Nutrient Partitioning and Dynamics in *Coriaria nepalensis* Wall Dominated Shrublands of Degraded Hills of Kumaun Himalaya

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Coriaria nepalensis is one of the shrubs which have the ability to mitigate the frequency of perilous natural events or natural calamities. This paper elucidates the nutrient dynamics of *C. nepalensis* shrublands in degraded hills of Kumaun Himalaya. The average nutrient concentration (N, P, and K) in aboveground components of *C. nepalensis* was in the following order: Foliage > Twigs > Branches > Bole wood, whereas in belowground components the order was: Fine roots > Lateral roots > Stump root. The order of contribution to total nutrient storage in vegetation was: Tree > Herbs > Shrubs. The proportion of nutrients stored in the shrub layer was in the order: N > K > P. The soil stored a maximum proportion of nutrients at each site (79.48–87.54% N, 70.47–87.88% P, 74.33–88.27% K). Maximum nutrient storage in soil and vegetation was recorded for site 3 (Barapatthar) and minimum for site 1 (Pines). The uptake of N, P, and K by vegetation ranged from 428 to 1,353 kg ha^{-1} yr^{-1}, 32–102 kg ha^{-1} yr^{-1}, and 109–479 kg ha^{-1} yr^{-1}, respectively. In the present study, the turnover time was 1.06–1.33 years for N, 1.03–1.15 years for P, and 1.02–1.13 years for K. Compartment models reflect the distribution of nutrients and net annual flux that will help to develop the management plan to maintain the fertility and productiveness of the degraded sites.

Keywords: compartment model, nutrient dynamics, nutrient content, retranslocation, turnover of nutrients

INTRODUCTION

The forest ecosystem production depends on the site condition and concentration of nutrients in the vegetation (trees, shrubs, and herbs) and soil pool, which are available in different amounts and play a major role in every plant's physiological activity. The functional and natural balance in the intra-system cycling of the given ecosystem determines the net flux and budget of the nutrients and affects the sustainability of the ecosystem (Bargali and Singh, 1997; Gautam and Mandal, 2018; Pang et al., 2020).

The status of the nutrients in the plant and soil pools are the key indicator of site quality in terms of potential productiveness and offers the best growing environment to the regenerative crops in the forest ecosystem (Raha et al., 2020; Ray et al., 2020). The nutrient budgeting and flux in the forest

ecosystem study helps toward soil health restoration and management plans, as well understanding the ecological paradigm of nutrient partitioning and resource utilization. In this perspective, the accumulation and transfer and nutrients among vegetation, litter, and soil have been explored by various researchers in various forests and plantations or shrublands across the world (Bargali et al., 1992; Lodhiyal et al., 1995; Mfilinge et al., 2002; Gautam and Mandal, 2018; Pang et al., 2020).

Deforestation and disturbances of various forms alter the nutrient availability and cycling in vegetation and soil compartments (Singh, 2021; Manral et al., 2022). Besides this, the presence of vegetation and species admixture in addition to biophysical characteristics of site and disturbance regimes also determine the stock and dynamics of the nutrient (Gautam and Mandal, 2018; Singh et al., 2022). Thus, the balance among the inputs and outputs i.e., fixation, deposition, weathering, leaching, and volatilization, etc. are the prime concern and management aspect for a better nutrient status of the forest ecosystem (Vitousek and Sanford, 1986; Bargali et al., 2018; Manral et al., 2020; Karki et al., 2021). Furthermore, the uptake of nutrient, its retention, and its release are the integral components of nutrient dynamics of the forest ecosystem. The imbalance among these components leads to degradation of soil health and fertility (Bargali et al., 2019).

Examining these dynamic aspects of nutrient and mineral cycling in the forest ecosystem, the present work was carried out to cover the aspects of nutrient cycling in *C. nepalensis* dominated shrublands with regards to biomass accumulation and net primary production (described in the first part of this paper—Awasthi et al., 2022). Moreover, the present work highlighted the information on concentration of nutrients, content, uptake, return, turnover, use efficiency, and cycling of nutrients in *C. nepalensis* dominated shrubland in Kumaun Himalaya in India.

MATERIALS AND METHODS

Study Sites
The present investigation was done in the Kumaun Himalayan region (Uttarakhand state) comprising five sites i.e., Pines (Site-1), Rusi (Site-2), Barapatthar (Site-3), Hanumangarhi (Site-4), and Takula (Site-5). The study area is placed between $29°21'57''$ N latitude and $79°27'23''$ E longitude. The species *C. nepalensis* occurred in patches, each surrounded by relatively large open areas with small woody plant cover. After the selection of study sites, the most prominent patches of *C. nepalensis* were selected for investigation and observations and the phyotosociological attributes of the sites were given in Awasthi et al. (2022).

The study area has a warm monsoon climate. The mean monthly temperature ranged from 12 to 32°C during summer and 1 to 7°C during winter. The highest annual rainfall in the region was recorded as 944.7 mm (August) whereas the lowest rainfall was observed to be 0 mm (November). The soils of the sites are sandy loam or sandy clayey loam.

Nutrient Analysis
The component of trees (bole wood, bark, branches, twigs, foliage, and reproductive parts), shrubs (bole wood, branches, twigs, and foliage), and herbs (aboveground and belowground parts) were collected from each site from 10 to 20 trees and shrubs of all the available species and brought to the laboratory in September 2019. The samples for the components of roots (stump, lateral, and fine) for both trees and shrubs were collected by digging out roots to approximately 1 m depth. Composite samples (3) of each component of the trees, shrubs, and herbs were oven dried at 60°C to constant weight. The samples were then millground to estimate the nutrient concentration. For each replicate a composite sample of 1.0 g of soil and plant material was analyzed for total nitrogen after digestion in 10 ml concentrated sulfuric acid using 5 g catalyst mixture (Potassium Sulfate and Cupric Sulfate in ratio of 9:1) with a quick digestion unit. The total nitrogen was determined by micro-Kjeldahl digestion and titration method (Kjeldahl, 1883; Peach and Tracey, 1956; Misra, 1968). Phosphorus and potassium were extracted by wet ashing of 0.5 g plant material, in an acid mixture, consisting of 10 ml H_2SO_4 + 3 ml HNO_3 + 1 ml $HClO_4$ following the method of Jackson (1958). Phosphorus was determined by spectrophotometry and potassium by flame photometry (Jackson, 1958). The total amount of nutrients in the vegetation was obtained by summing the amounts in the different components.

At each site, soil samples were collected from two depths i.e., 0–15 cm (surface layer) and 15–30 cm (sub-surface layer) in triplicate with the help of a soil corer. There was a total of 90 samples (5 sites × 3 seasons × 3 replicates × 2 depth layer). Air dried soil samples were passed through the 2 mm sieve to remove large soil particle and other waste material and then stored in plastic zipper bags for further chemical analysis. The chemical characteristics of the soil, i.e., total nitrogen (Kjeldahl, 1883), phosphorus (Olsen et al., 1954), and exchangeable potassium (Black, 1965) was analyzed following standard ecological methods. The amount of nutrients in both strata (10–15 and 15–30 cm) of soil was obtained by multiplying bulk density, soil volume, and nutrient concentration values (N, P, and K). The amounts of nutrients estimated in both strata were summed to obtain total nutrient content up to 30 cm depth.

Nutrient Uptake
Nutrient uptake was computed by multiplying the value of net primary productivity of different components by their respective nutrient concentration. Litter samples were collected from the litter traps at monthly intervals in different sites. The samples of foliage, twigs, bark, reproductive parts, and miscellaneous were separated and analyzed for nutrients. The nutrient concentration was multiplied by the weight of litter fall to compute the amount of nutrients transferred to the shrubland floor. The turnover rate (K) was calculated as Chaturvedi and Singh (1987).

$$K = A/A + F$$

Where, A is amount of nutrients added to the shrubland floor by litter fall, F is the nutrient content of the lowest value of the

standing crop of litter in the annual cycle. Turnover time (t) is the reciprocal of the turnover rate (K).

Nutrient Retranslocation

Percentage retranslocation of nutrients from senescing components i.e., foliage, twigs, bark, and reproductive parts to the perennial tissues was calculated following Vitousek and Sanford (1986) and Ralhan and Singh (1987).

$$R\,(\%) \,=\, (X-Y)/X \,\times\, 100$$

Where, R is nutrient retranslocation (%), X is the nutrient mass in mature green foliage, and Y is the nutrient mass in senesced components. X and Y were calculated on the basis of nutrient per unit weight of mature green and senesced components, respectively, multiplied by total amount of fall of respective litter component.

To estimate nutrient retranslocation, 20 g mature attached and freshly fallen senesced components were collected in August (peak month of leaf maturity) and November (component senescing period) 2018, respectively. Since rainfall is negligible in the region during leaves senescence (November), leaching is likely to have only a minimal effect on nutrient loss from the leaves (Ralhan and Singh, 1987). Percent nutrient retranslocation efficiency (PNRE) was calculated according to Finzi et al. (2001).

$$PNRE\% \,=\, A-B/A \,\times\, 100$$

Where, A is the nutrient in the live component, and B is the nutrient in the litter component.

Nutrient use efficiency (NUE) was calculated according to Vitousek (1984):

$$NUE = \frac{\text{Litter fall weight (g m}^{-2}\text{year}^{-1})}{\text{Nutrient content in litter fall (g m}^{-2}\text{year}^{-1})}$$

Nutrient Cycling

The compartment models of nutrients (N, P, K) dynamics were developed for site-1 to site-5. These compartment models represent the overall structure and functioning including nutrient stock and annual fluxes of nutrients in the ecosystem studied. The average values of nutrient content (kg ha^{-1}) are placed in the compartments. Net annual fluxes (of N, P, and K) between compartments are depicted by arrows (kg ha^{-1} yr^{-1}). The amount present in the soil to the depth of 30 cm is considered source and that associated with the decomposition is released into the soil for reuse.

RESULTS

Concentration of Nutrients

In the present study, the average nutrient concentration (N, P, and K) in the vegetation i.e., trees, shrubs and herbs varied from site to site because of the variation in species composition (**Table 1**). The concentration of nutrients in the aboveground components of trees was in the order: Reproductive parts > Foliage > Twigs > Branches > Bole

wood > Bark. In the belowground components, the order was: Stump root < Lateral roots < Fine roots. In shrubs, the order of nutrient concentration in aboveground components was: Foliage > Twigs > Branches > Bole wood while the order of the belowground components was the same as in trees. In the case of herbs, the nutrient concentrations in aboveground parts were always higher than in belowground parts. In the case of soil surface, the concentration of nutrients is generally higher in the surface layer (0–15 cm) than in the sub-surface layer (15–30 cm) due to presence of excessive organic matter on the surface layer (**Table 1**).

The mean concentration of N in every component across the sites was high in *C. nepalensis* as compared to the average concentration of shrub components. The high concentration N can be attributed to the high nitrogen fixing ability of *C. nepalensis*. Concentration of N in the foliage and fine roots of *C. nepalensis* was 226 and 165% higher than the average concentration in the foliage and fine roots of other shrubs, respectively, across the sites (**Table 2**). Concentration of phosphorus and potassium was more or less in a similar range in comparison to the other shrub species. Concentration of nutrients decreased in the order: N > K > P.

Standing State of Nutrients

Across the sites maximum nutrient (N, P, K) stock was recorded at site 3 (3,171 kg ha^{-1} N, 277 kg ha^{-1} P, and 1,037 kg ha^{-1} K) while the minimum nutrient stock (1,295 kg ha^{-1} N, 93 kg ha^{-1} P, and 433 kg ha^{-1} K) was recorded at site-1 (**Table 3**). In the tree layer, the relative contribution of aboveground components to the standing state of nutrients was generally in the order: Bole wood > Foliage > Branches > Twigs > Bole bark > Reproductive parts and contribution of belowground components was in the order: Stump root > Lateral roots > Fine roots. The order reported in shrubs was: Bole wood > Foliage > Branches > Twigs in aboveground components and Stump root > Lateral roots > Fine roots in belowground components. Herb aboveground parts recorded higher nutrient stock than belowground parts. Among vegetation types, trees contributed 21–51% N, 44–70% P, and 29–50% K; shrubs contributed 20–41% N, 7–9% P, and 22–31% K while herbs contributed 29–46% N, 32–49% P, and 23–44% K to the total vegetation nutrient stock (**Table 3**). The total nitrogen, phosphorus, and potassium content in the soil to a depth of 30 cm ranged from 7150.77 kg ha^{-1} (Site-2) to 12316.17 kg ha^{-1} (Site-3), 640.50 kg ha^{-1} (Site-1) to 812.24 kg ha^{-1} (Site-2), 3043.05 kg ha^{-1} (Site-4) to 3341.56 kg ha^{-1} (Site-2), respectively (**Table 3**). Generally, soil nutrient stock was greater than vegetation nutrient stock.

Retranslocation of Nutrients

The retranslocation of nutrients from senescing foliage, reproductive parts, twigs, and bark is given in **Table 4**. Across the sites, maximum nitrogen, phosphorus, and potassium were retranslocated by leaves (33–35% N, 61–97% P, and 79–81% K) and reproductive parts (30–42% N, 43–87% P, and 78–79% K) whereas minimum retranslocation was reported for bark. The general order of nutrients retranslocated from

TABLE 1 | Mean (± SE) concentration (%) of nitrogen, phosphorus, and potassium in different components of tree layer, shrub layer, herb layer, and soil across the selected sites.

Components		Sites				
		Site-1	Site-2	Site-3	Site-4	Site-5
Nitrogen						
Trees	Bole wood	0.37 ± 0.026	0.39 ± 0.006	0.76 ± 0.285	0.40 ± 0.036	0.76 ± 0.233
	Bole bark	0.07 ± 0.043	0.14 ± 0.065	0.09 ± 0.045	0.15 ± 0.058	0.09 ± 0.040
	Branches	0.52 ± 0.048	0.57 ± 0.065	0.90 ± 0.257	0.55 ± 0.054	0.92 ± 0.200
	Twigs	0.72 ± 0.050	0.79 ± 0.064	1.12 ± 0.258	0.71 ± 0.054	1.08 ± 0.201
	Foliage	1.43 ± 0.080	1.46 ± 0.056	1.70 ± 0.251	1.41 ± 0.062	1.81 ± 0.200
	Reproductive parts	1.68 ± 0.278	1.71 ± 0.318	1.95 ± 0.132	1.59 ± 0.299	2.09 ± 0.157
	Stump root	0.12 ± 0.007	0.14 ± 0.012	0.26 ± 0.086	0.13 ± 0.010	0.28 ± 0.077
	Lateral roots	0.15 ± 0.009	0.19 ± 0.009	0.35 ± 0.129	0.16 ± 0.010	0.35 ± 0.099
	Fine roots	0.16 ± 0.031	0.24 ± 0.006	0.48 ± 0.162	0.21 ± 0.011	0.42 ± 0.139
Shrubs	Bole wood	0.35 ± 0.167	0.76 ± 0.081	0.24 ± 0.126	0.46 ± 0.191	0.26 ± 0.131
	Branches	0.39 ± 0.183	0.83 ± 0.081	0.26 ± 0.135	0.53 ± 0.218	0.27 ± 0.134
	Twigs	0.94 ± 0.066	1.00 ± 0.023	0.82 ± 0.052	0.86 ± 0.078	0.82 ± 0.061
	Foliage	1.50 ± 0.241	1.61 ± 0.597	1.29 ± 0.182	1.43 ± 0.361	1.34 ± 0.194
	Stump root	0.44 ± 0.209	1.15 ± 0.040	0.31 ± 0.159	0.58 ± 0.236	0.38 ± 0.193
	Lateral roots	0.77 ± 0.037	0.94 ± 0.148	0.52 ± 0.264	0.89 ± 0.070	0.57 ± 0.288
	Fine roots	0.85 ± 0.081	1.72 ± 0.081	0.81 ± 0.067	0.98 ± 0.406	0.80 ± 0.071
Herbs	Aboveground	2.14 ± 0.057	2.07 ± 0.050	1.91 ± 0.094	1.82 ± 0.111	2.28 ± 0.095
	Belowground	1.28 ± 0.028	1.05 ± 0.052	1.10 ± 0.087	0.87 ± 0.050	1.39 ± 0.246
Soil	Average up to 0–30 cm	0.24 ± 0.03	0.26 ± 0.05	0.28 ± 0.06	0.33 ± 0.04	0.39 ± 0.04
Phosphorus						
Trees	Bole wood	0.06 ± 0.006	0.07 ± 0.003	0.06 ± 0.010	0.06 ± 0.009	0.06 ± 0.010
	Bole bark	0.01 ± 0.011	0.05 ± 0.025	0.02 ± 0.012	0.03 ± 0.014	0.01 ± 0.007
	Branches	0.09 ± 0.004	0.09 ± 0.003	0.08 ± 0.012	0.08 ± 0.004	0.07 ± 0.010
	Twigs	0.12 ± 0.009	0.09 ± 0.024	0.11 ± 0.008	0.10 ± 0.013	0.11 ± 0.008
	Foliage	0.16 ± 0.020	0.19 ± 0.026	0.14 ± 0.021	0.15 ± 0.017	0.15 ± 0.013
	Reproductive parts	0.15 ± 0.021	0.16 ± 0.027	0.11 ± 0.011	0.14 ± 0.023	0.13 ± 0.017
	Stump root	0.02 ± 0.002	0.02 ± 0.002	0.02 ± 0.008	0.01 ± 0.002	0.03 ± 0.012
	Lateral roots	0.03 ± 0.003	0.03 ± 0.005	0.03 ± 0.009	0.02 ± 0.004	0.02 ± 0.004
	Fine roots	0.11 ± 0.051	0.05 ± 0.002	0.18 ± 0.104	0.03 ± 0.007	0.03 ± 0.006
Shrubs	Bole wood	0.006 ± 0.003	0.015 ± 0.002	0.004 ± 0.002	0.008 ± 0.003	0.005 ± 0.002
	Branches	0.007 ± 0.003	0.018 ± 0.002	0.005 ± 0.003	0.009 ± 0.004	0.006 ± 0.003
	Twigs	0.036 ± 0.007	0.033 ± 0.012	0.031 ± 0.005	0.030 ± 0.007	0.033 ± 0.005
	Foliage	0.054 ± 0.008	0.046 ± 0.016	0.045 ± 0.006	0.043 ± 0.009	0.046 ± 0.007
	Stump root	0.002 ± 0.001	0.025 ± 0.021	0.002 ± 0.001	0.003 ± 0.002	0.006 ± 0.003
	Lateral roots	0.009 ± 0.004	0.007 ± 0.003	0.004 ± 0.001	0.006 ± 0.003	0.013 ± 0.008
	Fine roots	0.008 ± 0.004	0.018 ± 0.001	0.005 ± 0.003	0.011 ± 0.004	0.021 ± 0.003
Herbs	Aboveground	0.189 ± 0.014	0.146 ± 0.004	0.163 ± 0.012	0.152 ± 0.005	0.193 ± 0.038
	Belowground	0.074 ± 0.025	0.047 ± 0.032	0.072 ± 0.005	0.048 ± 0.031	0.068 ± 0.004
Soil	Average up to 0–30 cm	0.018 ± 0.002	0.022 ± 0.002	0.020 ± 0.001	0.021 ± 0.003	0.023 ± 0.003
Potassium						
Trees	Bole wood	0.14 ± 0.008	0.17 ± 0.034	0.15 ± 0.008	0.19 ± 0.029	0.20 ± 0.018
	Bole bark	0.02 ± 0.014	0.05 ± 0.030	0.03 ± 0.018	0.09 ± 0.040	0.07 ± 0.033
	Branches	0.35 ± 0.027	0.34 ± 0.010	0.28 ± 0.029	0.37 ± 0.056	0.32 ± 0.048
	Twigs	0.44 ± 0.032	0.52 ± 0.053	0.40 ± 0.032	0.54 ± 0.065	0.44 ± 0.064
	Foliage	0.70 ± 0.042	0.76 ± 0.038	0.64 ± 0.034	0.74 ± 0.078	0.66 ± 0.081
	Reproductive parts	0.94 ± 0.106	1.11 ± 0.050	0.92 ± 0.020	1.02 ± 0.112	1.18 ± 0.061
	Stump root	0.06 ± 0.008	0.06 ± 0.013	0.09 ± 0.033	0.13 ± 0.077	0.17 ± 0.059
	Lateral roots	0.08 ± 0.009	0.10 ± 0.006	0.14 ± 0.039	0.08 ± 0.028	0.14 ± 0.036
	Fine roots	0.11 ± 0.022	0.17 ± 0.006	0.16 ± 0.041	0.13 ± 0.041	0.17 ± 0.045
Shrubs	Bole wood	0.12 ± 0.055	0.30 ± 0.065	0.10 ± 0.056	0.14 ± 0.058	0.08 ± 0.040

(Continued)

TABLE 1 | (Continued)

Components		Sites				
		Site-1	Site-2	Site-3	Site-4	Site-5
	Branches	0.17 ± 0.079	0.38 ± 0.065	0.10 ± 0.051	0.18 ± 0.071	0.10 ± 0.049
	Twigs	0.38 ± 0.037	0.34 ± 0.057	0.31 ± 0.018	0.32 ± 0.039	0.33 ± 0.033
	Foliage	0.48 ± 0.033	0.48 ± 0.045	0.45 ± 0.022	0.44 ± 0.034	0.48 ± 0.032
	Stump root	0.14 ± 0.067	0.30 ± 0.014	0.12 ± 0.060	0.16 ± 0.093	0.13 ± 0.064
	Lateral roots	0.18 ± 0.085	0.33 ± 0.049	0.16 ± 0.080	0.25 ± 0.104	0.14 ± 0.071
	Fine roots	0.30 ± 0.027	0.41 ± 0.006	0.28 ± 0.026	0.29 ± 0.039	0.28 ± 0.023
Herbs	Aboveground	0.54 ± 0.106	0.63 ± 0.067	0.84 ± 0.049	0.68 ± 0.053	0.92 ± 0.036
	Belowground	0.32 ± 0.011	0.23 ± 0.003	0.25 ± 0.028	0.24 ± 0.042	0.36 ± 0.051
Soil	Average up to 0–30 cm	0.085 ± 0.001	0.089 ± 0.003	0.088 ± 0.003	0.090 ± 0.002	0.094 ± 0.002

litter to soil was K > P > N whereas the order for nutrient retranslocation by litter components was: Reproductive parts > Foliage > Twigs > Bark for nitrogen.

Nutrient Uptake

The uptake of nitrogen, phosphorus, and potassium by total vegetation ranged from 428.22 to 1352.95 kg ha^{-1} yr^{-1}, 31.66 to 102.27 kg ha^{-1} yr^{-1}, and 109.26 to 479.60 kg ha^{-1} yr^{-1}, respectively (**Table 5**). After the adjustment for internal cycling, the uptake of nitrogen, phosphorus, and potassium ranged from 427.00 to 1334.14 kg ha^{-1} yr^{-1}, 31.296 to 99.383 kg ha^{-1} yr^{-1}, and 107.87 to 872.81 kg ha^{-1} yr^{-1}1, respectively to the total vegetation (**Table 5**). Among the aboveground parts of the trees, the order of uptake was: Bole wood > Foliage > Branches > Twigs > Reproductive parts > Bole bark while among the belowground parts of the trees, the maximum uptake of N was reported for stump root followed by lateral roots and fine roots (**Table 5**). In shrubs, the uptake by aboveground components was generally in the order: Foliage > Bole wood > Twigs > Branches whereas in belowground components the order was: Fine roots < Lateral roots < Stump root (**Table 5**).

Nutrient Return Through Litter Fall

Average nutrient concentration across seasons in various litter components is given in **Table 6**. Concentration of nutrients

TABLE 2 | Mean nutrient concentration (Mean ± SE) (N, P, and K) in different components of *C. nepalensis* of 3 CBH classes (0–20, 20–40, and above 40 cm) of harvested sample (*n* = 3) across the sites.

Components	Nutrients		
	Nitrogen (%)	Phosphorus (%)	Potassium (%)
Bole wood	0.73 ± 0.023	0.013 ± 0.0003	0.22 ± 0.009
Branches	0.78 ± 0.012	0.015 ± 0.0004	0.27 ± 0.014
Twigs	0.89 ± 0.028	0.017 ± 0.0006	0.34 ± 0.022
Foliage	2.81 ± 0.015	0.018 ± 0.0006	0.48 ± 0.001
Stump roots	1.06 ± 0.037	0.005 ± 0.0000	0.36 ± 0.018
Lateral roots	1.24 ± 0.038	0.014 ± 0.0006	0.40 ± 0.012
Fine roots	1.72 ± 0.027	0.018 ± 0.0001	0.44 ± 0.021

in different litter components in diminishing order was: N > K > P, so the return of nitrogen to the floor was more in comparison to phosphorus and potassium. Maximum nutrient concentration was in foliage followed by miscellaneous litter, reproductive parts, twigs, and bark. Contribution of foliage to the nutrient return on soil was the maximum as compare to other components (**Table 7**). The amount of nitrogen, phosphorus and potassium returned by the total vegetation ranged from 395.90 (Site-1) to 1236.57 kg ha^{-1} yr^{-1} (Site-5), 30.12 (Site-1 and 2) to 91.37 kg ha^{-1} yr^{-1} (Site-5), and 98.61(Site-1) to 441.17 kg ha^{-1} yr^{-1} (Site-5), respectively. In comparison to the shrubs and trees, the return through herbs was maximum (**Table 7**).

Turnover for Nutrients on the Forest Floor

The values for the turnover rate (k, year^{-1}) and time (t, years) for nitrogen (N), phosphorus (P), and potassium (K) for different litter components across the selected sites are given in **Table 6**. In comparison to nitrogen and phosphorus, turnover rate for potassium was higher (N < P < K) (**Table 8**).

Percent Nutrient Retranslocation Efficiency

Percentage nutrient retranslocation efficiency for different litter components showed that, if the values were positive then it was capable of retranslocation of its nutrients before litter fall and if negative values were reported for PNRE then it could be interpreted that its nutrients were retained in the respective senescing components before falling on the soil. Potassium showed the highest PNRE among N, P, and K for all the components of litter fall (**Table 9**). The order of components on the basis of their PNRE was: Foliage > Reproductive parts > Twigs > Bark.

Nutrient Use Efficiency

Nutrient use efficiency (NUE) depends on the ability of efficient uptake of nutrients from soil by different components and also on their ability to store and use the nutrients. It also depends on transport, storage, mobilization, and usage within the plant, and even on the environment. The order

TABLE 3 | Nutrient content (kg ha^{-1}) in different layers of vegetation across the selected study sites (values in parenthesis are percentage of the total).

Components		Sites				
		Site-1	Site-2	Site-3	Site-4	Site-5
Nitrogen content						
Trees	Bole wood	119.72 (26.97)	156.29 (44.49)	467.79 (28.43)	142.76 (34.03)	234.24 (35.39)
	Bole bark	0.62 (0.14)	0.15 (0.04)	8.45 (0.51)	14.82 (3.53)	15.13 (2.29)
	Branches	102.83 (23.17)	72.31 (20.58)	392.08 (23.83)	108.23 (25.80)	159.51 (24.10)
	Twigs	59.35 (13.37)	33.16 (20.58)	236.23 (14.36)	56.12 (13.38)	77.93 (11.78)
	Foliage	138.69 (31.25)	60.68 (17.27)	431.39 (26.22)	67.15 (16.01)	120.03 (18.14)
	Reproductive parts	0.02 (0.001)	2.27 (0.65)	0.02 (0.001)	0.001 (0.0001)	0.60 (0.09)
	Stump root	17.04 (3.84)	17.75 (5.05)	82.68 (5.03)	19.42 (4.63)	35.20 (5.32)
	Lateral roots	5.15 (1.16)	5.71 (1.62)	23.41 (1.42)	8.43 (2.01)	14.89 (2.25)
	Fine roots	0.40 (0.09)	2.96 (0.84)	3.25 (0.20)	2.53 (0.60)	4.31 (0.65)
	Total	443.82	351.28	1645.30	419.45	661.85
Shrubs	Bole wood	133.25 (29.02)	185.11 (31.90)	178.31 (30.83)	196.06 (29.75)	240.99 (30.28)
	Branches	89.75 (19.55)	105.57 (18.19)	118.22 (20.44)	132.71 (20.13)	154.37 (19.40)
	Twigs	29.54 (6.43)	39.70 (6.84)	36.30 (6.28)	40.64 (6.17)	45.17 (5.68)
	Foliage	127.23 (27.71)	156.16 (26.91)	172.54 (29.83)	192.05 (29.14)	225.38 (28.32)
	Stump root	27.49 (5.99)	34.03 (5.86)	35.52 (6.14)	35.88 (5.44)	49.91 (6.27)
	Lateral roots	33.26 (7.24)	38.58 (6.65)	15.13 (2.62)	39.43 (5.98)	52.13 (6.55)
	Fine roots	18.63 (4.06)	21.12 (3.64)	22.31 (3.86)	22.33 (3.39)	27.79 (3.49)
	Total	459.15	580.26	578.34	659.10	795.75
Herbs	Aboveground	237.20 (60.39)	557.80 (67.64)	608.60 (64.24)	390.10 (75.81)	844.50 (68.77)
	Belowground	155.60 (39.61)	266.80 (32.36)	338.80 (35.76)	124.50 (24.19)	383.50 (31.23)
	Total	392.80	824.60	947.40	514.60	1228.00
Total vegetation		1295.77	1756.14	3171.03	1593.16	2685.60
Soil	Average up to 0–30 cm	9160.2	7150.8	12316.2	10581.1	11995.4
Phosphorus content						
Trees	Bole wood	15.01 (26.53)	27.08 (51.13)	52.82 (26.89)	23.70 (39.58)	29.81 (37.39)
	Bole bark	0.18 (0.32)	0.06 (0.10)	1.62 (0.82)	1.98 (3.31)	0.89 (1.11)
	Branches	15.46 (27.34)	10.67 (20.15)	44.60 (22.71)	15.78 (26.35)	20.80 (26.09)
	Twigs	8.60 (15.20)	3.89 (7.35)	28.06 (14.29)	8.00 (13.36)	9.85 (12.35)
	Foliage	12.30 (21.74)	7.06 (13.34)	57.49 (29.27)	7.14 (11.92)	13.14 (16.47)
	Reproductive parts	0.00 (0.00)	0.18 (0.33)	0.01 (0.01)	0.0001 (0.00)	0.05 (0.06)
	Stump root	3.97 (7.03)	2.11 (3.99)	7.29 (3.71)	1.92 (3.21)	3.19 (3.99)
	Lateral roots	0.92 (1.62)	1.14 (2.15)	2.97 (1.51)	1.06 (1.77)	1.47 (1.85)
	Fine roots	0.13 (0.23)	0.77 (1.45)	1.53 (0.78)	0.29 (0.48)	0.55 (0.68)
	Total	56.57	52.97	196.39	59.87	79.74
Shrubs	Bole wood	2.69 (41.29)	2.90 (38.13)	3.72 (50.95)	3.70 (41.02)	4.25 (38.13)
	Branches	1.63 (25.04)	2.12 (27.83)	1.88 (25.81)	2.25 (24.90)	2.96 (26.57)
	Twigs	0.53 (8.10)	0.71 (9.31)	0.24 (3.34)	0.70 (7.78)	1.01 (9.05)
	Foliage	0.96 (14.71)	1.09 (14.33)	1.03 (14.08)	1.34 (14.90)	1.73 (15.50)
	Stump root	0.15 (2.35)	0.16 (2.06)	0.33 (4.56)	0.19 (2.12)	0.33 (3.00)
	Lateral roots	0.37 (5.66)	0.41 (5.33)	0.06 (0.86)	0.59 (6.49)	0.57 (5.11)
	Fine roots	0.19 (2.86)	0.22 (2.96)	0.03 (0.44)	0.25 (2.78)	0.30 (2.65)
	Total	6.52	7.60	7.30	9.02	11.15
Herbs	Aboveground	21.00 (69.77)	39.30 (76.91)	52.00 (70.27)	32.60 (82.74)	71.50 (79.27)
	Belowground	9.10 (30.23)	11.80 (23.09)	22.00 (29.73)	6.80 (17.26)	18.70 (20.73)
	Total	30.10	51.10	74.00	39.40	90.20
Total vegetation		93.19	111.66	277.69	108.29	181.09
Soil	Average up to 0–30 cm	640.5	812.2	663.3	638.2	706.3
Potassium content						
Trees	Bole wood	33.24 (16.53)	53.54 (33.88)	114.37 (21.99)	53.72 (22.63)	116.04 (34.37)
	Bole bark	0.18 (0.09)	0.06 (0.04)	3.51 (0.68)	12.00 (5.05)	11.67 (3.46)
	Branches	66.50 (33.08)	38.78 (24.53)	127.98 (24.61)	76.89 (32.39)	93.80 (27.78)

(Continued)

TABLE 3 | (Continued)

Components		Sites				
		Site-1	Site-2	Site-3	Site-4	Site-5
	Twigs	32.51 (16.17)	22.95 (14.52)	85.76 (16.49)	45.25 (19.06)	37.01 (10.96)
	Foliage	57.67 (28.69)	28.61 (18.11)	157.81 (30.35)	35.25 (14.85)	44.96 (13.32)
	Reproductive parts	0.001 (0.00)	0.35 (0.22)	0.03 (0.00)	0.01 (0.00)	0.07 (0.02)
	Stump root	7.77 (3.87)	8.59 (5.44)	21.92 (4.22)	9.64 (4.06)	20.39 (6.04)
	Lateral roots	2.87 (1.43)	2.88 (1.82)	7.14 (1.37)	3.41 (1.44)	9.37 (2.77)
	Fine roots	0.28 (0.14)	2.29 (1.45)	1.46 (0.28)	1.21 (0.51)	4.33 (1.28)
	Total	201.02	158.05	519.98	237.37	337.63
Shrubs	Bole wood	45.40 (33.83)	51.15 (31.72)	60.62 (34.86)	58.35 (32.40)	68.13 (32.24)
	Branches	29.66 (22.10)	42.16 (26.15)	44.33 (25.49)	41.03 (22.78)	47.84 (22.64)
	Twigs	12.83 (9.56)	15.32 (9.50)	13.76 (7.91)	13.46 (7.47)	15.81 (7.48)
	Foliage	23.21 (17.30)	26.62 (16.51)	30.07 (17.29)	33.42 (18.56)	39.43 (18.65)
	Stump root	8.84 (6.58)	9.10 (5.64)	13.25 (7.62)	14.02 (7.79)	16.80 (7.95)
	Lateral roots	9.90 (7.38)	11.85 (7.35)	5.10 (2.93)	14.03 (7.79)	16.50 (7.81)
	Fine roots	4.36 (3.25)	5.06 (3.14)	6.78 (3.90)	5.79 (3.21)	6.83 (3.23)
	Total	134.20	161.26	173.91	180.10	211.34
Herbs	Aboveground	59.61 (60.66)	170.40 (74.83)	268.18 (78.04)	146.00 (81.29)	341.19 (77.59)
	Belowground	38.66 (39.34)	57.30 (25.17)	75.46 (21.96)	33.60 (18.71)	98.55 (22.41)
	Total	98.27	227.70	343.64	179.60	439.74
Total vegetation		433.49	547.01	1037.53	597.07	988.70
Soil	Average up to 0–30 cm	3273.6	3341.6	3041.2	3043.1	2871.4

TABLE 4 | Percentage retranslocation of nutrient from different plant parts during senescence.

Components	Nutrients	Sites				
		Site-1	Site-2	Site-3	Site-4	Site-5
Foliage	N	33.61	34.31	34.26	34.55	34.56
	P	97.36	75.25	74.7	61.82	64.35
	K	79.58	81.49	80.71	82.43	80.67
Reproductive parts	N	39.18	41.52	42.58	40.69	30.5
	P	87.07	43.41	66.79	56.43	62.74
	K	79.46	78.28	78.74	78.12	79.09
Twigs	N	25.04	18.19	26.28	25.5	36.38
	P	57.64	47.11	62.44	58.8	66.6
	K	76.72	58.71	77.63	80.1	77.66
Bark	N	6.45	29.32	13.8	8.01	11.42
	P	88.52	30.9	69.64	72.09	58.34
	K	75.24	56.14	76.5	82.05	74.18

of nutrients was: P > K > N and order of the components was: Twigs > Foliage > Bark > Miscellaneous < Reproductive parts (**Table 10**).

Nutrient Cycling

The direction of nutrient flux from soil to foliage or reproductive parts indicates a one-way movement, although it is well realized that the nutrients are utilized by the foliage in organic matter synthesis and that they are redistributing among different components at varying rates giving rise to internal recycling. The comparison of compartmental models (**Figures 1–5**) of different sites is described as follows;

The total quantity of nutrient stored in vegetation varied from site to site. Of the total nutrient 20.00–51.89% N, 44.03–60.70% P, and 28.89–50.12% K is distributed in the tree layer, 18.24–41.37% N, 2.63–8.33% P, and 16.76–30.96% K is distributed in the shrub layer and 29.88–46.96% N, 26.65–49.81% P, and 22.67–44.48% K is distributed in the herb layer. The allocation of uptake of N, P, and K in trees varied from 0.97 to 5.57%, 2.65 to 11.07%, and 1.72 to 5.19%, respectively. In shrubs, the uptake of N, P, and K varied from 3.69 to 8.28%, 0.59 to 1.29%, and 3.02 to 5.99%, respectively. In herbs the uptake of N, P, and K varied from 88.89 to 95.34%, 88.43 to 96.75%, and 89.63 to 95.26%, respectively.

TABLE 5 | The uptake of nutrient (kg ha^{-1} yr^{-1}) by different layers of vegetation across the selected sites (values in parenthesis are the percentage contribution).

Components		Sites				
		Site-1	Site-2	Site-3	Site-4	Site-5
Nitrogen						
Trees	Bole wood	3.010 (31.81)	2.874 (34.15)	21.245 (36.59)	4.705 (28.73)	16.576 (26.90)
	Bole bark	0.011 (0.12)	0.008 (0.10)	0.288 (0.50)	0.322 (1.97)	0.243 (0.39)
	Branches	2.138 (22.60)	2.514 (29.87)	14.636 (25.20)	3.422 (20.90)	14.044 (22.79)
	Twigs	1.073 (11.34)	0.831 (9.87)	5.975 (10.29)	1.369 (8.36)	5.877 (9.54)
	Foliage	2.806 (29.66)	1.631 (19.38)	7.689 (13.24)	5.870 (35.84)	20.989 (34.07)
	Reproductive parts	0.020 (0.21)	0.011 (0.13)	0.010 (0.02)	0.010 (0.06)	0.060 (0.10)
	Stump root	0.336 (3.55)	0.409 (4.86)	7.603 (13.09)	0.479 (2.92)	3.151 (5.11)
	Lateral roots	0.064 (0.68)	0.105 (1.25)	0.482 (0.83)	0.153 (0.93)	0.624 (1.01)
	Fine roots	0.004 (0.04)	0.034 (0.40)	0.141 (0.24)	0.047 (0.29)	0.050 (0.08)
	Total	9.46	8.42	58.70	16.38	61.61
Shrubs	Bole wood	3.52 (13.57)	2.62 (8.22)	10.87 (23.12)	8.51 (17.74)	11.69 (18.45)
	Branches	1.35 (5.20)	1.21 (3.79)	5.02 (10.69)	5.36 (11.18)	6.70 (10.58)
	Twigs	4.06 (15.63)	4.67 (14.64)	4.35 (9.26)	5.70 (11.88)	7.06 (11.14)
	Foliage	14.79 (56.99)	20.29 (63.66)	23.15 (49.25)	24.89 (51.90)	32.79 (51.76)
	Stump root	0.26 (1.01)	0.25 (0.78)	0.89 (1.89)	0.88 (1.83)	1.28 (2.02)
	Lateral roots	0.18 (0.69)	0.79 (2.46)	0.82 (1.74)	0.56 (1.17)	1.04 (1.65)
	Fine roots	1.80 (6.92)	2.06 (6.45)	1.90 (4.05)	2.06 (4.29)	2.79 (4.40)
	Total	25.96	31.87	47.00	47.96	63.34
Herbs	Aboveground	237.20 (60.39)	557.80 (67.64)	608.60 (64.24)	390.10 (75.81)	844.50 68.77)
	Belowground	155.60 (39.61)	266.80 (31.81)	338.80 (35.76)	124.50 (24.19)	383.50 (31.23)
	Total	392.80	824.60	947.40	514.60	1228.00
Total vegetation		428.22	864.89	1053.1	578.94	1352.95
After adjustment for retranslocation		427.00	864.17	1048.22	576.54	1334.14
Phosphorus						
Trees	Bole wood	0.412 (32.19)	0.545 (38.87)	1.945 (25.36)	0.706 (32.79)	3.851 (34.12)
	Bole bark	0.003 (0.23)	0.003 (0.21)	0.081 (1.06)	0.035 (1.63)	0.013 (0.12)
	Branches	0.355 (27.73)	0.463 (33.02)	1.285 (16.75)	0.484 (22.48)	2.688 (23.82)
	Twigs	0.168 (13.13)	0.102 (7.28)	0.488 (6.36)	0.245 (11.38)	1.243 (11.01)
	Foliage	0.268 (20.94)	0.224 (15.98)	0.924 (12.05)	0.615 (28.56)	3.183 (28.20)
	Reproductive parts	0.002 (0.16)	0.001 (0.07)	0.002 (0.03)	0.001 (0.05)	0.001 (0.01)
	Stump root	0.060 (4.69)	0.037 (2.64)	2.833 (36.93)	0.050 (2.32)	0.261 (2.31)
	Lateral roots	0.010 (0.78)	0.018 (1.28)	0.053 (0.69)	0.014 (0.65)	0.041 (0.36)
	Fine roots	0.001 (0.08)	0.009 (0.64)	0.059 (0.77)	0.004 (0.19)	0.006 (0.05)
	Total	1.280	1.402	7.671	2.153	11.287
Shrubs	Bole wood	0.069 (24.87)	0.041 (12.98)	0.229 (38.01)	0.158 (29.08)	0.207 (26.53)
	Branches	0.025 (8.83)	0.024 (7.73)	0.094 (15.56)	0.091 (16.72)	0.129 (16.49)
	Twigs	0.073 (26.10)	0.083 (26.56)	0.088 (14.67)	0.098 (18.13)	0.158 (20.22)
	Foliage	0.091 (32.68)	0.133 (42.59)	0.159 (26.37)	0.160 (29.38)	0.238 (30.48)
	Stump root	0.001 (0.51)	0.001 (0.36)	0.004 (0.75)	0.005 (0.88)	0.006 (0.77)
	Lateral roots	0.002 (0.72)	0.008 (2.64)	0.008 (1.40)	0.008 (1.54)	0.013 (1.71)
	Fine roots	0.018 (6.46)	0.022 (6.99)	0.020 (3.32)	0.023 (4.25)	0.030 (3.80)
	Total	0.278	0.313	0.603	0.543	0.780
Herbs	Aboveground	21.00 (69.77)	39.30 (76.91)	52.00 (70.27)	32.60 (82.74)	71.50 (79.27)
	Belowground	9.10 (30.23)	11.80 (23.09)	22.00 (29.73)	6.80 (17.26)	18.70 (20.73)
	Total	30.10	51.10	74.00	39.40	90.20
Total vegetation		31.658	52.815	82.274	42.096	102.267
After adjustment for retranslocation		31.296	52.629	81.222	41.547	99.383
Potassium						
Trees	Bole wood	0.963 (21.69)	1.230 (29.83)	4.192 (25.57)	2.060 (21.98)	8.434 (33.88)
	Bole bark	0.003 (0.07)	0.003 (0.07)	0.114 (0.70)	0.248 (2.65)	0.177 (0.71)
	Branches	1.529 (34.44)	1.448 (35.12)	4.487 (27.37)	2.538 (27.08)	6.881 (27.64)

(Continued)

TABLE 5 | (Continued)

Components		Site-1	Site-2	Site-3	Site-4	Site-5
		Site-1	**Site-2**	**Site-3**	**Site-4**	**Site-5**
	Twigs	0.634 (14.28)	0.581 (14.09)	1.831 (11.17)	1.137 (12.13)	2.200 (8.84)
	Foliage	1.137 (25.61)	0.669 (16.23)	2.975 (18.15)	2.655 (28.33)	6.131 (24.63)
	Reproductive parts	0.001 (0.02)	0.002 (0.05)	0.001 (0.01)	0.001 (0.01)	0.001 (0.01)
	Stump root	0.137 (3.09)	0.119 (2.89)	2.555 (15.58)	0.609 (6.50)	0.798 (3.21)
	Lateral roots	0.032 (0.72)	0.045 (1.09)	0.169 (1.03)	0.088 (0.94)	0.207 (0.83)
	Fine roots	0.003 (0.07)	0.026 (0.63)	0.071 (0.43)	0.037 (0.39)	0.066 (0.27)
	Total	4.44	4.12	16.39	9.37	24.90
Shrubs	Bole wood	1.19 (18.21)	0.72 (10.00)	3.87 (30.98)	2.52 (22.11)	3.30 (22.09)
	Branches	0.45 (6.81)	0.48 (6.68)	1.88 (15.10)	1.66 (14.55)	2.08 (13.88)
	Twigs	1.76 (26.90)	1.80 (24.94)	1.65 (13.22)	1.89 (16.55)	2.47 (16.51)
	Foliage	2.59 (39.58)	3.41 (47.24)	3.89 (31.17)	4.25 (37.28)	5.66 (37.82)
	Stump root	0.08 (1.27)	0.07 (0.91)	0.33 (2.67)	0.35 (3.06)	0.51 (3.41)
	Lateral roots	0.05 (0.82)	0.24 (3.34)	0.28 (2.21)	0.20 (1.76)	0.25 (1.70)
	Fine roots	0.42 (6.41)	0.49 (6.82)	0.58 (4.63)	0.53 (4.68)	0.68 (4.58)
	Total	6.55	7.22	12.48	11.40	14.96
Herbs	Aboveground	59.61 (60.66)	170.40 (74.84)	268.18 (78.04)	146.00 (81.29)	341.19 (77.59)
	Belowground	38.66 (39.34)	57.30 (25.17)	75.46 (21.96)	33.60 (18.71)	98.55 (22.41)
	Total	98.27	227.70	343.64	179.60	439.74
Total vegetation		109.26	239.04	372.51	200.37	479.60
After adjustment for retranslocation		107.865	238.148	368.969	197.067	472.81

TABLE 6 | Average concentration of nutrients (%) in different components in litter across seasons for the selected sites.

Components		Site-1	Site-2	Site-3	Site-4	Site-5
		Site-1	**Site-2**	**Site-3**	**Site-4**	**Site-5**
Nitrogen						
Tree	Foliage	1.43 ± 0.080	1.46 ± 0.056	1.70 ± 0.251	1.41 ± 0.062	1.81 ± 0.200
Shrub	Foliage	1.114 ± 0.075	1.270 ± 0.037	1.078 ± 0.037	1.266 ± 0.036	1.333 ± 0.039
	Reproductive parts	0.967 ± 0.040	1.076 ± 0.044	0.998 ± 0.043	0.963 ± 0.096	1.130 ± 0.046
	Twigs	0.380 ± 0.030	0.423 ± 0.034	0.435 ± 0.049	0.463 ± 0.066	0.445 ± 0.035
	Bark	0.285 ± 0.031	0.317 ± 0.035	0.305 ± 0.016	0.249 ± 0.034	0.333 ± 0.036
	Miscellaneous	0.984 ± 0.082	1.095 ± 0.092	1.239 ± 0.057	1.105 ± 0.010	1.150 ± 0.096
Herb	Foliage	2.14 ± 0.057	2.07 ± 0.050	1.91 ± 0.094	1.82 ± 0.111	2.28 ± 0.095
Phosphorus						
Trees	Foliage	0.16 ± 0.020	0.19 ± 0.026	0.14 ± 0.021	0.15 ± 0.017	0.15 ± 0.013
Shrub	Foliage	0.023 ± 0.006	0.024 ± 0.008	0.022 ± 0.006	0.026 ± 0.007	0.024 ± 0.007
	Reproductive parts	0.027 ± 0.005	0.028 ± 0.005	0.026 ± 0.005	0.028 ± 0.005	0.029 ± 0.006
	Twigs	0.029 ± 0.001	0.030 ± 0.006	0.027 ± 0.001	0.031 ± 0.002	0.031 ± 0.001
	Bark	0.018 ± 0.003	0.019 ± 0.003	0.018 ± 0.003	0.020 ± 0.003	0.020 ± 0.003
	Miscellaneous	0.031 ± 0.003	0.033 ± 0.003	0.038 ± 0.003	0.034 ± 0.003	0.034 ± 0.003
Herb	Foliage	0.189 ± 0.014	0.146 ± 0.004	0.163 ± 0.012	0.152 ± 0.005	0.193 ± 0.038
Potassium						
Tree	Foliage	0.70 ± 0.042	0.76 ± 0.038	0.64 ± 0.034	0.74 ± 0.078	0.66 ± 0.081
Shrub	Foliage	0.209 ± 0.009	0.220 ± 0.010	0.203 ± 0.009	0.225 ± 0.010	0.236 ± 0.011
	Reproductive parts	0.184 ± 0.004	0.194 ± 0.004	0.179 ± 0.004	0.197 ± 0.005	0.208 ± 0.004
	Twigs	0.089 ± 0.004	0.094 ± 0.005	0.086 ± 0.005	0.094 ± 0.004	0.100 ± 0.006
	Bark	0.095 ± 0.005	0.098 ± 0.010	0.091 ± 0.010	0.074 ± 0.005	0.106 ± 0.011
	Miscellaneous	0.199 ± 0.005	0.209 ± 0.006	0.193 ± 0.005	0.215 ± 0.006	0.225 ± 0.006
Herb	Foliage	0.54 ± 0.106	0.63 ± 0.067	0.84 ± 0.049	0.68 ± 0.053	0.92 ± 0.036

TABLE 7 | Amount of nutrient return (kg ha^{-1} yr^{-1}) by tree, shrub, and herb layer litter fall (values in the parenthesis are the percentage contribution).

Categories		Sites				
		Site-1	Site-2	Site-3	Site-4	Site-5
Nitrogen						
Trees	Aboveground	1.86 (99.63)	1.07 (96.49)	5.06 (97.21)	3.84 (98.77)	6.48 (99.26)
	Belowground	0.01 (0.21)	0.03 (3.06)	0.14 (2.71)	0.05 (1.21)	0.05 (0.77)
	Total	1.87	1.11	5.20	3.89	6.53
Shrubs	Foliage	0.91 (73.84)	1.09 (74.63)	0.96 (69.67)	1.11 (68.83)	1.42 (69.44)
	Reproductive parts	0.04 (3.42)	0.03 (2.17)	0.04 (3.01)	0.04 (2.69)	0.09 (4.47)
	Twigs	0.25 (20.18)	0.29 (20.10)	0.24 (17.72)	0.33 (20.69)	0.36 (17.80)
	Bark	0.02 (1.74)	0.02 (1.26)	0.03 (1.88)	0.02 (1.31)	0.04 (1.74)
	Total aboveground	1.22 (99.19)	1.43 (98.16)	1.27 (92.29)	1.51 (93.53)	1.91 (93.45)
	Total belowground	0.01 (0.65)	0.03 (1.92)	0.11 (7.68)	0.10 (6.21)	0.13 (6.57)
	Total	1.23	1.46	1.38	1.61	2.04
Herbs	Aboveground	237.20 (60.39)	557.80 (67.64)	608.60 (64.24)	390.10 (75.81)	844.50 (68.77)
	Belowground	155. 60 (39.61)	266.80 (32.36)	338.80 (35.76)	124.50 (24.19)	383.50 (31.23)
	Total	392.80	824.60	947.40	514.60	1228.00
Total vegetation		395.90	827.17	953.98	520.09	1236.57
Phosphorus						
Trees	Aboveground	0.007 (87.50)	0.055 (85.94)	0.234 (79.86)	0.235 (98.33)	1.135 (99.56)
	Belowground	0.001 (12.50)	0.009 (14.06)	0.059 (20.14)	0.004 (1.67)	0.006 (0.53)
	Total	0.0080	0.0640	0.2930	0.2390	1.1410
Shrubs	Foliage	0.0080 (46.23)	0.0091 (39.41)	0.0082 (45.05)	0.0144 (51.25)	0.0172 (52.41)
	Reproductive parts	0.0002 (1.35)	0.0008 (3.47)	0.0006 (3.45)	0.0008 (2.98)	0.0013 (3.92)
	Twigs	0.0086 (49.66)	0.0117 (50.38)	0.0077 (41.94)	0.0113 (40.37)	0.0117 (35.79)
	Bark	0.0002 (1.04)	0.0012 (5.33)	0.0006 (3.44)	0.0004 (1.57)	0.0011 (3.50)
	Total aboveground	0.0171 (98.28)	0.0229 (98.59)	0.0172 (93.89)	0.0270 (96.18)	0.0314 (95.64)
	Total belowground	0.0003 (1.72)	0.0003 (1.29)	0.0011 (6.01)	0.0011 (3.91)	0.0014 (4.27)
	Total	0.017	0.023	0.018	0.028	0.033
Herbs	Aboveground	21.00 (69.77)	39.30 (76.91)	52.00 (70.27)	32.60 (82.74)	71.50 (79.27)
	Belowground	9.10 (30.23)	11.80 (23.09)	22.00 (29.73)	6.80 (17.26)	18.70 (20.73)
	Total	30.10	51.10	74.00	39.40	90.20
Total vegetation		30.12	51.19	74.31	39.67	91.37
Potassium						
Trees	Aboveground	0.232 (98.72)	0.124 (82.67)	0.574 (88.99)	0.467 (92.66)	1.185 (94.72)
	Belowground	0.003 (1.28)	0.026 (17.33)	0.071 (11.01)	0.037 (7.34)	0.066 (5.28)
	Total	0.235	0.150	0.645	0.504	1.251
Shrubs	Foliage	0.066 (63.81)	0.072 55.13)	0.066 (52.25)	0.070 (54.68)	0.098 (54.39)
	Reproductive parts	0.003 (3.35)	0.003 (2.18)	0.004 (2.94)	0.004 (3.03)	0.007 (3.68)
	Twigs	0.023 (21.94)	0.043 33.15)	0.022 (17.13)	0.026 (20.37)	0.037 (20.65)
	Bark	0.003 (2.74)	0.006 (4.33)	0.004 (2.77)	0.002 (1.60)	0.005 (2.84)
	Total aboveground	0.095 (91.83)	0.124 94.78)	0.095 (75.08)	0.102 (79.68)	0.148 (81.56)
	Total belowground	0.008 (7.77)	0.007 (5.34)	0.032 (24.92)	0.026 (20.32)	0.033 (18.44)
	Total	0.103	0.131	0.127	0.128	0.181
Herbs	Aboveground	59.61 (60.66)	170.40 (74.84)	268.18 78.04)	146.00 (81.29)	341.19 (77.59)
	Belowground	38.66 (39.34)	57.30 (25.16)	75.46 (21.96)	33.60 (18.71)	98.55 (22.41)
	Total	98.27	227.70	343.64	179.60	439.7
Total vegetation		98.61	227.98	344.41	180.23	441.17

DISCUSSION

Concentration of Nutrients

The concentration of the nutrient in the plant parts depends upon the nutrient stock in the soil and their available form to the plant. Further, the concentration may vary among different plant components and age of the plants and their growth phase. The order of concentration of nutrients in the various components varied significantly and was highest for N followed by K and P. The foliage to root nutrient concentration ratio ranged between 1.20 and 2.09 (**Table 2**) which is within the range reported for high altitude shrubs of central Himalaya (Garkoti, 1996). The low leaf:root nutrient concentration and accumulation of nutrients in perennial parts suggested the nutrient conservation strategy of *C. nepalensis*. Highest concentration in foliage and fine roots are due to their higher metabolic activity. The present

TABLE 8 | Turnover rate (k, yr^{-1}) and turnover time (t, year) of the nutrients on the shrub floor across selected sites.

Nutrients	Components	Site-1		Site-2		Site-3		Site-4		Site-5	
		k	T	k	t	k	t	k	t	k	t
Nitrogen	Foliage	0.87	1.15	0.84	1.19	0.78	1.28	0.75	1.33	0.79	1.27
	Reproductive parts	0.90	1.11	0.81	1.24	0.78	1.29	0.91	1.10	0.87	1.14
	Twigs	0.93	1.08	0.91	1.09	0.89	1.13	0.88	1.14	0.90	1.11
	Bark	0.94	1.07	0.94	1.06	0.90	1.11	0.84	1.19	0.75	1.33
Phosphorus	Foliage	0.87	1.15	0.93	1.07	0.91	1.10	0.95	1.05	0.91	1.09
	Reproductive parts	0.93	1.08	0.97	1.03	0.94	1.06	0.94	1.06	0.87	1.14
	Twigs	0.91	1.10	0.95	1.06	0.91	1.10	0.94	1.06	0.93	1.08
	Bark	0.92	1.09	0.96	1.04	0.90	1.11	0.90	1.11	0.94	1.06
Potassium	Foliage	0.94	1.07	0.98	1.02	0.96	1.04	0.95	1.05	0.94	1.07
	Reproductive parts	0.93	1.08	0.96	1.04	0.97	1.03	0.94	1.06	0.95	1.05
	Twigs	0.97	1.03	0.95	1.05	0.93	1.08	0.96	1.04	0.96	1.04
	Bark	0.96	1.04	0.98	1.02	0.96	1.04	0.88	1.13	0.94	1.06

TABLE 9 | Percent nutrient retranslocation efficiency (%) at different selected sites for different litter components.

Nutrients	Components	Site-1	Site-2	Site-3	Site-4	Site-5
Nitrogen	Foliage	60.45	54.91	61.71	55.06	52.66
	Reproductive parts	55.48	50.45	54.05	55.67	47.97
	Twigs	54.04	48.85	47.41	44.03	46.29
	Bark	43.64	37.28	39.67	50.83	34.14
Phosphorus	Foliage	63.74	40.82	65.59	57.77	61.23
	Reproductive parts	52.63	50.63	55.04	50.23	49.36
	Twigs	43.82	41.44	46.68	40.05	39.94
	Bark	46.94	44.69	49.64	43.20	43.27
Potassium	Foliage	68.43	66.77	69.32	66.09	64.35
	Reproductive parts	64.98	63.14	65.97	62.52	60.46
	Twigs	63.30	61.42	64.39	61.25	58.62
	Bark	62.38	60.83	63.84	59.52	57.98

TABLE 10 | Nutrient use efficiency of different components of litter across the selected sites.

Nutrients	Components	Site-1	Site-2	Site-3	Site-4	Site-5
Nitrogen	Foliage	43.60	46.37	48.15	48.62	57.64
	Reproductive parts	3.30	2.32	3.34	3.17	5.35
	Twigs	105.15	102.34	92.05	125.97	155.04
	Bark	15.88	16.20	19.51	14.73	23.78
	Miscellaneous	5.55	6.93	6.13	5.35	8.59
Phosphorus	Foliage	2134.78	2483.43	2404.76	2268.76	3159.83
	Reproductive parts	117.87	88.42	129.78	118.45	209.09
	Twigs	1396.61	1451.41	1474.10	1766.75	2250.80
	Bark	245.07	266.92	339.58	230.04	401.07
	Miscellaneous	176.13	230.00	199.74	173.82	290.59
Potassium	Foliage	232.22	267.49	255.47	267.53	325.44
	Reproductive parts	17.29	12.84	18.59	17.06	29.04
	Twigs	449.23	462.97	463.77	574.36	686.50
	Bark	47.89	52.22	65.53	44.73	75.03
	Miscellaneous	27.44	36.32	39.33	27.49	43.91

study showed that either foliage or bole wood contributed the maximum nutrient storage which depends upon the species composition, vegetation structure, and nutrient percentage in species (Sharma and Sharma, 2013; Gong et al., 2017; Gautam and Mandal, 2018) but Negi et al. (1983), Frederic et al. (2010), and Pang et al. (2020) have suggested that the contribution of foliage and bole wood in various forests of the world is intermediate with regard to nutrient storage. The present finding was similar to values reported by Ovington and Madgwick (1959) for scots pine plantations and post oak-black jack forest, Perala and Alban (1982) for *Populus*, *Picea,* and pines stands, Adhikari et al. (1995) for *Q. semecarpifolia* and *Abies pindrow* forests, Sharma and Sharma (2013) for *Acacia senegal*, *A. tortilis,* and *E. camaldulensis* forests and Gautam and Mandal (2018) for tropical moist forests. In the soil more nutrients are concentrated in the upper layer because most of the microbial communities and their activities are confined in this layer (Pant et al., 2017; Padalia et al., 2018; Manral et al., 2022) along with the nutrient leaching from the vegetation layer.

Standing State of Nutrients

The standing state of nutrients depends upon the intake potential and inherent characteristics of the species. In this study, the nutrient accumulated in soil and vegetation showed a positive correlation. Similar findings were also reported by Singh and Singh (1991) and Pang et al. (2020). In shrubs the maximum storage of nutrients was generally reported from bole wood and it tended to be lower than storage in trees because of differences in biomass. Due to the high biomass accumulation in bole (Awasthi et al., 2022) nutrient storage becomes high in this component. Herb aboveground parts stored higher nutrients than in belowground parts and its contribution ranged from 29.88 to 46.96% N, 26.6 to 49.81% P, and 22.67 to 41.63% K to the total vegetation (Rawat and Singh, 1988; Bargali et al., 1992; Lodhiyal et al., 1995). The range of nutrient stock on the basis of percent contribution to total storage in different vegetation layers was: Trees > Herbs > Shrubs which was also reported by Lodhiyal and Lodhiyal (2003).

Contribution of litter fall to the total storage was the minimum through vegetation, litter, and soil. Nutrient storage in litter ranged from 8.38 to 15.52 kg N ha^{-1}, 0.31 to 0.55 kg P ha^{-1}, and 1.64 to 2.94 kg K ha^{-1}. The annual N and P return through litter fall reported for certain temperate forests was 14.1–125.0 kg N ha^{-1} and 1.7–10.0 kg P ha^{-1}, respectively (Ovington and Madgwick, 1959; Van Cleve and Noonan, 1975) which was higher than the values recorded in the present study. Adhikari et al. (1995) and Pang et al. (2020) also reported higher nutrient contribution by litter in comparison to the present study.

Retranslocation of Nutrients

The retranslocation of nutrients from the senescing tissues is one of the factors affecting the concentration of nutrients in the litter (Liu et al., 2001). It allows the plants to utilize the nutrients in the various growth cycle that are added in to the soil through the leaves or foliage and fine roots. In foliage, the N and P concentrations are important because it determines the cyclic phase of nutrients and C as well as the food web and chain in the forest ecosystem (Chapin et al., 2011). The values of the P retranslocated by twigs (47.11–66.60%) in this study were in a similar bracket as reported by Attiwill et al. (1978) for *Eucalyptus oblique* (61.1%), and Rawat and Singh (1988) for oak forest (47.8%), whereas the K retranslocated by twigs (58.71–80.10%) was higher than reported by Gautam and Mandal (2018) in mixed forests (41%) and Lodhiyal and Lodhiyal (2003) in Shisham plantation (34.8–37.3%) in Kumaun Himalaya. Bargali et al. (1992) reported 87.9–93.3% K retranslocation in *Eucalyptus* plantations, which was much higher than reported in the present study. This may be due to the higher K concentration of foliage litter in *C. nepalensis* shrublands than *Eucalyptus* plantations. The highest retranslocation rate (30–97%) was recorded for P than K (56–82%) and N (6–34%) which showed a reverse trend as maximum concentration of nutrients in foliage was in the order: N > P > K (**Table 1**). The retranslocation rate showed insignificant correlation with soil as well as foliage nutrient stock.

Nutrient Uptake

The nutrient uptake depends upon the nutrient stock, its available forms, root system, and rhizosphere biology as well as ecology. Beside this, the species and its age and site condition also affect and determine the update of nutrients. The range of nutrient uptake (kg ha^{-1} yr^{-1}) by different vegetation layers across the sites revealed that the order of uptake by different vegetation layers was inversely proportional to the size of the plants: Herbs > Shrubs > Trees for N and Herbs > Trees > Shrubs for P and K. Earlier studies also reported the variations in the order of contribution by different vegetation layers e.g., Singh and Singh (1991) reported the order: Shrubs > Trees > Herbs whereas Rawat and Singh (1988), Garkoti and Singh (1994), Lodhiyal and Lodhiyal (2003), and Gautam and Mandal (2018) reported the order: Trees > Herbs > Shrubs. These findings suggested that the required nutrient is extracted by plants from the soil in proportions that vary from species to species. The magnitude of annual uptake in the present study was higher than the values reported by Rawat and Singh (1988) in an oak forest, Garkoti and Singh (1994) in Maple, Birch and *Rhododendron* forests, and Gautam and Mandal (2018) in a tropical moist forest.

Nutrient Return Through Litter Fall

The nutrient return from litter takes place through decomposition processes followed by nutrient release. The nutrient release and cycling process alters as well as being dependent upon the turnover of litter and turnover time. Further, the concentration of nutrient in litter and amount of litter also affects the level of nutrient returns in the soil compartment. The values of nutrient return through litter fall in the present study were higher than reported by Rawat and Singh (1988), Bargali et al. (1992), Rana et al. (2007), Paudel et al. (2015), Novak et al. (2020), and Pang et al. (2020). The contribution of foliage in total ranged from 68.83 to 74.63% N, 39.41 to 52.41 P, and 52.25 to 63.81% K which is lower than reported by Klinge (1968), Rawat and Singh (1988), and Rana et al. (2007) whereas Paudel et al. (2015), and Novak et al. (2020)
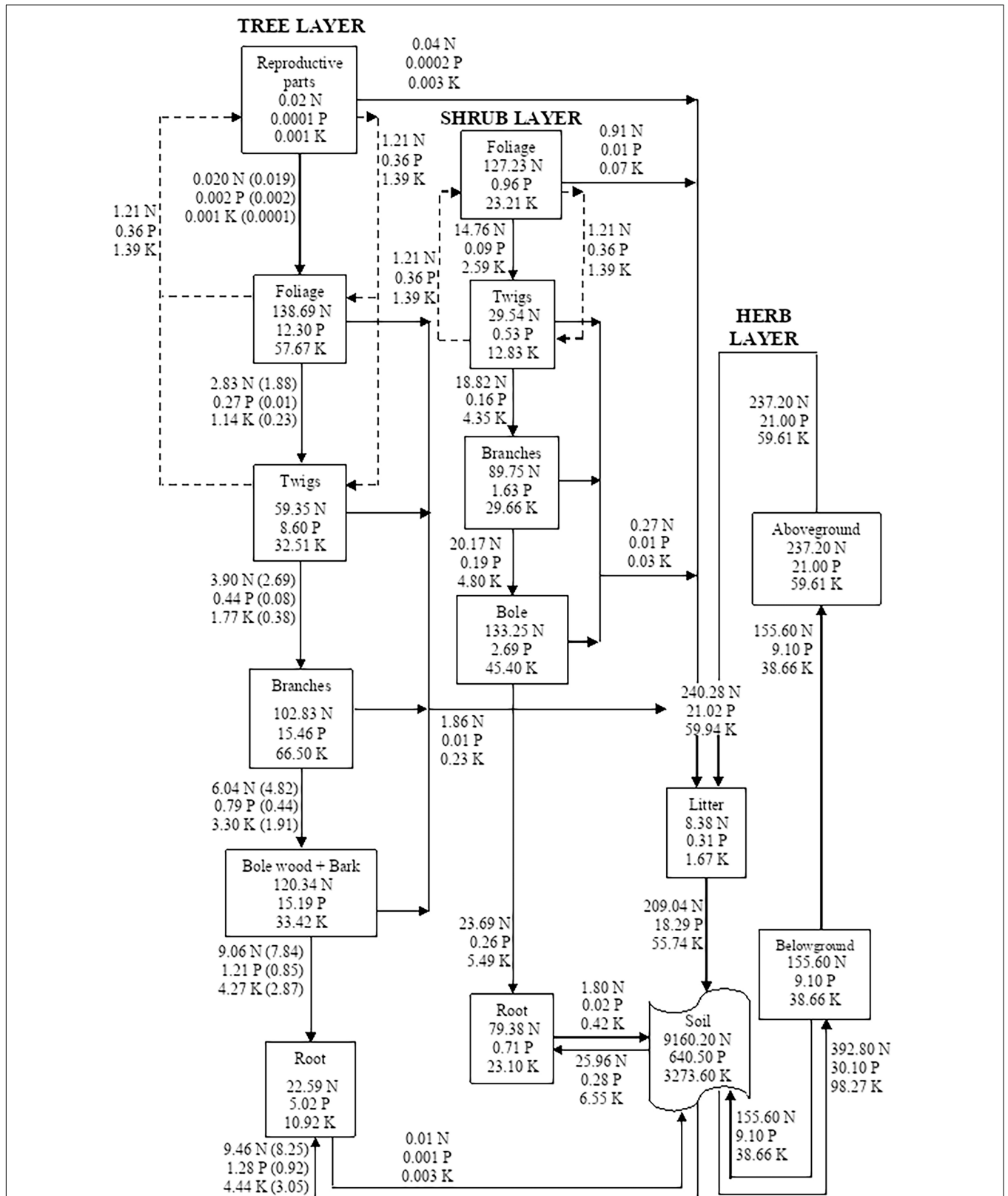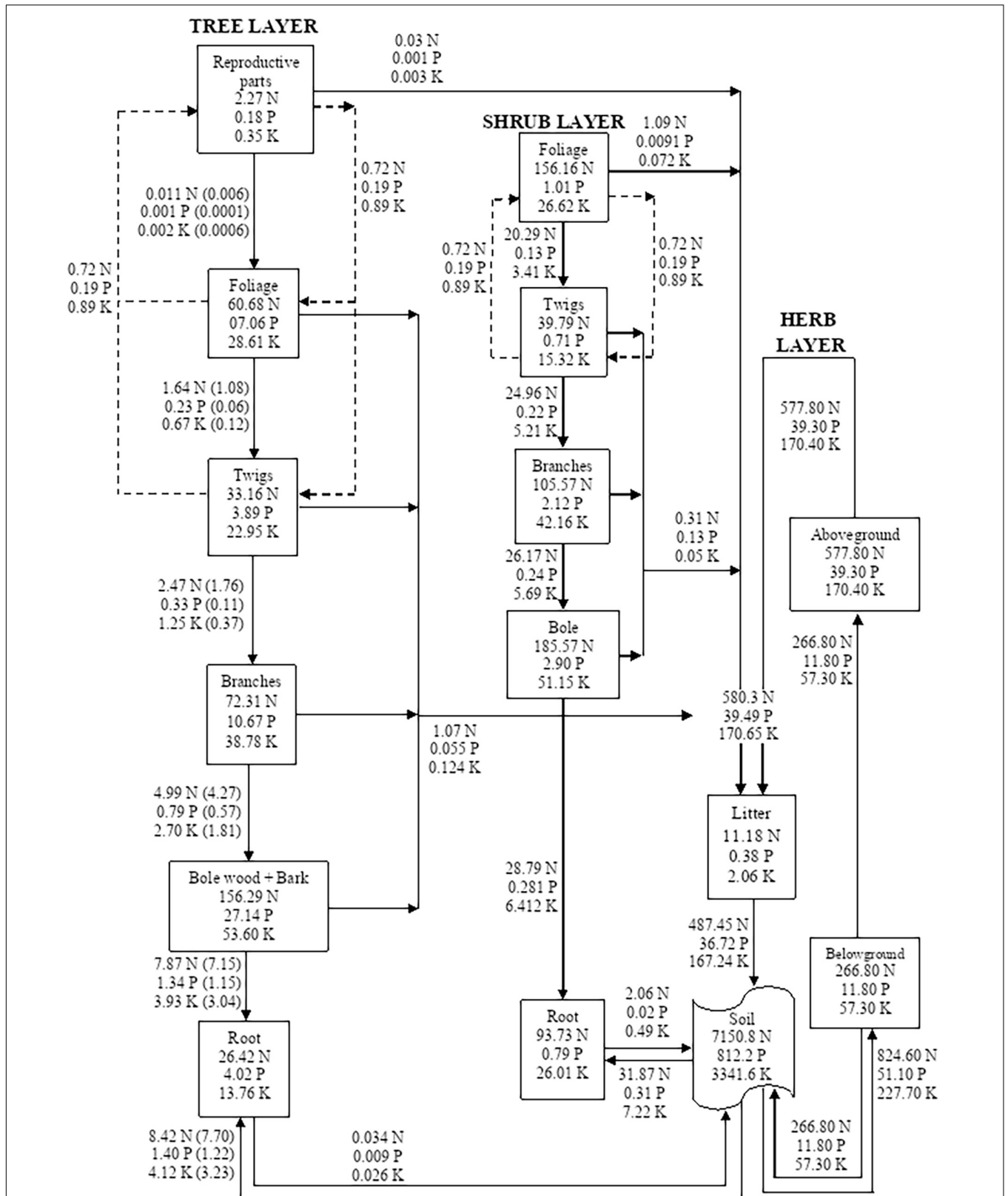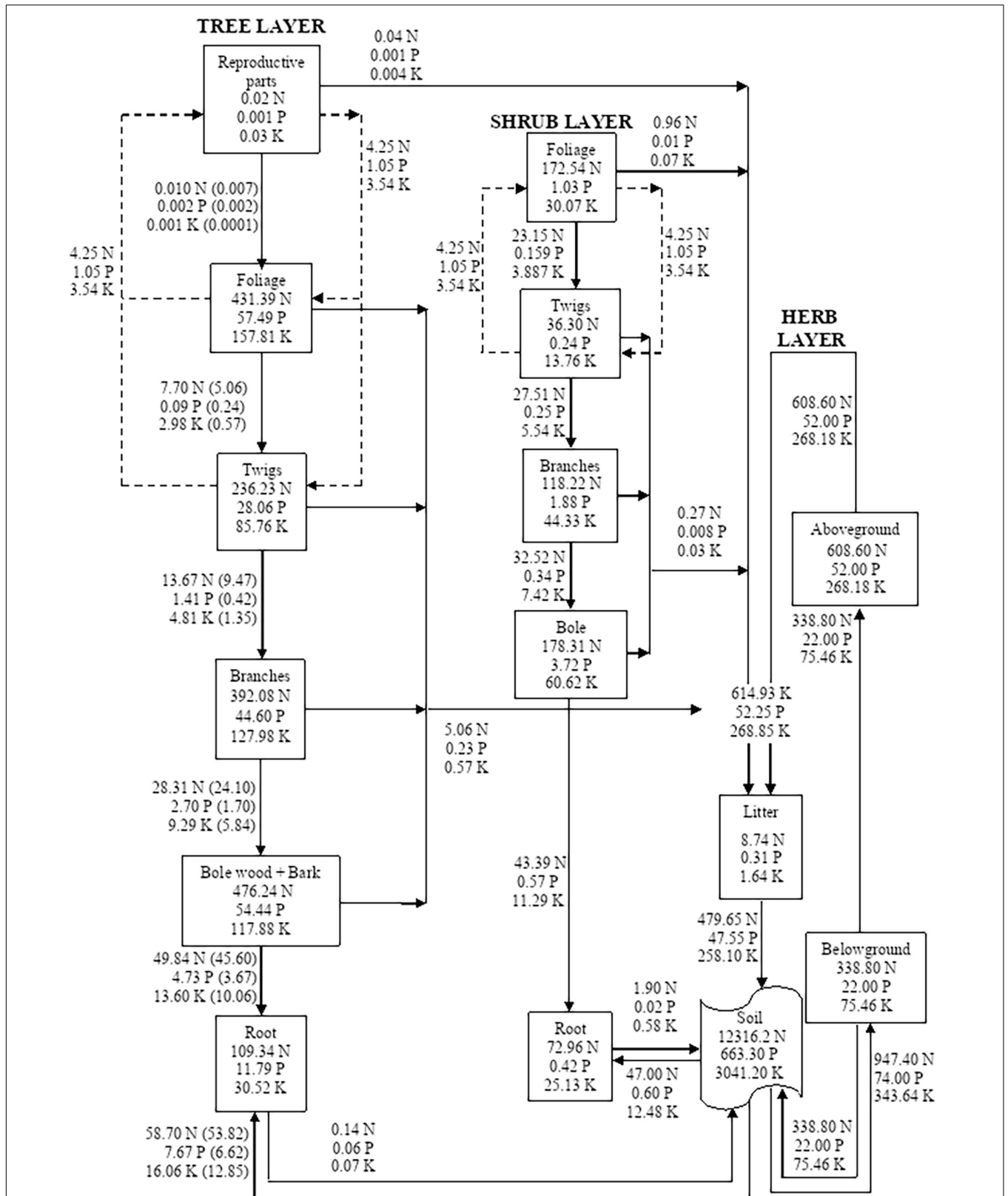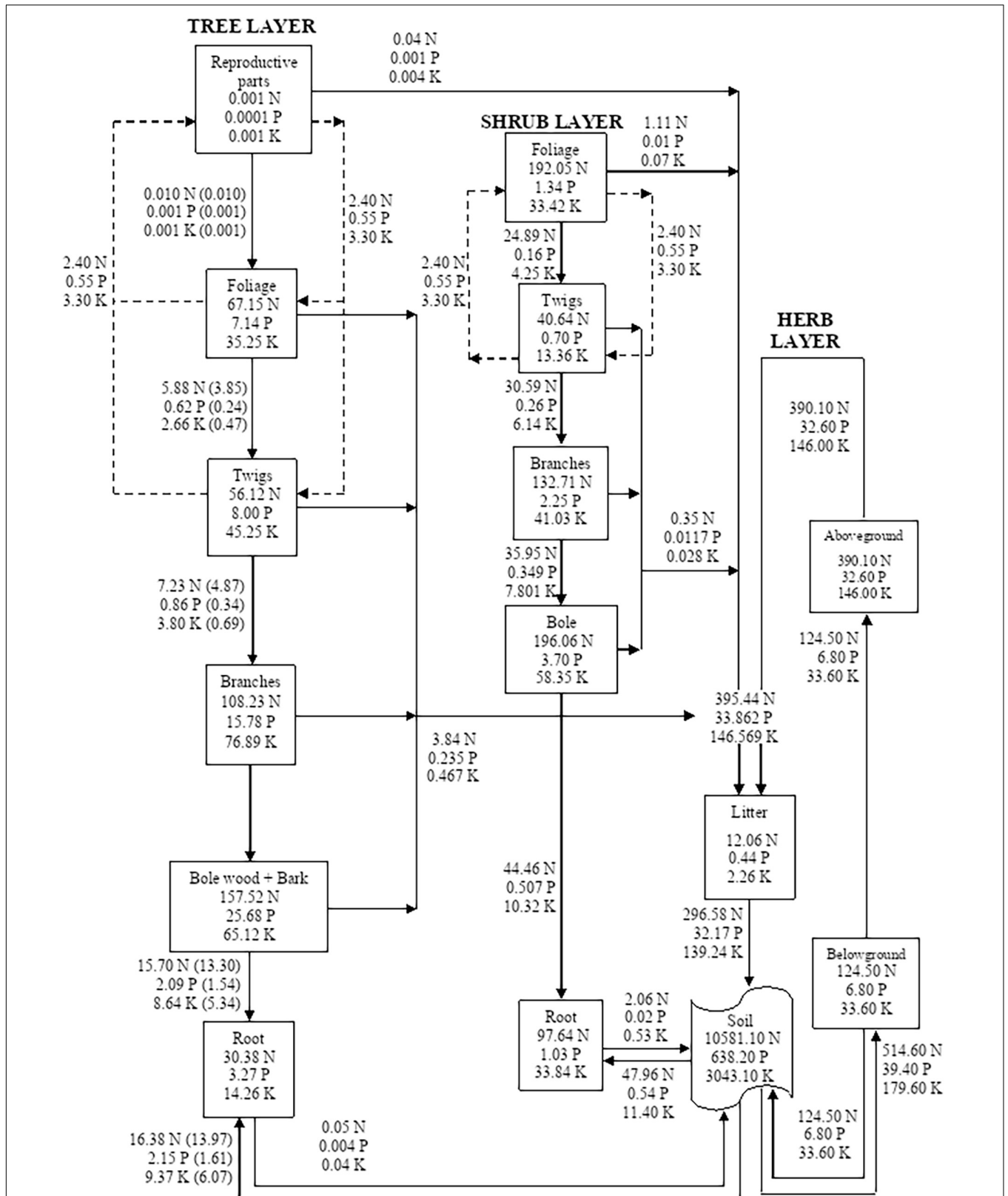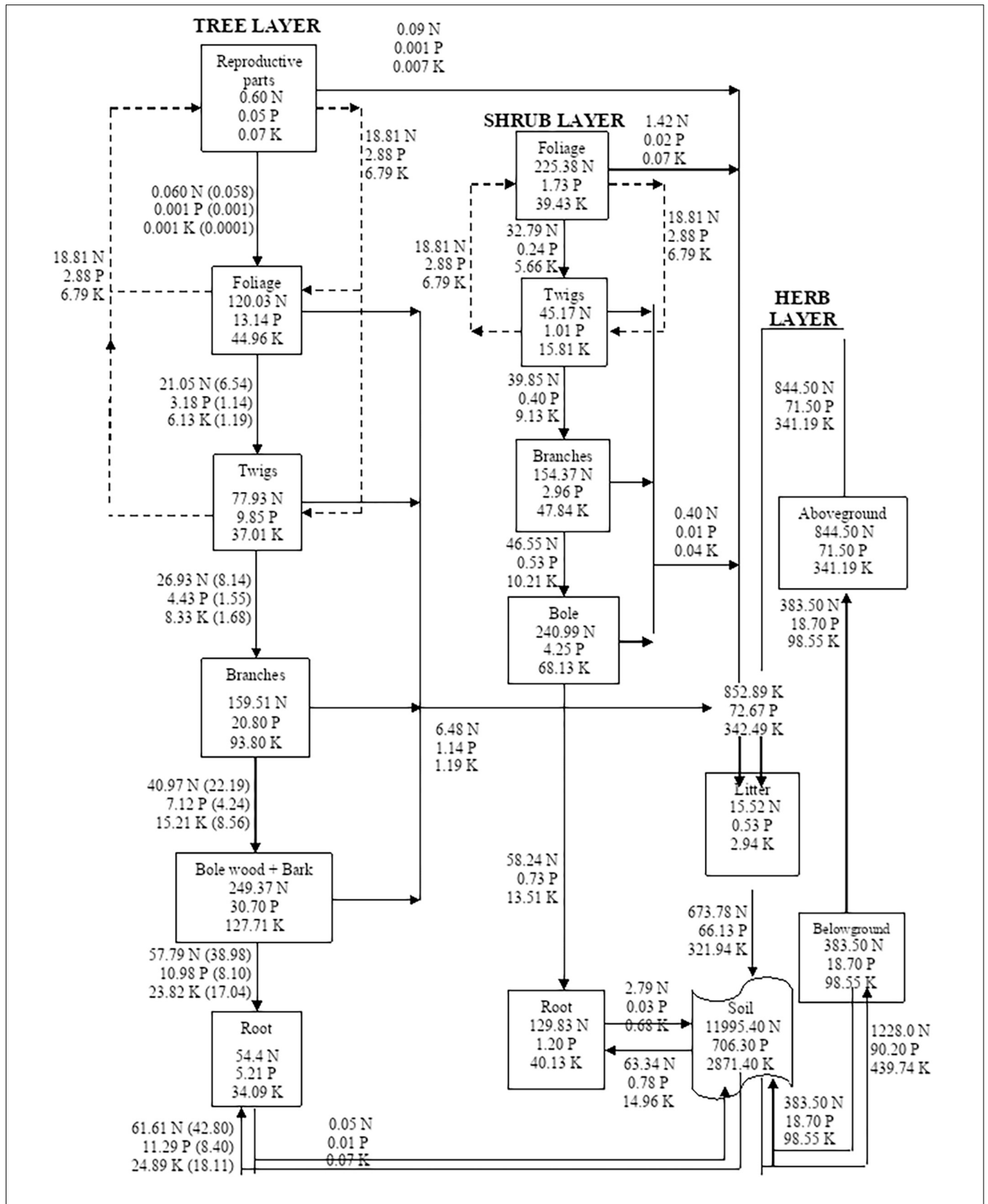
FIGURE 1 | Compartment models showing the distribution and cycling of nitrogen (N), phosphorus (P), and potassium (K) in tree, shrub, and herb at site-1. Rectangle represents a compartment for standing state of nutrients from one compartment to the next compartment. Units are kg ha^{-1} yr^{-1} for flows between compartments. Values in parenthesis are after adjustment for internal cycling. Recycling between reproductive parts, foliage, twigs, and bole is shown by dotted lines.

FIGURE 2 | Compartment models showing the distribution and cycling of nitrogen (N), phosphorus (P), and potassium (K) in tree, shrub, and herb at site-2. Rectangle represents a compartment for standing state of nutrients from one compartment to the next compartment. Units are kg ha^{-1} yr^{-1} for flows between compartments. Values in parenthesis are after adjustment for internal cycling. Recycling between reproductive parts, foliage, twigs, and bole is shown by dotted lines.

FIGURE 3 | Compartment models showing the distribution and cycling of nitrogen (N), phosphorus (P), and potassium (K) in tree, shrub, and herb at site-3. Rectangle represents a compartment for the standing state of nutrients from one compartment to the next compartment. Units are kg ha^{-1} yr^{-1} for flows between compartments. Values in parenthesis are after adjustment for internal cycling. Recycling between reproductive parts, foliage, twigs, and bole is shown by dotted lines.

FIGURE 4 | Compartment models showing the distribution and cycling of nitrogen (N), phosphorus (P), and potassium (K) in tree, shrub, and herb at site-4. Rectangle represents a compartment for standing state of nutrients from one compartment to the next compartment. Units are kg ha^{-1} yr^{-1} for flows between compartments. Values in parenthesis are after adjustment for internal cycling. Recycling between reproductive parts, foliage, twigs, and bole is shown by dotted lines.

FIGURE 5 | Compartment models showing the distribution and cycling of nitrogen (N), phosphorus (P), and potassium (K) in tree, shrub, and herb at site-5. Rectangles represent compartment for standing state of nutrients from one compartment to the next compartment. Units are kg ha^{-1} yr^{-1} for flows between compartments. Values in parenthesis are after adjustment for internal cycling. Recycling between reproductive parts, foliage, twigs, and bole is shown by dotted lines.

reported a similar range of 55.23–70.51% of nutrient return through foliage in various forests. Nutrient return by leaves was followed by twigs, reproductive parts, and bark. High nutrient content in the litter enhanced the decomposition processes and nutrient return to the soil as compared to other vegetation types.

Turnover for Nutrients on the Forest Floor

The litter deposition and its decomposition are the key ecological processes of nutrient cycling. The rate and time of decomposition affects the nutrient release and stock in the forest soils. The turnover time for N in this study was a little longer than those for other nutrients (P and K) and these results are consistent with the observations of Lang and Formann (1978) because K is soluble and is more readily leached from the organic matter and therefore, recycles faster than structurally bound elements like N and P. Slower turnover of N and P in the litter layer also appears to be due to re-translocation in the plant before senescence, thereby reducing the relative amounts of these nutrients in litter fall (Rawat and Singh, 1988). Bargali et al. (1992) in a *Eucalyptus* plantation and Nonghuloo et al. (2020) in a coniferous forest reported a turnover ranging between 0.3 and 1.35 years which was in a similar range to that reported in this study whereas Gosz et al. (1973) in northern deciduous hardwood forests, Singh and Singh (1991) in a dry tropical forest, Rawat and Singh (1988) in an oak forest, Foster and Morrison (1976) in a pine forest, Garkoti and Singh (1994) in a temperate forest of Western Himalaya and Gautam and Mandal (2018) in a tropical moist forest reported the turnover time for nutrients to be between 1.47 and 15.4 years which is higher than the turnover time reported in this study.

Nutrient Use Efficiency

Plants that recycle a large proportion of their nutrients internally are less dependent on uptake from the soil to meet subsequent nutrient requirements. Nutrient use efficiency of a species is also an important consideration in managed systems but in natural systems it is regulated by the structure and functioning of the ecosystems. The nutrient retranslocation prior to senescence and litter fall increased the nutrient use efficiency in the forests (Chapin et al., 2011). High nutrient use efficiency under low nutrient availability drives infertile ecosystems toward greater nutrient deficiency (Shaver and Melillo, 1984). The nutrient use efficiency in the present study was in a similar range as in the *Shorea robusta* forest (128 N, 1525 P, and 258 K; Singh and Singh, 1987); *Populus deltoides* plantation (160 N; 1379 P; Lodhiyal et al., 1995), Puetro Rico forest (128–357 N, 833–1,428 P; Wang et al., 1991), *P. roxburghii* forest (129 N, 1,130 P, and 219 K; Chaturvedi and Singh, 1987), and Costa-rica forest (95–150 N, 433–962 P; Hiremath et al., 2002). However, the present values of nutrient use efficiency were lower than reported for eucalypt plantations (198 N, 3,180 P, and 362 K; Bargali et al., 1992), *Pinus thunbergii* forest (66–263 N; 1,552–3,771 P; Enoki et al., 1997), five plantation-grown trees (135–480 N, 750–3,750 P; Son and Gower, 1991) and mangrove forests (167–322 N, 2,905–5,053 P; Alongi et al., 2005).

Nutrient Cycling

The total amount of nutrient uptake (N, P, K) by vegetation after adjusting for internal cycling ranged from 427.00 to 1334.14 kg N ha^{-1} yr^{-1}, 31.30 to 99.38 kg P ha^{-1} yr^{-1}, and 107.87 to 472.82 kg K ha^{-1} yr^{-1}, respectively. The decrease in the calculated uptake was due to adjustment of internal retranslocation. The recycling supports a portion of the production of new foliage and other components and that will decrease the demands of nutrients from the soil.

The soil compartment received nutrients consequent to release by decomposition of litter and roots. Annually, 240.28–852.89 kg N ha^{-1}, 21.02–72.67 kg P ha^{-1}, and 59.94–342.50 kg K ha^{-1} were released into the soil through total litter fall (*C. nepalensis* foliage + twigs + reproductive parts + bark + tree aboveground + herb leaf litter). The release of nutrients by fine roots (trees + shrubs + herbs) ranged between 124.65 and 383.68 kg N ha^{-1}, 6.81 and 18.71 kg P ha^{-1}, and 33.66 and 98.65 kg K ha^{-1} across the selected sites.

CONCLUSION AND IMPLICATION FOR RESTORATION OF DEGRADED HILLS

Himalayan mountains are sub-surface flow systems and are hence prone to landslides and landslips. Nutrient and water limitations are two limiting factors to plant growth and stand productivity in these degraded lands and needs to reduce their insidious effects with selection of suitable plant species. This study reported that in nutrient concentration and stock (1,295–12,316 kg ha^{-1} N, 93–277 kg ha^{-1} P, and 433–1,037 kg ha^{-1} K) in *C. nepalensis* dominated shrublands was more than other shrub species of the region like *Lantana camara* and *Arundinaria falcata*. Through annual litter fall the *C. nepalensis* released 240.28–852.89 kg ha^{-1} N, 21.02–72.67 kg ha^{-1} P, and 59.94–342.50 kg ha^{-1} K to the soil. In addition, the *C. nepalensis* shrubland showed efficient nutrient retranslocation (34–62% N, 41–65% P, and 57–69% K) and conservation (use) mechanism. Gautam and Mandal (2018) reported that the plants with high nutrient concentration have a higher percentage of N and P in soluble inorganic form and retranslocate a larger proportion of N and P than plants with low nutrient status. The higher nutrient retranslocation efficiency support the production of new foliage and branches in a successful growing season and minimize the demand from the soil. Therefore, in landslide affected degraded hills of Kumaun Himalaya, conserving and establishing *C. nepalensis* shrubland is a better management strategy to improve soil conditions by utilizing its biological nitrogen-fixation ability and nutrient-cycling through nutrient-rich litter.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

PA collected the data and prepared the first draft. KB and SB guided the research, reviewed, and modified the manuscript. KK helped in manuscript preparation and analysis. MJ helped in editing the manuscript. All authors contributed to the article and approved the submitted version.

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