Annals of Botany **89**: 273–282, 2002
doi:10.1093/aob/mcf036, available online at www.aob.oupjournals.org

Performance of an Age Series of *Alnus*–cardamom Plantations in the Sikkim Himalaya: Nutrient Dynamics

G. SHARMA, R. SHARMA, E. SHARMA† and K. K. SINGH*

G. B. Pant Institute of Himalayan Environment and Development, Sikkim Unit, P.O. Tadong, Gangtok, Sikkim-737102, India

Received: 11 May 2001 Returned for revision: 20 July 2001 Accepted: 22 November 2001

Nutrient cycling, nutrient use efficiency and nitrogen fixation in an age series of *Alnus*–cardamom plantations were studied in the eastern Himalaya. The impact of stand age (5, 10, 15, 20, 30 and 40 years) on the nutrient dynamics of mixtures of N_2-fixing (*Alnus nepalensis*) and non-N_2-fixing (large cardamom) plants was assessed. Foliar nutrient concentrations of *Alnus* decreased with advancing age groups of plantations and showed an inverse relationship with stand age. Annual N fixation increased from the 5-year-old stand (52 kg ha^{-1}), peaking in the 15-year-old stand (155 kg ha^{-1}) and then decreased with increasing plantation age. Nitrogen and phosphorus uptake was lowest in the 40-year-old stand, and highest in the 15- and 5-year-old stand, respectively. Nutrient storage in understorey cardamom was very high: up to 31 % N and 59 % P of the stand total in the 15-year-old stand. Nutrient use efficiency was higher (with faster turnover times) in younger stands and decreased (with slower turnover times) in older plantations. Nitrogen retranslocation showed a strong positive relationship with stand age, while that of P was inversely related to stand age. Nutrient standing stock, uptake and return were also highest in the 15-year-old stand. Nitrogen and P cycling in *Alnus*–cardamom plantations was functionally balanced. Nutrient cycling and dynamics indicated that *Alnus*–cardamom plantations performed sustainably up to 15–20 years. The management practice should be altered to incorporate replantation after this age.

Key words: *Alnus nepalensis*, *Amomum subulatum* (large cardamom), nitrogen fixation, nutrient use efficiency, nutrient cycling, phosphorus, plantation age, turnover time.

INTRODUCTION

Nutrient elements play fundamental roles in the physiological activities of plants. The primary production of plantations is influenced by the availability of nutrients, and this in turn depends on distribution and rates of cycling. The concentration of nutrients within any part of an ecosystem usually depends upon a functional balance within the system. Information is scarce on the functional balance of nutrients within ecosystems where mixtures of N_2-fixing and non-N_2-fixing plants are managed.

Nutrient dynamics in relation to plantation age are important, given that the structure and function of plantations do not remain constant as stands mature. This was reported in pure monoculture plantations of alder (Sharma, 1993) in Himalaya and in lodgepole pine (Binkley *et al.*, 1995) in North America. Binkley *et al.* (1992) and DeBell *et al.* (1997) have studied nutrient availability and performance of mixtures of different percentage combinations of N_2-fixing *Albizia* and non-N_2-fixing *Eucalyptus*. However, information on nutrient dynamics for mixtures of N_2-fixing and non-N_2-fixing stands with respect to stand age and maturity is limited. Establishment of plantation mixtures of large cardamom (*Amomum subulatum* Roxb.) and N_2-fixing Himalayan alder (*Alnus nepalensis* D. Don) is a common practice in the eastern Himalaya. These *Alnus*–cardamom plantations provide a good system for understanding the impact of stand age on the performance of mixtures of N_2-fixing and non-N_2-fixing plants.

This paper deals with studies on the concentration, standing state, uptake, return, turnover and cycling of nutrients, nutrient use efficiency and nitrogen fixation in an age series of plantation mixtures of *Alnus* and cardamom in the Sikkim Himalaya.

MATERIALS AND METHODS

Three experimental sites selected for the study are located at Kabi, Thekabong and Sumik in Sikkim of the eastern Himalaya. For details of the location, climate and plantation of these study sites see Sharma *et al.* (2002). Large cardamom is a perennial cash crop cultivated under shade trees, predominantly *Alnus nepalensis*. The selected *Alnus*–cardamom stands at each of the three study sites represent plantations of an age sequence of 5, 10, 15, 20, 30 and 40 years. The stands at each of the sites are closely comparable; the structural and functional differences are attributed to the age of the plantations.

Sample plots 30 × 40 m were established at each of the six age series of plantation stands in all three sites, giving 18

* For correspondence: Fax +91-3592-31090, e-mail singhkk20@hotmail.com

† Present address: Mountain Farming Systems Division, International Centre for Integrated Mountain Development, GPO Box 3226, Kathmandu, Nepal

plots in total. All plant and soil samplings were made from these sample plots. Plant samples of different components (leaf, twig, catkin, branch, bole, root and root nodules of *Alnus*; leaf, pseudo-stem, capsule, rhizome and root of cardamom) were collected in replicates (n = 9; three samples × three sites) from stands in all six age groups. These samples were oven dried at 80 °C to a constant weight to determine fresh : dry weight ratios and were then ground to pass through a 2-mm sieve. Total N was analysed using a modified Kjeldahl method and P using the ascorbic acid method (Anderson and Ingram, 1993). Nutrient retranslocation during senescence of leaves and twigs on *Alnus* trees was calculated by the difference in nutrient contents in intact and senescent parts (Rawat and Singh, 1988).

Standing biomass, net primary productivity, litter production and cardamom yield of the same stands, estimated by Sharma *et al.* (2002), were used to quantify nutrient contents in different plant components, floor-litter and their flow rates. Nutrient contents in different plant components were obtained by multiplying the dry weight of the components by their mean nutrient concentration. Tree litterfall was estimated monthly over a 2-year period (1998–1999) using five litter traps of 1 m^2 collecting area in each sample plot; data were pooled to give annual values. Cardamom tillers that fruited in the current year were slashed after harvest (because they do not fruit again) and left on the stand floor. Nutrient flow from tree litterfall and slashed cardamom tillers was estimated by multiplying by the nutrient concentration. The mean nutrient content of the floor litter was estimated by analysing samples in different layers at five random (1 × 1 m) areas in each of the plots. Decomposition rates were calculated by enclosing litter fractions separately in nylon bags; data of all the fractions were pooled to give annual nutrient release.

Root nodules of five average-sized *Alnus* trees from all 18 plots were recovered for estimation of biomass and nutrient contents. Nutrient release from root nodules of *Alnus* was estimated using nodule turnover, a decomposition rate conversion factor (Sharma and Ambasht, 1986) and the nutrient concentration in root nodules.

Nitrogen fixation was estimated by the acetylene (C_2H_2) reduction assay (Stewart *et al.*, 1967) using a Perkin Elmer 8700 gas chromatograph, and by adopting a $C_2H_2 : N_2$ conversion factor of 3 : 1 (Hardy *et al.*, 1973). Nitrogen fixation by each age class of *Alnus* root nodules (young, medium and old) over a season was determined by the product of its mean biomass and nitrogen fixation rate. The values of all the nodule age classes were summed to give seasonal fixation, and the seasonal totals through the year together represented annual fixation.

Soil samples (n = 5) were collected at two soil depths (0–15 and 15–30 cm) from all 18 plots during the rainy, winter and spring seasons. Samples were air dried, ground to pass through a 2 mm sieve and used for nutrient analysis. Soil total N and total P were estimated by modified Kjeldahl and ascorbic acid methods, respectively (Anderson and Ingram, 1993). The amount of nutrients in each soil horizon (0–15 and 15–30 cm) was estimated using bulk density, soil volume and nutrient concentration values. The amount of nutrients estimated in both the horizons was summed to obtain total nutrient contents to a depth of 30 cm.

TABLE 1. *Range of nitrogen (N) and phosphorus (P) concentrations of* Alnus *tree and cardamom components in an age series of* Alnus*–cardamom plantation stands*

Plant components	Nutrients	Concentration range (%)
Alnus		
Leaf	N	2·631–3·641
	P	0·151–0·205
Twig	N	0·781–0·950
	P	0·017–0·052
Catkin	N	2·430–2·705
	P	0·130–0·182
Branch	N	0·591–0·656
	P	0·003–0·006
Bole	N	0·331–0·355
	P	0·002–0·004
Root	N	1·201–1·531
	P	0·004–0·007
Cardamom		
Leaf	N	1·973–2·155
	P	0·091–0·167
Pseudo-stem	N	0·325–0·607
	P	0·032–0·088
Capsule	N	0·849–1·000
	P	0·089–0·094
Rhizome	N	0·310–0·621
	P	0·002–0·004
Root	N	0·543–0·630
	P	0·054–0·092

Each value represents the sample mean, n = 9.

The values of nutrient contents of different plant components of both *Alnus* and cardamom were summed to obtain nutrient storage in vegetation. The sum of nutrient contents of *Alnus* trees, understorey cardamom and floor-litter represented the standing state of a stand. Annual nutrient uptake was the sum of the production of nutrients in all plant components. In the case of nitrogen, the difference between total annual uptake and fixation in a stand was the net uptake from the soil. Nutrient retention was the difference between annual uptake and return through decomposition of the stand floor-litter and root nodules. Turnover time of nutrients in the standing vegetation was computed by taking the ratios of standing state and the annual uptake (Chaturvedi and Singh, 1987; Sharma, 1993). The turnover time for each nutrient on the stand floor was calculated following Olson (1963).

RESULTS

Nutrient concentrations and standing states

The range of nutrient concentrations of *Alnus* and cardamom components in the age series of *Alnus*–cardamom plantations is presented in Table 1. Concentrations of nutrients were highest in leaves and lowest in boles of *Alnus*, and highest in leaves and lowest in rhizomes of cardamom. The highest concentration of N in *Alnus* leaves was 11 times greater than the lowest concentration in the bole, while in

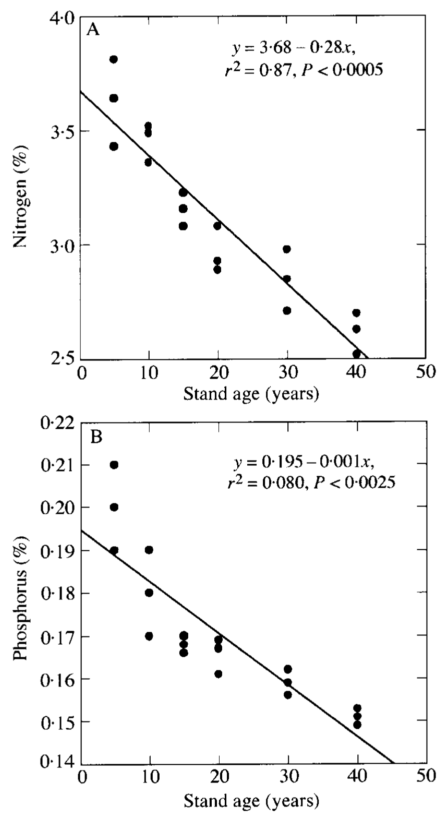

FIG. 1. Relationships between foliar N (A) and P (B) concentrations in *Alnus* in the age series of *Alnus*–cardamom plantation stands.

cardamom it was seven times greater in the leaf than in the rhizome. There was tremendous variation between components in P concentration: it was approx. 100-fold higher in the leaf (highest value) than in the bole (lowest value) of *Alnus*, and approx. 84 times greater in the leaf than in the rhizome of cardamom. Mean N concentrations of different components of *Alnus* decreased in the order leaf > catkin > root > twig > branch > bole. A similar order was recorded for P except there was a higher concentration in the twig than in the root. In cardamom, N concentrations followed the order: leaf > capsule > root > pseudo-stem > rhizome. A similar trend was recorded for P except that the pseudo-stem had a distinctly higher concentration than the rhizome. Foliar nutrient concentrations of *Alnus* decreased with increasing plantation age and showed an inverse relationship with stand age (Fig. 1). Both N and P concentrations of foliage decreased by approx. one-quarter in the 40-year-old stand compared with that of the 5-year-old stand.

Stand total and component-wise standing stocks of nutrients are presented in Table 2. Standing states of N doubled between the 5- and 15-year-old stands, and then increased slightly to peak in the 40-year-old stand. The standing state of N was 2·43 times greater in the 40-year-old stand than in the 5-year-old stand. The standing state of P also increased 2·5-fold from the 5- to the 15-year-old stand, and then decreased to a value of 7 kg ha^{-1} in the 40-year-old stand. Increment in perennial parts such as branch, bole and root of *Alnus* mainly contributed to the nutrient increase in biomass. The contribution of different components of cardamom to the standing state began to decrease once the stand reached 15 years of age.

Nitrogen fixation

Nitrogen fixation by the shade tree *Alnus* was estimated seasonally in the age series of *Alnus*–cardamom plantations (Table 3). The highest fixation was recorded during the peak growing season extending from July to September. Although the lowest rate of fixation was recorded during the winter months, its contribution was quite substantial in the 10- and 15-year-old stands (Table 3). Annual fixation increased from 52 kg ha^{-1} in the 5-year-old stand to a peak value of 155 kg ha^{-1} in the 15-year-old stand. Annual fixation was essentially static (58 and 59 kg ha^{-1}, respectively) in 30- and 40-year-old plantations.

Nutrient return to floor and turnover rates

Annual inputs of nutrients to the floor were predominantly by litterfall of *Alnus* (leaf and twig, and catkin) and slashed cardamom tillers. Total nutrient return to the stand floor from both *Alnus* and cardamom ranged from 3·57 kg ha^{-1} per year P and 62 kg ha^{-1} per year N in the 40-year-old stand to 7·35 kg ha^{-1} per year P and 163 kg ha^{-1} per year N in the 15-year-old stand (Table 4). The contribution of *Alnus* leaf and twigs to both nutrient pools was always highest (59–69 % N; 45–62 % P) in all the stands. The contribution of cardamom leaf and pseudo-stem ranged from 17 to 44 % P and 17 to 32 % N. Floor-litter biomass and its nutrient contents increased from the 5-year-old stand to peak in the 15-year-old stand and then declined to the lowest value in the 40-year-old stand (Table 5). Nitrogen in the floor litter was 2·48–3·43 times greater and P was 2·54–4·51 times greater than the annual input through litterfall and slashed cardamom tillers.

The values of turnover rates and times for different nutrients on the stand floor are given in Table 8. The turnover time of N ranged from 2·5 years in the 5-year-old stand to 3·4 years in the 30-year-old stand. P turnover time also ranged from a similar minimum value of 2·5 years in the 5-year-old stand to a highest value of 4·5 years in the 15-year-old stand. The turnover rate of N ranged from 0·29 in the 30-year-old stand to 0·40 in the 5-year-old stand, and P ranged from 0·22 in 15- and 20-year-old stands to 0·39 in the 5-year-old stand.

Nutrient uptake, retranslocation and turnover time

Nutrient uptake from the soil, retention in biomass and return to the soil, and standing states in the age series of plantation stands are presented in Table 6. Nitrogen uptake (including biological fixation) was lowest (90 kg ha^{-1} per

TABLE 2. *Standing state of nutrients (kg ha⁻¹) in different* Alnus *and cardamom components in the age series of* Alnus–*cardamom plantation stands*

Stand age (years)	Nutrients	Alnus LT	Alnus CT	Alnus BR	Alnus BO	Alnus RT	Cardamom CL	Cardamom PS	Cardamom RR	Stand total
5	N	42·04 ± 2·61	7·35 ± 0·94	43·71 ± 4·21	51·88 ± 9·61	106·33 ± 14·29	12·82 ± 1·23	6·79 ± 0·65	42·09 ± 6·00	313
	P	2·43 ± 0·14	0·39 ± 0·05	0·29 ± 0·03	0·28 ± 0·01	0·83 ± 0·06	0·94 ± 0·09	1·14 ± 0·11	0·14 ± 0·01	6
10	N	61·94 ± 2·66	11·49 ± 1·66	55·66 ± 7·30	66·23 ± 5·77	122·93 ± 5·27	26·69 ± 6·16	14·85 ± 3·43	65·54 ± 15·09	425
	P	2·86 ± 0·14	0·67 ± 0·11	0·37 ± 0·05	0·36 ± 0·03	1·31 ± 0·02	1·70 ± 0·39	2·98 ± 0·69	0·30 ± 0·01	11
15	N	54·15 ± 3·18	13·91 ± 1·91	87·16 ± 20·80	115·38 ± 32·80	178·67 ± 52·00	48·57 ± 20·02	25·65 ± 10·56	131·56 ± 26·65	655
	P	2·56 ± 0·06	0·81 ± 0·12	0·59 ± 0·14	0·63 ± 0·18	1·61 ± 0·23	3·67 ± 1·51	4·68 ± 1·93	0·58 ± 0·12	15
20	N	44·45 ± 5·32	14·81 ± 2·13	112·53 ± 20·77	158·18 ± 29·13	242·25 ± 34·64	21·98 ± 2·14	19·30 ± 1·89	54·27 ± 3·98	668
	P	2·37 ± 0·29	0·99 ± 0·14	0·76 ± 0·14	0·87 ± 0·16	1·86 ± 0·15	1·77 ± 0·17	2·44 ± 0·24	0·24 ± 0·02	11
30	N	34·64 ± 3·06	14·04 ± 1·85	121·03 ± 21·48	194·65 ± 33·46	246·12 ± 43·26	14·60 ± 4·46	8·28 ± 2·57	24·68 ± 7·65	658
	P	1·77 ± 0·16	0·85 ± 0·14	0·81 ± 0·15	0·97 ± 0·18	1·39 ± 0·19	1·01 ± 0·32	1·93 ± 0·38	0·18 ± 0·05	9
40	N	30·88 ± 0·49	13·78 ± 2·46	165·57 ± 44·36	264·74 ± 19·00	266·09 ± 54·76	6·31 ± 2·02	2·86 ± 0·98	9·38 ± 1·01	760
	P	1·63 ± 0·02	0·79 ± 0·14	1·11 ± 0·29	1·44 ± 0·43	1·46 ± 0·24	0·28 ± 0·58	0·28 ± 0·09	0·03 ± 0·004	7

Values are means of three site replicates (± s.e.; *n* = 9).
LT, Leaf and twig; CT, catkin; BR, branch; BO, bole; RT, root and root nodule; CL, cardamom leaf; PS, pseudo-stem; RR, root and rhizome; N, nitrogen; P, phosphorus.

TABLE 3. *Seasonal course of nitrogen fixation (kg ha⁻¹) by* Alnus *trees in the age series of* Alnus–*cardamom plantations based on acetylene reduction assays*

	Stand age (years) 5	10	15	20	30	40
October–December	15 ± 2	35 ± 3	48 ± 5	41 ± 5	15 ± 3	15 ± 2
January–March	5 ± 1	14 ± 2	14 ± 1	8 ± 2	6 ± 1	5 ± 1
April–June	14 ± 1	25 ± 2	23 ± 3	19 ± 3	13 ± 2	11 ± 2
July–September	18 ± 2	54 ± 7	70 ± 8	44 ± 7	24 ± 3	28 ± 3
Total annual fixation	52	128	155	112	58	59

Values are means of three site replicates (± s.e.).

TABLE 4. *Annual input of nitrogen and phosphorus (kg ha⁻¹) to the stand floor through litter production in the age series of* Alnus–*cardamom plantation stands*

Stand age (years)	Nutrients	*Alnus* leaf and twig	*Alnus* catkin	Cardamom leaf and pseudo-stem	Stand total
5	N	63·52 ± 2·61	7·35 ± 0·94	26·06 ± 0·55	96·93
	P	2·49 ± 0·14	0·39 ± 0·52	2·28 ± 0·05	5·16
10	N	75·09 ± 2·70	11·49 ± 1·66	27·69 ± 2·18	114·27
	P	2·54 ± 0·12	0·67 ± 0·11	2·40 ± 0·19	5·61
15	N	97·86 ± 3·20	13·31 ± 1·91	51·36 ± 1·03	162·53
	P	3·96 ± 0·10	0·81 ± 0·12	2·58 ± 0·52	7·35
20	N	68·53 ± 5·32	14·81 ± 2·13	22·11 ± 5·05	105·45
	P	3·00 ± 0·28	0·99 ± 0·14	2·01 ± 0·46	6·00
30	N	64·88 ± 3·10	14·03 ± 1·85	16·44 ± 1·71	95·36
	P	3·16 ± 0·16	0·85 ± 0·11	1·39 ± 0·14	5·40
40	N	36·80 ± 0·50	13·78 ± 2·46	11·74 ± 0·69	62·32
	P	2·18 ± 0·02	0·79 ± 0·14	0·60 ± 0·03	3·57

Values are means of three site replicates (± s. e.; *n* = 9).

year) in the 40-year-old stand and highest (239 kg ha^{-1} per year) in the 15-year-old stand. Phosphorus uptake also showed a similar pattern, having the lowest value (3·83 kg ha^{-1} per year) in the 40-year-old stand and the highest (10·60 kg ha^{-1} per year) in the 15-year-old stand. Annual return of N to that of uptake ranged from 32 to 58 % and was higher in younger stands, whereas that of P ranged from 44 to 66 % and was highest in the 15- and 20-year-old stands.

Standing states of N, including that of the floor-litter, were lower (554 kg ha^{-1}) in the 5-year-old stand and highest (1084 kg ha^{-1}) in the 15-year-old stand; thereafter values decreased slightly with increasing age of the stand. Phosphorus in the standing states was also highest (48 kg ha^{-1}) in the 15-year-old stand; it increased from the 5- to the 15-year-old stand and then declined with advancing age.

Nutrient retranslocation from the senescent *Alnus* leaves is presented in Fig. 2. Nitrogen retranslocation rates were lower in the youngest stand and increased with plantation age. In the case of P the opposite was true; values were highest in the youngest plantations and decreased with advancing age. Nitrogen retranslocation showed a strong positive relationship with stand age while the relationship was negative with P.

The turnover time of N in the standing vegetation of both *Alnus* and cardamom increased from 1·83 years in the 5-year-old stand to reach the highest value (8·32 years) in the 40-year-old stand. Overall turnover time for P was low, ranging from 1·1 years in the 5-year-old stand to 1·83 years in the 40-year-old stand. The turnover time of both nutrients varied little in the cardamom components; however, the turnover time of N increased greatly after the 15-year-old stand in *Alnus* whereas it remained nearly constant for P (Table 7). Turnover rate and time of plantation floor are given in Table 8.

TABLE 5. *Floor-litter biomass and nutrient content in the age series of* Alnus–*cardamom plantation stands*

Stands age (years)	Floor-litter (t ha^{-1})	Nutrients (kg ha^{-1})	
		Nitrogen	Phosphorus
5	18·51 ± 0·25	240·63 ± 18·19	13·14 ± 2·45
10	23·16 ± 2·06	305·71 ± 10·73	22·00 ± 5·77
15	34·91 ± 1·24	429·39 ± 11·52	33·16 ± 4·89
20	28·05 ± 1·44	339·41 ± 12·42	26·96 ± 1·23
30	24·27 ± 0·58	327·65 ± 13·49	18·20 ± 1·9
40	14·67 ± 1·04	176·04 ± 14·00	11·88 ± 2·68

Values are means of three site replicates.

Nutrient use efficiency and nutrient cycling

Nutrient use efficiency (kg annual net primary productivity per kg nutrient taken up) for both N and P decreased with plantation age (Table 9). Nitrogen use efficiency was 98 in the 5-year-old stand, decreasing with increasing age to 81 in the 40-year-old stand. Similarly, P use efficiency in the 5-year-old stand was 2439 and decreased with increasing age to a minimum value of 1914 in the 40-year-old stand. Average P use efficiency of all stands was approx. 25 times greater than that of N use efficiency.

Computation of the ratio nutrient uptake: energy fixation efficiency takes into account both above- and below-ground production of plantations, and the ratio nutrient release: energy dissipated is based on floor-litter and root nodule disappearance (Table 10). Nitrogen and P uptake per unit energy fixed remained almost constant in the younger stands and increased slightly with plantation age. The amount of nutrient released per unit energy dissipated was highest in the 5-year-old stand and decreased with increasing age to a minimum value in the 30-year-old stand.

Nitrogen distribution and flow rates in the components of the 5-, 15- and 40-year-old plantation stands are presented in Fig. 3. Annual N uptake from soil in the 5-year-old stand was 1·4 times greater than that of the 15-year-old stand and 3·8 times that of the 40-year-old stand. Nitrogen fixation was highest in the 15-year-old stand, which was three times greater than that of the 5-year-old stand and 2·6 times that of the 40-year-old stand. Approx. 61 % of total annual N uptake is allocated to above-ground components in *Alnus* and 15 % in cardamom in the 15-year-old stand. The allocation shifted to 87 % in *Alnus* and just 4 % in cardamom in the 40-year-old stand. Nitrogen exit in terms of cardamom capsules (agronomic yield) was greatest (2·89 kg ha^{-1} per year) in the 15-year-old stand, being 2·8

TABLE 6. *Uptake, retention, return and standing state of nutrients in the age series of* Alnus *–cardamom plantation stands*

Nutrients	Stand age (years)	Uptake	Return	Retention	Standing state (kg ha^{-1})†
		(kg ha^{-1} per year)			
Nitrogen	5	171·04*	71·26	99·78	553·64
	10	202·36*	102·37	99·99	731·04
	15	238·83*	126·46	112·37	1084·44
	20	168·85*	68·93	99·92	1006·87
	30	150·47*	66·50	83·97	970·84
	40	90·12*	44·97	45·15	926·14
Phosphorus	5	6·86	3·77	3·09	19·58
	10	8·77	4·88	3·89	32·55
	15	10·60	5·56	5·04	48·29
	20	7·62	3·74	3·88	38·26
	30	6·79	3·09	3·70	27·11
	40	3·83	2·51	1·32	18·90

Values are pooled from three site replicates.
* Includes biological nitrogen fixation.
† Includes floor litter nutrient.

times higher that of the 5-year-old stand and 7·6 times that of the 40-year stand.

Phosphorus distribution and flow rates in the components of both *Alnus* and cardamom in 5-, 15- and 40-year-old plantation stands are presented in Fig. 4. Annual P uptake from the soil was highest in the 15-year-old stand (10·6 kg ha^{-1} per year) being 1·5 times greater than that of the 5-year-old stand and 2·8 times that of the 40-year-old stand. In stands up to 15 years of age, allocation of P from the annual uptake remained between 30 and 40 % in large cardamom and decreased with increasing stand age to just 6 % in 40-year-old stands. In the oldest stands (40 years), 93 % of annual P uptake from the soil was allocated to above-ground components of *Alnus*. Phosphorus exit from the system in the form of agronomic yield was highest in the 15-year-old stand (0·29 kg ha^{-1} per year), being 2·4 times greater than that of the 5-year-old stand and 7·25 times that of the 40-year-old stand.

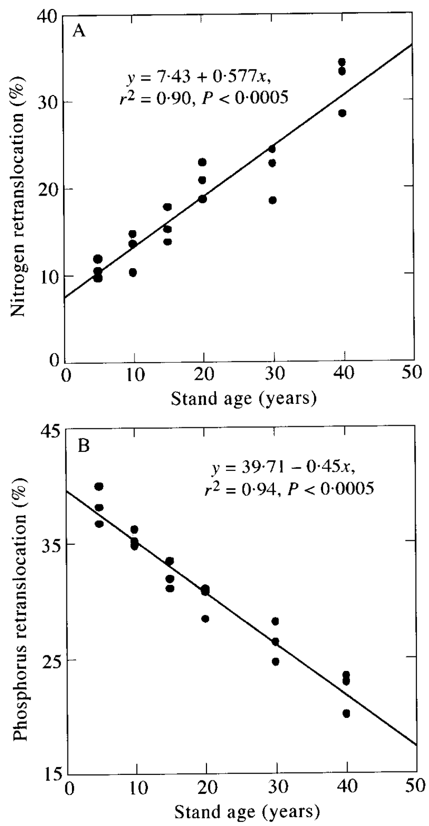

FIG. 2. Relationships between N (A) and P (B) retranslocation from *Alnus* leaves and stand age in the age series of *Alnus*–cardamom plantation stands.

DISCUSSION

Nitrogen concentrations in different plant components of *Alnus* were higher than in the analogous components of cardamom. This is attributed to high rates of N_2-fixation by *Alnus* (Sharma and Ambasht, 1984; Sharma *et al.*, 1994). Foliar nutrient (N and P) concentrations in *Alnus* decreased consistently from the young to the older plantations. A similar trend was recorded in *Alnus rubra* by DeBell and Radwan (1984). This result suggests that the supplies of these nutrients may become limiting beyond a certain age in older plantation stands.

The distribution of nutrients in different components in an age series of *Alnus*–cardamom 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. Similar results were reported by Sharma (1993) in an age series of *Alnus nepalensis* plantations, and by Rawat and Singh (1988) in *Quercus* forests in central Himalaya. Ranges of standing states of nutrients (N: 313–760 kg ha^{-1}; P: 6–15 kg ha^{-1}) in the present study can be compared with the range given for deciduous forests (530–1200 kg ha^{-1} for N and 40–100 kg ha^{-1} for P; Rodin and Bazilevich, 1967; Duvigneaud and Denaeyer De-Smet, 1970; Nihlgard, 1972). The standing state of N is within the same range while that of P is much lower in the present study. Nutrient storage in understorey cardamom was very high (N: 2–31 %; P: 8–59 %) and was highest in the 15-year-old stand. Normally, the contribution

TABLE 7. *Turnover time (years) of nutrients in the standing vegetation of* Alnus *and cardamom in the age series of* Alnus–*cardamom plantation stands*

Stand age (years)	Nitrogen			Phosphorus		
	Alnus	Cardamom	Stand total	*Alnus*	Cardamom	Stand total
5	1·87	1·69	1·83	0·89	1·02	1·10
10	2·08	2·16	2·10	1·12	1·32	1·20
15	2·66	3·23	2·74	0·89	2·17	1·43
20	4·18	2·78	3·95	1·25	2·07	1·48
30	4·96	2·06	4·62	1·09	2·08	1·31
40	8·67	3·09	8·32	1·78	2·68	1·83

Values are pooled for three site replicates.

TABLE 8. *Turnover rate* (k) *and turnover time* (t, *years*) *of nutrients on stand floor in the age series of* Alnus–*cardamom plantations*

Stand age (year)	Nitrogen		Phosphorus	
	k	*t*	*k*	*t*
5	0·40	2·5	0·39	2·5
10	0·37	2·6	0·26	3·9
15	0·38	2·7	0·22	4·5
20	0·31	3·2	0·22	4·4
30	0·29	3·4	0·29	3·6
40	0·35	3·0	0·30	3·4

Values are pooled from three site replicates.

TABLE 9. *Nutrient use efficiency in the age series of* Alnus–*cardamom plantation stands*

Stand age (years)	Total net primary productivity (t ha^{-1} per year	Nutrient use efficiency	
		Nitrogen	Phosphorus
5	16·73	97·81	2439
10	19·57	96·71	2231
15	22·40	93·71	2111
20	14·72	87·18	1934
30	13·06	86·79	1923
40	7·35	81·34	1914

Values are pooled from three site replicates.

TABLE 10. *Ratios between nutrient uptake (NU) and net energy fixation (NEF), and nutrient release (NR) and energy dissipation (ED) in an age series of* Alnus *–cardamom plantation stands*

Ratio	Stand age (years)	Nitrogen	Phosphorus
NU : NEF	5	0·531	0·021
	10	0·520	0·023
	15	0·538	0·024
	20	0·554	0·025
	30	0·577	0·026
	40	0·585	0·030
NR : ED	5	0·67	0·024
	10	0·52	0·022
	15	0·46	0·019
	20	0·31	0·012
	30	0·28	0·012
	40	0·37	0·013

NU and NR are quantified as kg ha^{-1} per year and NEF and ED as kJ ha^{-1} per year.

Values are pooled from three site replicates.

of understorey vegetation in temperate forests and plantations is below 2 % (Whittaker *et al.*, 1979; Rawat and Singh, 1988; Sharma, 1993). The higher nutrient storage in understorey cardamom in the present study is mainly attributed to the management of this cash crop.

Total annual N_2 fixation in monoculture stands of different ages of *Alnus nepalensis* has been reported to range from 29 to 117 kg ha^{-1}, the highest values being recorded in the youngest stand (Sharma and Ambasht, 1988). However, in the present study *A. nepalensis* in combination with cardamom showed slightly higher N_2 fixation, ranging from 52 to 155 kg ha^{-1} per year. N_2 fixation in all plantation stands was highest during the rainy season (July–September). The average annual N_2 fixation recorded in this study (155 kg ha^{-1}) was higher than that recorded in *A. rubra* (130 kg ha^{-1}; Binkley, 1981) or in *A. nepalensis* (117 kg ha^{-1}; Sharma and Ambasht, 1988). Newton *et al.* (1968) reported annual N_2 fixation as high as 320 kg ha^{-1} in 2- to 15-year-old *A. rubra* stands. The contribution of N_2 fixation to total uptake ranged from 30 to 65 %, with the highest contribution being recorded in 10-, 15- and 20-year-old stands.

Annual input of N and P to the plantation floor through litterfall and slashed pseudo-stems of cardamom increased from the youngest stand to peak in the 15-year-old stand and then decreased with further increase in plantation age. The contribution of cardamom to the total annual input ranged from 17 to 32 % for N and 17 to 44 % for P. The concentration increased from the youngest stand to peak in the 15-year-old stand and then decreased with advancing age, exactly following the N_2 fixation trend. This indicates that nitrogen levels in the cardamom components were also influenced by N_2 fixation, either because the element was available to cardamom following fixation by *Alnus*, or because *Alnus* did not compete for soil N so more was available. However, the contribution of cardamom to P input was highest in the youngest stand and decreased with advancing age to a minimum value in the oldest stand.

Nutrient retranslocation of senescent *Alnus* leaves was positively related to stand age in the case of N, and negatively related in the case of P. The retranslocation of N in young *Alnus* trees was minimal because this nutrient was sufficiently available through fixation; however, with advancing age the demand increased as the contribution from fixation decreased causing greater retranslocation. In the case of P, its demand for growth was high in younger stands where effective retranslocation was recorded. It decreased with advancing stand age. *Alnus* showed entirely different physiological behaviour for N and P at different ages, governed mostly by demand and availability of these nutrients.

Nutrient use efficiency may be expected to drop as utilization of that nutrient increases because availability of some other resource (e.g. water, energy or light) limits production (Melillo and Gosz, 1983; Binkley *et al.*, 1992). The nutrient use efficiencies for both N and P in monoculture plantations of *A. nepalensis* decreased with plantation age (Sharma, 1993). In the case of mixed *Alnus* and cardamom plantations studied here, the nutrient use efficiencies were generally consistent with the above hypothesis and decreased with plantation age. *Alnus*–cardamom mixed stands used P less efficiently compared with pure stands of the same species of *Alnus* (Sharma,

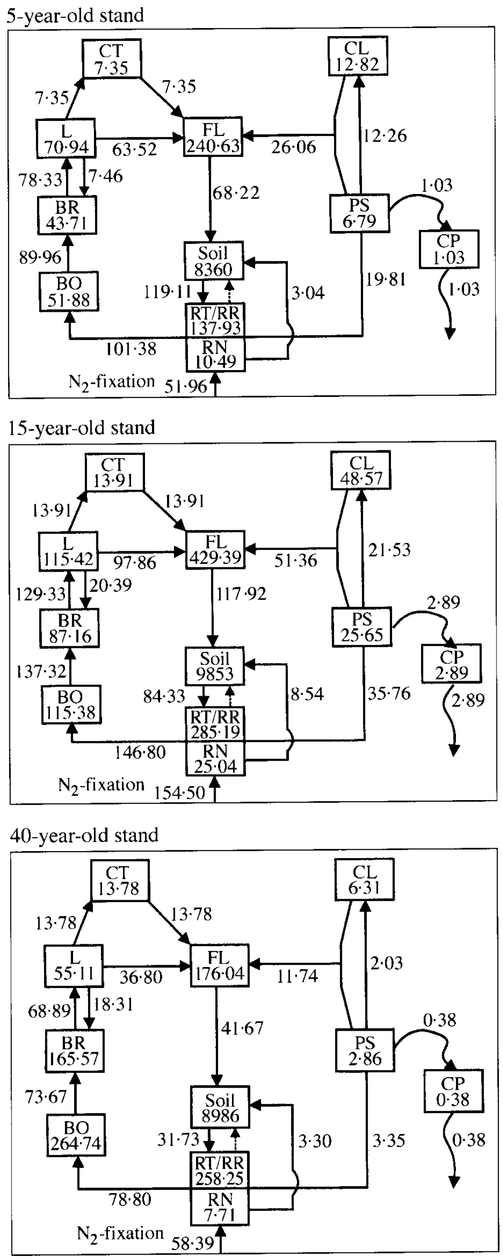

FIG. 3. Distribution of N flow rates in components of *Alnus* and cardamom in 5-, 10- and 40-year-old *Alnus*–cardamom plantations. Units are kg ha^{-1} for compartments and kg ha^{-1} per year for flows. Soil total N is presented for the upper 30 cm. L, Leaf; CT, catkin; BR, branch; BO, bole; RT/RR, root/rhizome; RN, root nodule; FL, floor-litter; CL, cardamom leaf; PS, pseudo-stem; CP, capsule.

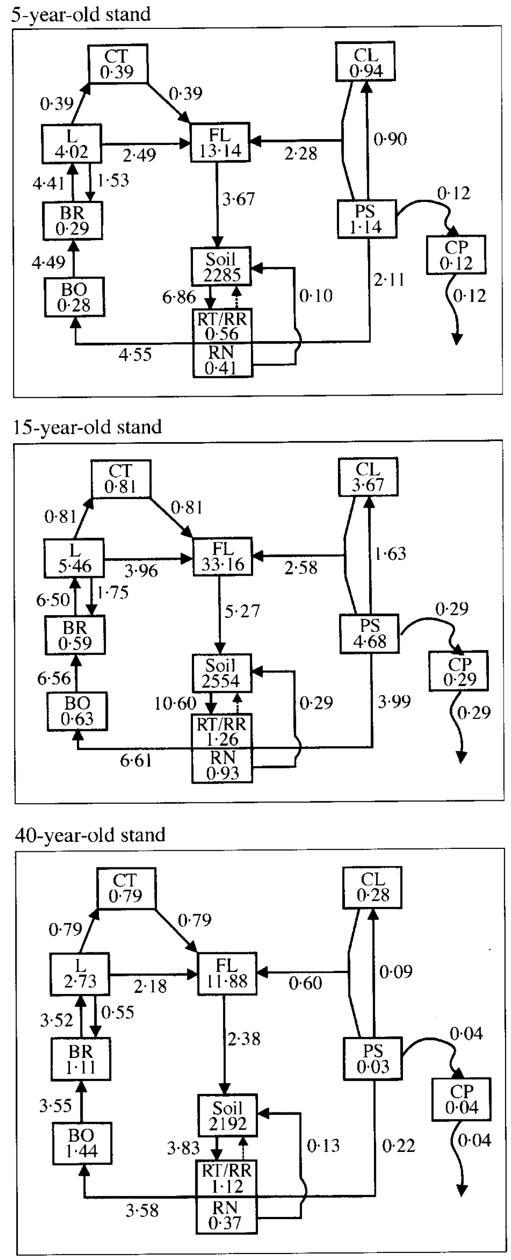

FIG. 4. Distribution of P flow rates in components of *Alnus* and cardamom in the 5-, 10- and 40-year-old *Alnus*–cardamom plantations. Units are kg ha^{-1} for compartments and kg ha^{-1} per year for flows. Soil total P is presented for upper 30 cm. L, Leaf; CT, catkin; BR, branch; BO, bole; RT/RR, root/rhizome; RN, root nodule; FL, floor-litter; CL, cardamom leaf; PS, pseudo-stem; CP, capsule.

1993). The *Alnus*–cardamom plantations also used N less efficiently compared with mixed *Alnus rubra*–conifer stands in the USA. Comparison between *A. rubra* and conifers showed *A. rubra* to be less efficient than conifers (Binkley *et al*., 1992).

Total uptake in *Alnus*–cardamom plantations was 90–239 kg ha^{-1} per year for N and 3·8–10·6 kg ha^{-1} per year for P, being lower for N and higher for P compared with monoculture plantations of *A. nepalensis* (Sharma, 1993). Rawat and Singh (1988) estimated nutrient uptake in a Himalayan oak forest and reported values of 230 kg ha^{-1} per year for N and 13 kg ha^{-1} per year for P. These comparisons show that pure *Alnus* plantations have higher N uptake and lower P uptake and, in the mixed stands, cardamom N uptake decreases while P uptake increases. The low P uptake in pure *A. nepalensis* stands was attributed to a negative effect of *Alnus* on the P economy, mostly by increasing soil acidity (Sharma, 1993), causing phosphate to react with Fe and Al to form less soluble compounds (Brozek, 1990; Sharma *et al*., 1997). Furthermore, a heavy accumulation of organic matter in soils of pure *Alnus* plantation stands could have shifted P from a plant-available pool to an organically bound pool (Sharma, 1993). The combination of *Alnus* with cardamom is a system where N and P uptakes are balanced compared with either pure stands of N_2-fixing species or non-N_2-fixing species. Therefore, plantation systems with a mixture of N_2-fixing and non-N_2-fixing species, such as *Alnus*–cardamom, are advantageous in balancing N and P cycling.

The turnover time in standing vegetation reflects the rate of nutrient cycling, and the mean turnover time of P was lower than that of N. The turnover time of P remained between 1 and 2 years in plantations of all ages, while that of N increased from 2 years in youngest stand to more than 8 years in the oldest stand. The N turnover of the stand was more affected by the *Alnus* component than by cardamom. Sharma (1993) also reported a lower turnover time of P than of N in an age series of pure *A. nepalensis* plantations; however, turnover times were greater for both N and P than in the mixed *Alnus*–cardamom plantations of the present study. The turnover time of nutrients on the plantation floor, however, was slightly higher for P than for N. This finding suggests that P cycling in vegetation was much quicker than N in stands with a mixture of N_2-fixing and non-N_2-fixing species.

The nutrient budget showed substantial N loss from the system by the 40-year-old stand compared with younger plantations. The 40-year-old stand has less N in the soil (approx. 800 kg N ha^{-1} less), and slightly more N in vegetation (approx. 100 kg N ha^{-1} more), giving a net loss of 700 kg N ha^{-1} (or 30 kg N ha^{-1} per year). At the same time, N fixation is supposed to be in the order of 100 kg N ha^{-1} per year for a total input of approx. 2500 kg N ha^{-1} over 25 years. In the 25-year period a large amount of N is lost from the system. This is attributed mainly to shade tree biomass removal as a thinning practice (373 trees fewer in the 40- compared with the 10-year-old stand). Leaching loss from soil and exit from the system in the form of cardamom agronomic yield were also other important causes of nutrient imbalance.

Consistently high net primary production in the age series of *Alnus*–cardamom conforms with marked retention of nutrients by the plants over the annual cycles. The ratio of nutrient uptake and net energy fixation remained fairly similar in *Alnus*–cardamom plantations of all the ages. However, N and P uptake per unit energy fixed in monocultures of *A. nepalensis* stands was higher than the results of the present study and the ratios increased with plantation age (Sharma, 1993).

The performance of cardamom under the influence of N_2-fixing *Alnus* in an age series of plantations with regards to nutrient use efficiencies, nutrient dynamics and cycling suggests the system is sustainable up to 20 years, and replanting both *Alnus* and cardamom after 15–20 years would be highly beneficial.

ACKNOWLEDGEMENTS

The authors are grateful to the Director, G. B. Pant Institute of Himalayan Environment and Development for providing facilities. This work is a part of a project funded by the Indian Council of Agricultural Research, New Delhi.

LITERATURE CITED

Anderson JM, Ingram JSI. 1993. *Tropical soil biology and fertility: A handbook of methods.* Wallingford, UK: CAB International.

Binkley D. 1981. Nodule biomass and acetylene reduction rates of red alder and Sitka alder on Vancouver Island, B.C. *Canadian Journal of Forest Research* **11**: 281–286.

Binkley D, Smith FW, Son Y. 1995. Nutrient supply and decline in leaf area and production in lodgepole pine. *Canadian Journal of Forest Research* **25**: 621–628.

Binkley D, Sollins P, Bell R, Sachs D, Myrold D. 1992. Biogeochemistry of adjacent conifer and alder/conifer stands. *Ecology* **73**: 2022–2033.

Brozek S. 1990. Effect of soil changes caused by red alder (*Alnus rubra*) on biomass and nutrient status of Douglas fir (*Pseudotsuga menziesii*) seedlings. *Canadian Journal of Forest Research* **20**: 1320–1325.

Chaturvedi OP, Singh JS. 1987. Structure and function of pine forest of central Hmalaya. II. Nutrient dynamics. *Annals of Botany* **60**: 253–267.

DeBell DS, Radwan MA. 1984. Repeated coppicing of cottonwood and alder effects soil properties. *Agronomy Abstracts* **258**.

DeBell DS, Cole TG, Whitesell C. 1997. Growth, development and yield in pure and mixed stands of *Eucalyptus* and *Albizia*. *Forest Science* **43**: 286–298.

Duvigneaud P, Denaeyer De-Smet S. 1970. Biological cycling of minerals in temperate deciduous forests. In: Reichle DE, ed. *Analysis of temperate forest ecosystems.* New York: Springer-Verlag, 199–225.

Hardy RWF, Burns RC, Holston RD. 1973. Applications of the acetylene-ethylene assay for measurement of nitrogen fixation. *Soil Biology and Biochemistry* **5**: 47–81.

Melillo JM, Gosz J. 1983. Interactions of biogeochemical cycles in forest ecosystems. In: Bolin B, Cook R, eds. *The major biogeochemical cycles and their interactions.* New York: Wiley, 177–221.

Newton MBA, Hassan El, Zavitkovski J. 1968. Role of red alder in western Oregon forests succession. In: Trappe JM, Franklin JF, Tarrant RF, Hassans GM, eds. *Biology of alder.* Portland, Oregon: USDA Forest Service, PNW Forest Range Experimental Station, 73–83.

Nihlgard B. 1972. Plant biomass, primary production and distribution of chemical elements in a beech and a planted spruce forest in southern Sweden. *Oikos* **23**: 69–81.

Olson JS. 1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* **44**: 322–331.

Rawat YS, Singh JS. 1988. Structure and function of oak forest in central Himalaya. II. Nutrient dynamics. *Annals of Botany* **62**: 413–427.

Rodin LE, Bazilevich NI. 1967. *Production and mineral cycling in terrestrial vegetation*. Edinburgh: Oliver and Boyd.

Sharma E. 1993. Nutrient dynamics in Himalayan alder plantations. *Annals of Botany* **67**: 329–336.

Sharma E, Ambasht RS. 1984. Seasonal variation in nitrogen fixation by different ages of root nodules of *Alnus nepalensis* plantations in the eastern Himalayas. *Journal of Applied Ecology* **21**: 265–270.

Sharma E, Ambasht RS. 1986. Root nodule age-class transition, production and decomposition in an age sequence of *Alnus nepalensis* plantation stands in the Eastern Himalayas. *Journal of Applied Ecology* **23**: 689–701.

Sharma E, Ambasht RS. 1988. Nitrogen accretion and its energetics in Himalayan alder plantations. *Functional Ecology* **2**: 229–235.

Sharma G, Sharma E, Sharma R, Singh KK. 2002. Performance of an age series of *Alnus*-cardamom plantations in the Sikkim Himalaya: Productivity, energetics and efficiencies. *Annals of Botany* **89**: 261–272.

Sharma R, Sharma E, Purohit AN. 1994. Dry matter production and nutrient cycling in agroforestry systems of cardamom grown under *Alnus* and natural forest. *Agroforestry Systems* **27**: 293–306.

Sharma R, Sharma E, Purohit AN. 1997. Cardamom, mandarin and nitrogen-fixing trees in agroforestry systems in India's Himalayan region. I. Litterfall and decomposition. *Agroforestry Systems* **35**: 235–253.

Stewart WDP, Fitzgerald GP, Burris RH. 1967. *In situ* studies on N_2-fixation using the acetylene reduction technique. *Proceedings of the National Academy of Sciences, USA* **58**: 2071–2078.

Whittaker RH, Likens GE, Bormann FH, Eaton JH, Siccama TG. 1979. The Hubbard Brook ecosystem study: Forest nutrient cycling and element behaviour. *Ecology* **60**: 203–220.