharma & Ambasht 1991). The inverse relationships of efficiencies against plantation age and exponential relationships between efficiencies suggest that the immature plantations function as the most productive system, while the intermediate and mature plantations are relatively less and the least productive, respectively.

Agroforestry Systems

Biomass, net primary production and crop yield were studied in cardamom-based agroforestry systems with and without N_2-fixing *A. nepalensis* tree associates in the Sikkim Himalaya (Sharma et al. 1994). A cardamom-based agroforestry with *A. nepalensis* tree associate was designated as *Alnus*-cardamom and mixed tree species associate as forest-cardamom stand. Density and basal area of trees were 517 trees/ha and 5.6 m^2/ha, and 850 trees/ha and 6.3 m^2/ha, respectively in the *Alnus*-cardamom and forest-cardamom agroforestry stands. Cardamom were planted in equal density in both the stands and after nearly 6 years the tiller number (96400/ha) and basal area (22.5 m^2/ha) in the *Alnus*-cardamom stand achieved 2.26 times higher than the forest-cardamom stand (Sharma et al. 1994).

Annual litter production was much higher in *Alnus*-cardamom than in forest-cardamom stand (table 3). The agroforestry floor litter weight was

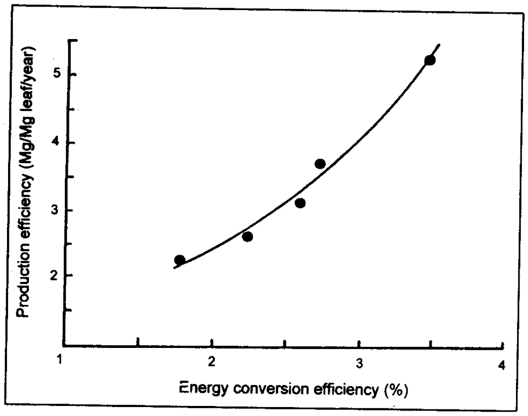

Figure 3. Relationship ($y = 0.870\ e^{0.513}x$; $F_{1,3} = 183$, $P < 0.005$; $r^2 = 0.984$) between production efficiency and energy conversion efficiency in age series of *A. nepalensis* plantations (*after Sharma and Ambasht 1991*)

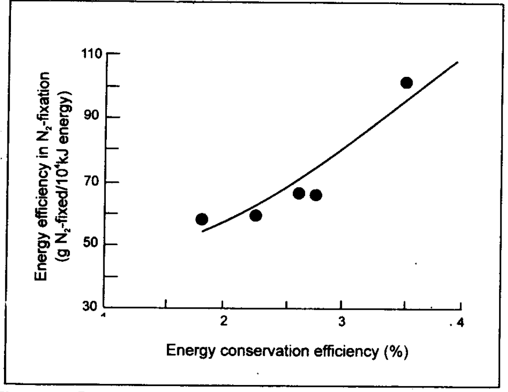

Figure 4. Relationship ($y = 29.343\ e^{0.340x}$; $F_{1,3} = 26$, $P < 0.025$; $r^2 = 0.897$) between energy efficiency in N_2-fixation and energy conversion efficiency in age series of *A. nepalensis* plantations (*after Sharma and Ambasht 1991*)

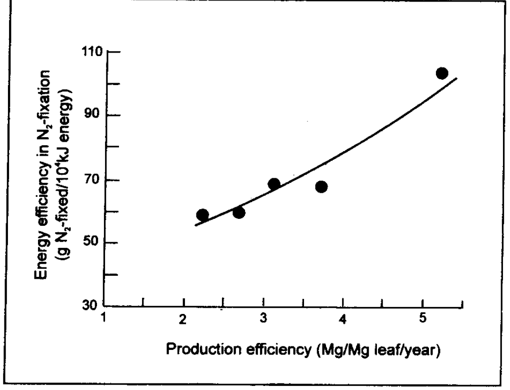

Figure 5. Relationship ($y = 36.99\ e^{0.189}x$; $F_{1,3} = 46$, $P < 0.01$; $r^2 = 0.938$) between energy efficiency in N_2-fixation and production efficiency in age series of *A. nepalensis* plantations (*after Sharma and Ambasht 1991*)

also higher in *Alnus*-cardamom stand (table 3). Contribution of *Alnus* litter was 39% and cardamom 61% to the stand total annual litter flow to floor in the *Alnus*-cardamom system (Sharma et al. 1997a). The 57% of annual litter production is decomposed while 43% accumulated on the floor. In contrary, mixed tree species litter contributed 64% and just 36% by cardamom to the stand total annual litter production in the other stand. The rate of accumulation of litter on the floor was 49% in the forest-cardamom stand.

The litter production and its disappearance rates were respectively 1.59 and 1.79 times higher in *Alnus*-cardamom than the forest-cardamom stand (Sharma et al. 1994, 1997a). Binkley et al. (1992) also found much greater litterfall in mixed stands with N_2-fixing associate (*A. rubra*) than in stands containing only non-N_2-fixing trees. The litter from N_2-fixing species generally decomposes faster than litter of non-N_2-fixing species and the addition of N_2-fixer litter may accelerate the decomposition of other litter types. This has been shown by Taylor et al. (1989) who found that leaf litter of *Alnus crispa* in litter bags would require about 11.5 years to reach 95% decomposition, compared with 14.5 years for leaf litter from *Populus trimuloides*. They also reported *Populus* litter mixed with *Alnus* litter in the same bag decomposed as rapidly as the *Alnus* litter.

Total biomass was 28% higher in the *Alnus*-cardamom stand, and tree biomass slightly higher for *Alnus* despite its lower stand density (table 5). The contribution of cardamom biomass to stand total biomass was 34% in *Alnus*-cardamom and 18% in the forest-cardamom stand. The stand total biomass, and tiller number, basal area and biomass of cardamom crop was much higher under the influence of *Alnus*. Binkley et al. (1992) have also reported that at a low-fertility site in USA, biomass of the *Alnus*-conifer stand exceeded by 69% to that of the pure conifer stand.

Annual net primary productivity of *Alnus* trees was slightly higher than mixed tree species in spite of its lower stand density, but the cardamom productivity was more than double under the influence of *Alnus* (table 5). The agronomic yield of cardamom also increased by 2.2 times under the canopy of *Alnus*. Similarly, annual net primary productivity at the age 28 in the mixed stand of Douglas-fir and *Alnus* was 2.5 times higher compared to pure Douglas-fir stand (Binkley 1992).

Table 5. *Biomass and productivity of components in cardamom based agroforestry systems of the Mamlay watershed in Sikkim (after Sharma* **et al 1994)**

Agroforestry systems	Components	Biomass (kg/ha)	Productivity (kg/ha/year)
Alnus-cardamom	Tree (*Alnus*)		
	Bole	9475	1515
	Branch	3199	484
	Leaf & twig	1674	2851*
	Root	4414	592
	Tree total	18762	5442
	Cardamom		
	Leaf	1493	1004
	Pseudo-stem	5082	3415
	Root	2631	528
	Capsule	454	454
	Cardamom total	9660	5401
	Stand total	28422	10843
Forest-cardamom	Tree (Mixed subsp.)		
	Bole	10712	1576
	Branch	2543	244
	Leaf & twig	1212	2905*
	Root	3874	489
	Tree total	18341	5214
	Cardamom		
	Leaf	661	453
	Pseudo-stem	1925	1216
	Root	1105	413
	Capsule	205	205
	Cardamom total	3896	2287
	Stand total	22237	7501

*Tree leaf and twig production estimated on standing trees was corrected using litterfall data.

Alnus-cardamom intercrop grown in the middle hills of eastern Nepal was studied as a model highland agroforestry system (Zomer & Menke 1993). Sixty-six sites were sampled in four districts of the Kosi and Mechi Zones. Annual *Alnus* biomass production was estimated at 14 Mg/ha/year for a typical plantation cycle, with an average 11 Mg/ha/year annual increase in standing biomass after tree thinning. Tree component standing biomass accumulation was estimated by site index classes, and used to derive a predictive equation for average total standing biomass (273 Mg/ha) at a plantation reference age of 25 years. Cardamom crop production reduces substantially after its 20 years age (Singh et al. 1989, Zomer & Menke 1993).

Nutrient Cycling

Nutrient elements play an important role in physiological activities of plants. The primary production of an ecosystem is influenced by the availability of nutrients, and this in turn depends on distribution and rates of cycling. The nutrients within any part of an ecosystem usually depends upon a functional balance within the system. Nutrient cycling is a function of many factors such as microclimate, species composition, stand age, biotic stress on the system etc. Nutrient cycling rates is an important indicator of plant performance and it can be utilized in evaluating sustainability at systems level. The nutrient cycling studies in *A. nepalensis* have been made in an age series of plantations and in large cardamom based agroforestry in the Sikkim Himalaya (Sharma 1985, 1993, Sharma et al. 1994), and its role in shifting agriculture sustenance in north-eastern India have been emphasized (Ramakrishnan 1992).

Role in Shifting Agriculture

Shifting agriculture or jhum is the major economic activity in the north-eastern India. This highly organized agroecosystem was based on empirical knowledge accumulated through centuries as was in harmony with the environment as long as the jhum cycle was long enough to allow the forest and the soil fertility lost during the cropping phase to recover. Increased human population pressure and decline in land area resulting from extensive deforestation for timber has caused shortening of jhum cycle (Ramakrishnan 1992) and the practice of shifting cultivation is turning less productive and unsustainable. Allocated areas of operation for a shifting cultivator has been decreasing substantially in recent years. *A. nepalensis* has been an important fallow species in the jhum system. With the rapid transfer of nutrients from the soil to the vegetation during the early phase of the fallow period, rapid depletion of nutrients occurs in the soil even though losses by leaching and runoff are greatly reduced. It is only after 10 years of fallow regrowth that overall soil fertility improves through a net transfer of nutrients back to the soil. The 10-year cycle is therefore considered to be the shortest one possible for the regeneration of the system, unless the fallow has an accelerated regrowth rate. This can be achieved by introducing species such as *A. nepalensis* which improve soil fertility through a rapid recycling of nutrients with a fast turnover of leaves and through high rates of biological N_2-fixation (Ramakrishnan 1992). During one cropping phase the jhum system may lose about 600 kg/ha, of which no more than half is recovered during the subsequent 5-year fallow period. A shortened fallow based on the introduction of a variety of legumes and non-leguminous symbiotic N_2-fixing trees (such as *Albizia* spp. and *Alnus nepalensis*) during the fallow phase is able to restore soil fertility. Therefore, *A. nepalensis* has a major nutrient balancing role in a shortened fallow. *A. nepalensis* also coppices readily as observed in Nagaland jhum systems and may be harvested after the same-5-year interval, thus providing the farmer with marketable poles and restore the soil fertility at the same time (Ramakrishnan 1992, 1994).

Plantations

Nutrient cycling study in an age series of *A. nepalensis* plantations have been made by Sharma (1993). The nitrogen concentration in different components of *A. nepalensis* trees was high which is attributed to high rate of N_2-fixation. Foliar nitrogen concentration of *A. nepalensis* (3.5%) is comparable to 3.1% reported in *A. rubra* stand (Binkley 1983). Phosphorus concentration ranged from 0.08 to 0.10% in the twig and leaf component of *A. nepalensis* (Sharma 1993), and was lower than 0.14-0.23% reported in *A. rubra* by Binkley (1983). Potassium in *A. nepalensis* was within the reported range, whereas calcium values were lower than the reported values for temperate species (Woodwell et al. 1975, Sharma 1993).

The level of nutrients in a given soil is the net outcome of input and output from the system. Soil *p*H ranged from 4.1 to 5.2 and the nutrients were higher in the upper than lower soil horizons in an age series of *A. nepalensis* plantations (Sharma et al. 1985). Mean total nitrogen concentration estimated up to a depth of 30 cm soil was high (ranged between 0.454% and 0.723% among plantation stands) and it increased with plantation stand age. Concentrations of available phosphorus, and exchangeable potassium and calcium in soil of *A. nepalensis* plantations were relatively low (Sharma et al. 1985). Binkley (1983) also reported an increase in total soil nitrogen and a decrease in extractable cations under fertile *A. rubra* stands. Soil nutrient contents upto a 30cm depth are presented in table 6. Total nitrogen and available phosphorus increased with plantation age. Exchangeable potassium and

Table 6. *Nutrients in standing state (kg/ha) of live-biomass, litterfall contents (kg/ha/year), forest-floor litterlayer contents (kg/ha) and soil contents (kg/ha) upto 30 cm depth in an age series of **A. nepalensis** plantations (after Sharma 1993)*

Plantation age/yr	Components	Nutrients			
		N	P	K	Ca
7	Standing state	1371	12	379	180
	Litterfall	195	6	38	11
	Forest-floor	453	12	68	53
	Soil*	12990	113	113	124
17	Standing state	2106	16	658	349
	Litterfall	212	7	39	11
	Forest-floor	612	17	92	72
	Soil*	15115	117	180	197
30	Standing state	2632	22	871	482
	Litterfall	237	8	46	13
	Forest-floor	608	17	92	72
	Soil*	16082	181	151	92
46	Standing state	3109	24	1072	619
	Litterfall	252	8	46	18
	Forest-floor	773	21	116	91
	Soil*	18720	212	154	82
56	Standing state	3513	27	1263	757
	Litterfall	248	8	45	12
	Forest-floor	975	27	147	115
	Soil*	18720	199	158	95

*N=total nitrogen, P=available phosphorus, K=exchangeable potassium, and Ca=exchangeable calcium

calcium contents in soil were higher in the 17-year plantation as compared to the 7-year, and the values lowered to remain nearly the same in mature plantations (table 6).

The distribution of nutrients in different components in an age series of *A. nepalensis* plantations depended considerably on component biomass and nutrient concentration. The standing state of nutrients in different components increased with increase in their biomass and the role of nutrient concentration was minimized (Sharma 1993). The standing state of nitrogen was 2.56, phosphorus 2.26, potassium 3.33 and calcium 4.21 times more in the live components of the 56-year plantation, than in the 7-year-old plantation (table 6).

Litter falling to the forest floor is normally regarded as the main route by which nutrients move from the canopy to the soil. Approximately 70% of the annual uptake of macro-elements is returned via litterfall in temperate forests, but this largely depends on tree age. Younger plantations of *A. nepalensis* retained more macro-nutrients than older plantations (tables 6 and 7). The total annual inputs (kg/ha) via tree litterfall in *A. nepalensis* plantations were: 183-232 nitrogen, 4.9-7.0 phosphorus, 33.5-39.5 potassium and 9.2-10.8 calcium (Sharma 1993). Forest floor litter weight of the same plantation stands increased with stand age (table 3). This has caused increasing accumulation of nutrients on the forest-floor with stand age (table 6). Litterfall, decomposition and nutrient release in these age series of *A. nepalensis* plantations have been made by Sharma and Ambasht (1987).

Seasonal and annual nitrogen accretions and nitrogen fixation of these age series stands have been dealt earlier in this article. Nutrient uptake in an age series of *A. nepalensis* plantations is presented in table 7. Rawat and Singh (1988) estimated nutrient uptake in a Himalayan oak forest and reported 230 nitrogen, 13 phosphorus, 259 calcium and 76 kg/ha/year potassium. The nitrogen uptake was higher in *A. nepalensis* plantations than in the oak forest, potassium uptake was similar while phosphorus and calcium uptake were lower. The low phosphorus uptake can be attributed to a negative effect of *Alnus* on the phosphorus economy mostly by increasing soil acidity, which causes a transition of phosphate into less soluble compounds with iron and aluminium (Brozek 1990). Furthermore, a heavy accumulation of organic matter in soils of *A. nepalensis* stands could have shifted phosphorus from a plant available mineral pool to an organically bound pool. The total nutrient uptake and accumulation in *A. nepalensis* stands was in the order N>K>Ca>P (table 7). Cote and Camire (1987) reported higher uptake and more accumulation of potassium than calcium in young trees of *A. glutinosa*, and explained this to be due to the relatively better availability of potassium compared to calcium. They expected that on a longer term basis, calcium should accumulate more than potassium. Similarly in *A. nepalensis* stands, uptake and accumulation of potassium was more than calcium, and remained higher even at the maturity of the stands.

The values of turnover rates and times for different nutrients on the forest floor of *A. nepalensis* are given in table 8. The turnover time of nutrients on the forest floor of northern hardwoods in USA (Gosz et al. 1973) ranged between 2.0 and 15.4 years, and the range of 1.8-9.3 years in *A. nepalensis* stands

Table 7. *Uptake, retention, return and standing state of nutrients in an age series of A. nepalensis plantations (after Sharma 1993)*

Nutrient	Plantation age (years)	Uptake (kg/ha/ year)	Retention (kg/ha/ year)	Return (kg/ha/ year)	Standing state# (kg/ha)
Nitrogen*	7	356	231	125	1834
	17	292	135	157	2723
	30	292	126	166	3244
	46	291	120	171	2386
	56	276	121	155	4491
Phosphorus	7	7.01	3.15	3.86	24.52
	17	7.13	2.41	4.72	33.29
	30	8.82	3.60	5.22	38.31
	46	8.90	3.66	5.24	45.50
	56	8.63	3.41	5.22	53.76
Potassium	7	90.02	56.53	33.49	449
	17	67.40	31.57	35.83	750
	30	67.12	28.71	38.41	963
	46	61.07	21.34	39.73	1189
	56	53.44	14.89	38.55	1410
Calcium	7	38.62	26.58	12.04	233
	17	27.72	13.70	14.02	421
	30	25.77	10.76	15.01	554
	46	22.12	8.20	13.92	710
	56	17.88	3.69	14.19	872

*Includes biological fixation (see table 2).
#Includes nutrient in the forest-floor litterlayer.

Table 8. *Turnover rate (k) and turnover time (t, years) of nutrients on the forest floor in an age series of A. nepalensis plantations (after Sharma 1993)*

Plantation age (years)	Nutrients							
	N		P		K		Ca	
	k	*t*	*k*	*t*	*k*	*t*	*k*	*t*
7	0.43	2.32	0.48	2.07	0.55	1.80	0.19	5.07
17	0.34	2.89	0.38	2.58	0.42	2.36	0.15	6.54
30	0.39	2.56	0.49	2.01	0.50	1.98	0.18	5.54
46	0.32	3.06	0.37	2.65	0.39	2.53	0.13	7.15
56	0.25	3.93	0.30	3.23	0.30	3.27	0.10	9.32

Table 9. *Nutrient use efficiencies of an age series of A. nepalensis plantations (after Sharma 1993)*

Plantations age (years)	Nutrient use efficiency#			
	N	P	K	Ca
7	70	3578	279	649
17	69	2818	298	725
30	66	2187	287	749
46	57	1875	273	755
56	48	1534	248	741

#Calculated as the annual production of biomass (kg) per kg of nutrients taken up.

is lower. The turnover time for nitrogen, phosphorus and potassium was less and that of calcium was greater. Potassium is soluble and is more readily leached from the organic matter, and nitrogen being high in the *Alnus* litter showed faster turnover. Therefore nitrogen and potassium recycled faster than structurally bound calcium found in the form of pectates.

Nutrient use efficiency (kg annual net primary productivity per kg nutrient taken up) may be expected to drop as utilization of that nutrient increases, because availability of some other resource (such as water, energy, or light) limits production (Binkley et al. 1992). The nutrient use efficiencies of the *A. nepalensis* plantations were generally consistent with this hypothesis. Nutrient use efficiencies in these plantations decreased with plantation age for all nutrients except for calcium (table 9). The *A. nepalensis* plantations as a whole used nitrogen and potassium less efficiently compared to *A. rubra*-conifer stands of USA (Binkley et al. 1992). Binkley et al. (1992) also reported that *A. rubra* is much less efficient than conifers in nutrient use efficiency.

Consistently high net primary production in an age series of *A. nepalensis* plantations (table 4) is in conformity with marked retention of nutrients by the vegetation over the annual cycles. Computation of the ratios (nutrient uptake) : (net energy fixed) takes into account both aboveground and belowground production of plantations, and the ratios (nutrient released) : (energy dissipated) are based on litter and root nodule disappearance (table 10). Nitrogen, phosphorus and potassium uptake per unit energy fixed increased with the plantation age. The amount of nutrient released per unit of energy dissipated in all *A. nepalensis* stands is always greater than the amount absorbed per equivalent net energy fixed, indicating nutrient uptake to be a higher energy consuming process than release. Nutrient uptake is expected to be more expensive than release in stands dominated by fast growing species.

Agroforestry systems

Nitrogen and phosphorus concentrations of different tissues of *Alnus* were higher than those of mixed tree species in cardamom based agroforestry studied by Sharma et al. (1994). This is consistent with higher nutrient concentrations of N_2-fixing *Alnus* as compared to conifer in mixed condition (Binkley

1983). Nitrogen and phosphorus concentrations of intact leaf and freshly fallen leaf of *Alnus* and mixed tree species were estimated and given in table 11. Back translocation of nitrogen was 3.9% and phosphorus 22.6% in *Alnus* leaf while it was 17.5% nitrogen and 31.4% phosphorus in mixed tree species. Absolute amounts of nitrogen and phosphorus back translocations were respectively 2.3 and 1.2 times higher in mixed tree species of the forest-cardamom stand than *Alnus* of the *Alnus*-cardamom stand. Lower back translocation of nitrogen and phosphorus in *Alnus* and mixed tree species is because of higher availability and uptake of these elements in the *Alnus*-cardamom stand. The general concept of inverse relationship between availability and conservation stands well. *Alnus* has more availability of these elements than mixed tree species and hence recorded lower back translocation indicating its poor conservation strategy.

Table 10. *Ratios between nutrient uptake and net energy fixation, and nutrient release and energy dissipation in an age series of A. nepalensis plantations (after Sharma 1993)*

Ratio*	Plantation age (yr)	Nutrient N	P	K	Ca
Nutrient uptake: energy fixation	7	0.846	0.017	0.214	0.092
	17	0.887	0.022	0.205	0.084
	30	0.936	0.028	0.215	0.083
	46	1.085	0.033	0.228	0.082
	56	1.284	0.040	0.248	0.083
Nutrient release: energy dissipation	7	1.506	0.047	0.403	0.145
	17	1.481	0.046	0.338	0.132
	30	1.349	0.042	0.312	0.122
	46	1.401	0.043	0.325	0.114
	56	1.281	0.043	0.318	0.117

*Nutrient uptake (kg/ha/year); nutrient release (kg/ha/year); net energy fixation (10^6 kJ/ha/year; and energy dissipation (10^6 kJ/ha/year). Data on net energy fixation and energy dissipation are taken from Sharma and Ambasht (1991).

Table 11. *Nitrogen and phosphorus concentration (mg/g) of intact and freshly fallen leaf, and back translocation (%) of tree species from cardamom based agroforestry systems in the Mamlay watershed. Values are mean* (n = *10)* ± SE *(after Sharma* et al *1994)*

Agroforestry systems	Species	Leaf type/translocation	Nitrogen	Phosphorus
Alnus-cardamom	*Alnus*	Intact leaf	26.0 ± 0.69	1.68 ± 0.16
		Freshly fallen leaf	25.0 ± 1.37	1.30 ± 0.18
		Back translocation	3.85	22.62
Forest-cardamom	Mixed subsp.	Intact leaf	18.3 ± 0.38	1.53 ± 0.12
		Freshly fallen leaf	15.1 ± 0.39	1.05 ± 0.09
		Back translocation	17.49	31.37

Soil total nitrogen level up to 30 cm depth of the forest-cardamom stand was 1.19 times higher than the *Alnus*-cardamom stand (figure 6). The annual retention of nitrogen in plant components and litter was not much different in both the *Alnus*-cardamom (56.1 kg/ha/year) and forest-cardamom (49.6 kg/ha/year) stands. Annual uptake, standing state, return to soil and exit of nitrogen from the systems were, respectively, 1.79, 1.92, 2.86 and 2.27 times higher in *Alnus*-cardamom than the forest-cardamom stand. Soil inorganic phosphorus up to the 30 cm depth was higher in *Alnus*-cardamom than the forest-cardamom (figure 7). Total annual phosphorus uptake, standing state, return to soil and exit from the systems were, respectively, 2.02, 1.80, 2.62 and 2.13 times higher in *Alnus*-cardamom than the forest-cardamom stand. The annual retention of phosphorus in plant components and litter was 6.3 kg/ha/year in the *Alnus*-cardamom stand and 3.8 kg/ha/year in the forest-cardamom stand (figure 7).

The annual uptake and return of nitrogen to the soil in the *Alnus*-cardamom stand were higher than the forest-cardamom stand which is attributed to nitrogen fixation by *Alnus*. The rates of phosphorus uptake and return through litterfall and decomposition were also higher in *Alnus*-cardamom than the forest-cardamom stand which has probably resulted from an increase in the rate of phosphorus supply, attributable to geochemical and biological factors influenced by *Alnus*. Potential geochemical factors could be rhizosphere acidification (Gillespie & Pope 1989) and biological factors could be rooting depth (Malcolm et al. 1985), soil enzyme activity (Ho 1979) and organic chelates (Ae et al. 1990).

The nitrogen and phosphorus cycling in the cardamom-based agroforestry system appeared very malleable (flexible) under the influence of N_2-fixing *Alnus*. Binkley (1992) have also reported generally higher uptake and return of all nutrients and greater magnitude of malleability of nutrient cycles as an influence of N_2-fixing *Alnus* consistent with the findings of the study made by Sharma et al. (1994, 1997b). But there is no understanding on the mechanisms that give rise to this malleability.

Nutrient use efficiency is the ratio of annual net primary productivity and nutrient uptake. The nitrogen use efficiency was 73 and 93, and phosphorus 823 and 1151 in the *Alnus*-cardamom

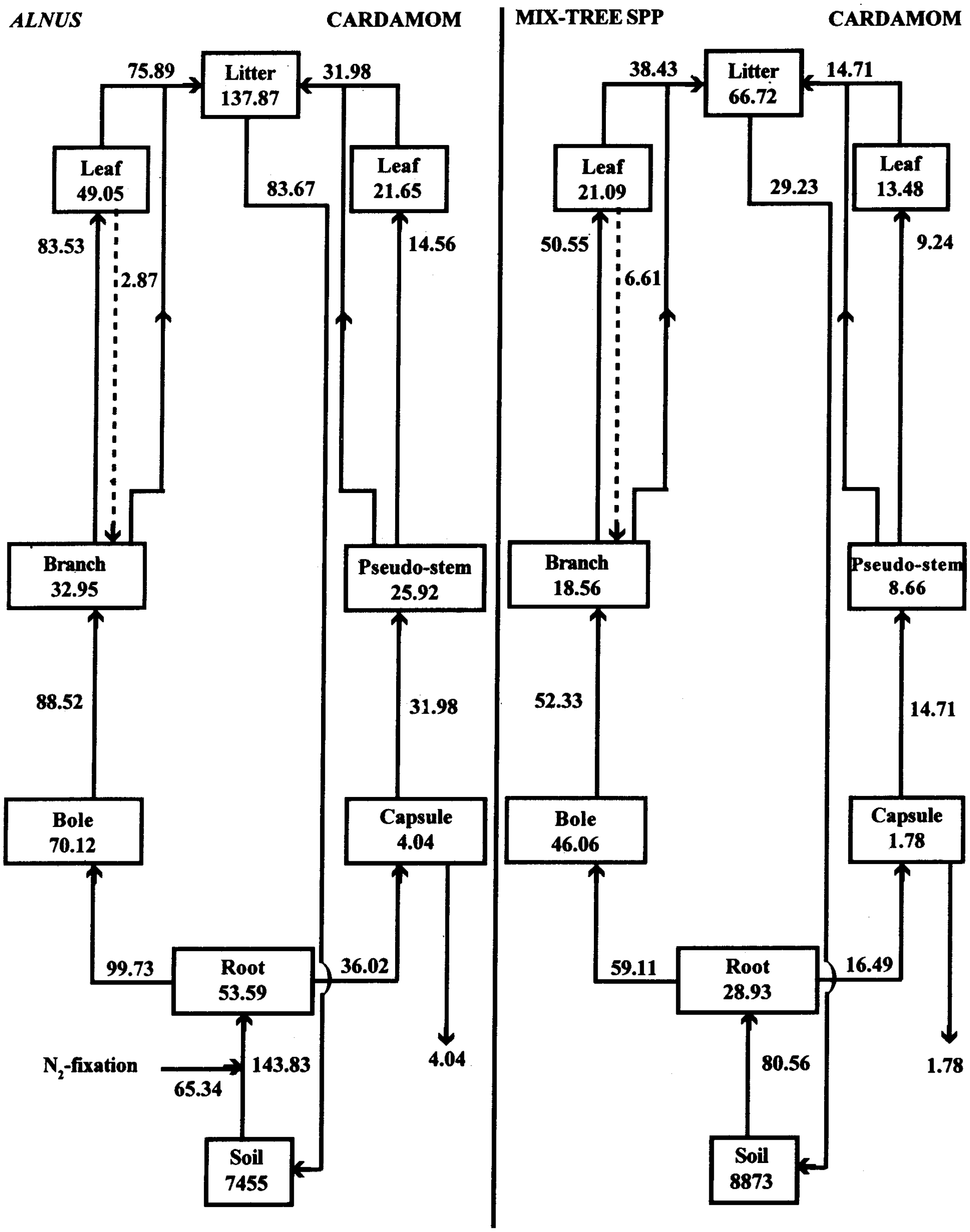

Figure 6. Distribution of nitrogen and flow rates in the components of *Alnus*-cardamom and forest-cardamom agroforestry systems in the Mamlay watershed. Units are kg/ha for compartments and kg/ha/year for flows. Soil total nitrogen is presented for top 30 cm depth. Broken lines indicate back translocation of nitrogen from leaf to branch before abscission *(after Sharma et al. 1994)*

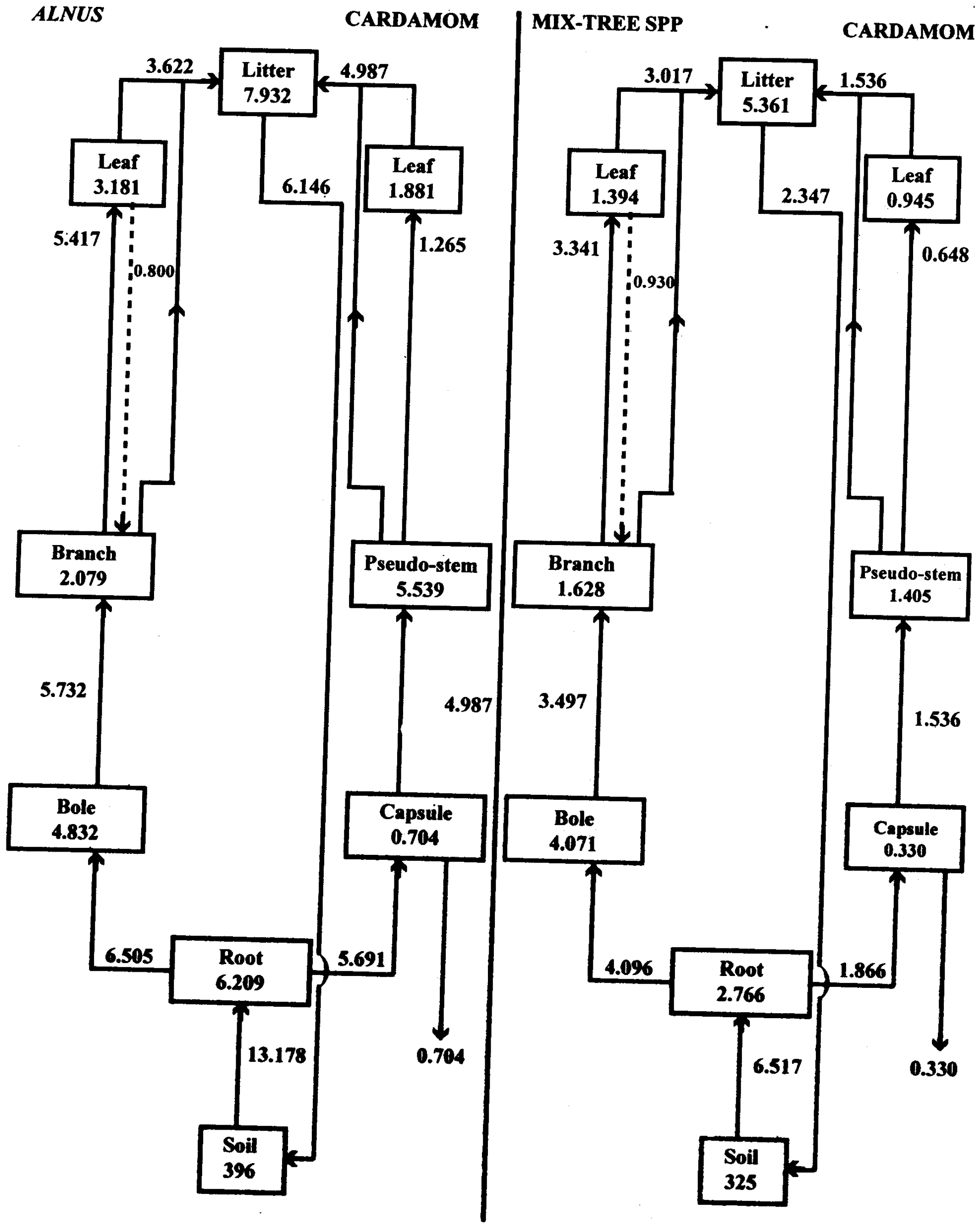

Figure 7. Distribution of phosphorus and flow rates in the components of *Alnus*-cardamom and forest-cardamom agroforestry systems in the Mamlay watershed. Units are kg/ha for compartments and kg/ha/year for flows. Soil inorganic-phosphorus is presented for top 30 cm depth. Broken lines indicate back translocation of phosphorus from leaf to branch before abscission (*after Sharma et al. 1994*)

and forest-cardamom stands, respectively (Sharma et al. 1994). Nutrient use efficiencies in the cardamom based agroforestry systems were generally consistent with the hypothesis that efficiency drops as utilization of that nutrient increases because availability of some other resource limit production. It decreased as an influence of N_2-fixing *Alnus*, a pattern consistent with the expectation that efficiency should decrease with increasing rates of uptake.

The agroforestry system under the influence of *A. nepalensis* was more productive having faster rates of nutrient cycling. The poor nutrient conservation and low nutrient use efficiency of this species and alleability of nutrient cycling under its influence make it an excellent associate promoting higher availability and faster cycling of nutrients.

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