NUTRIENT CYCLING IN DISTURBED TROPICAL DRY DECIDUOUS TEAK FOREST OF SATPURA PLATEAU, MADHYA PRADESH, INDIA

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PANDE, P. K. 2004. Nutrient cycling in disturbed tropical dry deciduous teak forest of Satpura Plateau, Madhya Pradesh, India. In this paper, distribution of different nutrients in different life forms, their allocation in different tree components and nutrient cycling in some teak forests of Satpura Plateau are described. The nutrients in tree biomass were higher for disturbed and mature sites (I and II) as compared with younger and undisturbed sites (III and IV). The allocation of nutrients was higher for bole and lowest for leaves, irrespective of sites. The accumulation of nutrients in bole was higher for disturbed and mature sites whereas the trend was reverse for leaves. The contribution of belowground nutrients in tree biomass was higher for disturbed site I and lower for undisturbed site III. Tree, shrub and herb, contributed 87–94, 0.73–6 and 3.47–6.69% nutrients in aboveground biomass at different sites respectively. Nutrient uptake by trees was 41–51% of the total uptake at different sites, while herbs contributed 42–52% to the total uptake. Nutrient use efficiency as per unit biomass was higher for herbs followed by shrub and trees, irrespective of sites. The contribution of teak in total tree biomass nutrients were 62.66, 70.08, 84.60 and 99.92% for site I, II, III and IV respectively. The young and undisturbed sites showed higher contribution of nutrients in teak.

Key words: Biomass – nutrient return – nutrient uptake – nutrient use efficiency

PANDE, P. K. 2004. Kitaran nutrien hutan jati daun luruh kering tropika yang diceroboh di Dataran Tinggi Satpura, Madhya Pradesh, India. 2004. Kertas kerja ini menerangkan tentang taburan sesetengah nutrien dalam jenis tumbuhan yang berbeza, jumlahnya dalam bahagian pokok yang berbeza dan kitaran nutrien di beberapa hutan jati di Dataran Tinggi Satpura. Nutrien dalam biojisim pokok lebih tinggi di hutan yang diceroboh dan matang (tapak I dan tapak II) berbanding hutan yang lebih muda dan tidak diceroboh (tapak III dan tapak IV). Nutrien di semua tapak lebih tinggi dalam batang pokok dan paling rendah dalam daun. Nutrien yang terkumpul dalam batang lebih tinggi di tapak yang diceroboh dan matang. Sebaliknya, nutrien dalam daun lebih tinggi di tapak muda yang tidak diceroboh. Sumbangan nutrien bawah tanah dalam biojisim pokok lebih tinggi di tapak I yang diceroboh tetapi rendah di tapak III yang tidak diceroboh. Pokok, pokok renik dan pokok herba di keempat-empat tapak ini masing-masing menyumbang 87–94%, 0.73–6% dan 3.47–6.69% nutrien daripada jumlah biojisim atas tanah. Ambil-naik nutrien oleh pokok dan pokok herba masing-masing adalah 41–51% dan 42–52% daripada keseluruhan ambil-naik. Keberkesanan penggunaan nutrien dari segi seunit biojisim lebih tinggi untuk pokok herba, diikuti oleh pokok renik dan pokok. Sumbangan pokok jati dalam keseluruhan biojisim pokok masing-masing adalah 62.66%, 70.08%, 84.60% dan 99.92% untuk tapak I, II, III dan IV. Sumbangan nutrien lebih tinggi dalam pokok jati di tapak muda yang tidak diceroboh.

Introduction

Disturbances play a great role in the tropical dry deciduous forests of Satpura. The long-term ecosystem dynamics of these forests are greatly affected by biotic and abiotic periodic disruptions. Disturbances also affect the nutrient cycling of these forests. Therefore, nutrient cycling of these forests has an important role in the understanding of various processes and functions of these natural ecosystems. Nutrient cycling is very important for the management of disturbed forests.

A lot of work has been done on the aspect of nutrient cycling in India and in other countries (Turner & Lambert 1983, George 1984, Negi 1984, Sharma & Pande 1989, Negi *et al.* 1995, Cairns *et al.* 1997). Most of the studies pertain to nutrient cycling for different plantation and natural forest ecosystems. Little emphasis has been made to study nutrient cycling at disturbed ecosystems. Hence, the objectives of the present investigation were to investigate: (1) the distribution of different nutrients in different life forms, (2) their allocation in different tree components, (3) nutrient uptake, retention and return, and (4) nutrient cycling. All these aspects were compared and analysed as per the disturbance magnitude of the selected sites.

Materials and methods

Study site

The study sites are located in south Chhindwara forest division, comprising the Sillevani range and Khutama beat (site I, Amla-55 L, compartment no. 348; site II, Amla-6, compartment no. 345-B; site III, Amla-45 compartment no. 346-A and site IV is a 16-year-old plantation in the large gap inside the forest of site I), of Chhindwara district, Madhya Pradesh, India. The study area is situated between 20° 28' to 22° 49' N latitude and 78° 40' to 79° 24' E longitude at an elevation of 410–457 m asl. As per the classification of Champion and Seth (1968), the forests of the area are categorised under group 5 A/(1b) as tropical dry deciduous forest. The Forest Department of Chhindwara has classified the site as undulating rock of decan trap. The soil is sandy loam and alluvium occurs along the 'nalas'. The other important features of the site are given in Table 1.

Floristic composition

Three communities were identified as *Tectona grandis-Lagerstroemia parviflora-Ougeinia oojeinensis* (site I); *T. grandis-Diospyros melanoxylon-Butea monosperma-Miliusa tomentosa* (site II) and *T. grandis-Chloroxylon swietenia-L. parviflora-D. melanoxylon* (site III). Shrub layer at all the sites comprised mainly saplings of *T. grandis, D. melanoxylon, L. parviflora* and *Butea monosperma. Triumfetta rhombifolia, Indigofera trifoliata, Oplismenus burmanni, Cyperus kyllingia, Sida rhombifolia, S. acuta* were the common herb species at the sites. Well-known medicinal plants like *Hemidesmus indicus, Achyranthes aspera, Hyptis suaveolens, Ageratum conyzoides* were also recorded from these sites.

Table 1 Characteristics of the study site in Chhindwara district, Madhya Pradesh, India

Site	Density (t ha^{-1})	Total basal area[1] (cm^2 ha^{-1})	k[2] (year^{-1})	Litter production (kg ha^{-1} year^{-1})	Soil pH[3]	N (kg ha^{-1})	P (kg ha^{-1})
I	690	155 487 2 (225)	2 26	3305 26 (1267)	7 95	71	19 8
II	950	148 823 5 (157)	3 33	4535 77 (1246)	7 99	413	18 2
III	1630	95 642 8 (59)	2 57	3275 94 (1001)	7 99	413	19 2
IV	2500	132 081 4 (52 83)	2 26	3305 26 (1267)	7 95	71	19 8

[1] Values in parentheses are mean basal area, [2] Decomposition constant (k), the values of 'k' were calculated using l/x_{ss}, where l = litter production and x_{ss} = litter accumulation (Olson 1963), [3] Soil depth 0–20 cm

Climate

The climate of the area is monsoonal with seasonal rainfall. Total precipitation recorded in 1998 was 1247 mm with a maximum of 235 mm in September. The annual mean maximum and minimum temperatures in that year were 29 and 20 °C respectively with an average mean temperature of 25 °C. June (34 °C) and December (17 °C) were the hottest and coldest months of the year respectively.

Magnitude of disturbance

The degree of past disturbances was estimated by calculating coefficient of determination (r^2) between density-diameter relationship (Schmelz & Lindsey 1965, Robertson *et al.* 1978). The magnitude of r^2 indicates the degree to which a stand approximates a balanced structure. A value of r^2 closer to '1' means the system is more balanced (Robertson *et al.* 1978). From the r^2 values for all tree species, the degree of disturbance was found to follow the order: 0.58 (site III) > 0.18(II) > 0.05 (I). These r^2 values were non-significant for both negative power and negative exponential function. However, site I was most disturbed while site III was the least disturbed site. Details in this regard are given in Pande (2001). As per the mean basal area, site III is taken as the younger site while sites II and I as the mature sites.

Biomass studies

Biomass studies in the Sillevani range and Khutama beat were conducted in 1998 using harvested method of stratified tree technique (Peterken & Newbould 1966). Twenty quadrats (size 10 × 10 m for trees, 3 × 3 m for shrubs and 1 × 1 m for herbs) were laid randomly along the transect at each site. Girth at breast height (GBH) and height of each tree were measured. In order to have better distribution of sample trees over the population, the number of trees was divided into different girth classes. Sample trees for each girth class were selected as being nearest to the average of each class (Ovington *et al.* 1967). These sample trees were felled and roots were excavated for the determination of underground biomass. The whole tree biomass was recorded for different components, namely, twig, branch, bole and root, and presented as oven-dry weight values. The mean diameter was also calculated to estimate shrub biomass for different species. The harvest method was used for estimating herb biomass.

The calculated biomass for each sample tree of each girth class was divided by age. Age was determined by volume tables and further confirmed by counting growth rings. The density of each diameter class was multiplied by the biomass of the respective girth class. This exercise was done for each species. Finally, all the values were summed to obtain the net primary productivity (NPP), which was then multiplied by per cent nutrient concentration to determine the nutrient uptake. The biomass values were used to estimate nutrient allocation in different tree components, life forms and nutrient uptake.

Litter studies

Five permanent litter plots (5 × 5 m) were randomly placed at each site. All the plots were cleared and swept clean of any deposited debris. This deposited debris was sorted into leaves, twigs and miscellaneous (consisting of litter of other than the main species and of other unidentified organic matter) (Sharma & Pande 1989). All the components were given as oven-dry weight values.

Phosphorus was determined by ammonium-molybdate-blue method (Vogal 1961). K and Ca were determined using flame photometric method and Mg, using atomic absorption spectrophotometer. Nitrogen was determined by Kjeldhal method. All the results are in oven-dry weight values. Chemical analysis for each component of biomass was conducted for all tree, shrub and herb species, and the various litter fractions.

Per cent nutrient concentration was multiplied by the magnitude of different component of biomass of different life forms. This is to determine the contribution of nutrients by the various components of the different life forms at the different sites.

Results and discussion

Allocation of nutrients in different life forms

The allocation of different nutrients in the biomass of trees, shrubs and herbs is given in Table 2. Tree biomass nutrients as per cent of total biomass nutrients are in the order: 95.09 (IV) > 92.77(I) > 91.50(II) > 81.33(III). The trend showed that nutrients in tree biomass were generally higher for disturbed and mature sites than of the less disturbed and younger sites, except site IV. This is the reflection of maturity of stand. However, site IV, being a high density plantation inside the forest, showed higher tree biomass and nutrient content. The per cent allocation of nutrients in shrub was higher for site III (11.67), followed by sites I (3.03)), II (2.04) and IV (1.53). The low nutrients in shrub at site IV is a reflection of dense, undisturbed and younger nature of the plantation, which provides less space and resources for shrubs to grow. The per cent allocation of nutrients in herbs was higher for undisturbed site III (6.99) followed by sites II (6.46), I (4.20) and IV (3.39). Herb biomass at site IV has the least nutrients due to low herb and high trees biomass. Further, the high tree density does not allow much scope for the invasion and growth of herbs (Table 2).

Table 2 Nutrients content (kg ha^{-1}) in total biomass

Component/nutrient	N	P	K	Ca	Mg	Total
Site I						
Aboveground biomass nutrient						
Tree	588.070	253.810	387.240	952.920	430.770	2612.810 (94.66)
Shrub	25.639	2.935	5.242	11.439	6.415	51.671 (1.87)
Herb	25.388	3.563	18.622	37.259	11.641	96.473 (3.47)
Total (A)	639.090	260.310	411.100	1001.600	448.830	2760.954 (100)
Belowground biomass nutrients						
Tree	54.793	27.623	60.504	188.820	94.314	426.049 (82.77)
Shrub	11.353	2.671	9.425	14.813	9.2950	47.5568 (9.24)
Herb	5.245	1.887	9.4543	17.561	6.9784	41.122 (7.9)
Total (B)	71.391	32.181	79.383	221.190	110.590	514.730 (100)
Total (A + B)						
Tree	642.860	281.430	447.750	1141.100	525.090	3038.230 (92.77)
Shrub	36.993	5.610	14.667	26.252	15.710	99.228 (3.03)
Herb	30.634	5.450	28.076	54.816	18.619	137.595 (4.20)
Grand total	710.490	292.490	490.490	1222.170	559.420	3275.050 (100)
Site II						
Aboveground biomass nutrient						
Tree	608.180	240.670	368.680	742.555	271.060	2231.136 (92.79)
Shrub	7.197	2.580	4.042	9.301	5.595	28.714 (1.19)
Herb	38.583	5.660	27.796	58.783	13.854	144.673 (6.02)
Total (A)	653.960	248.910	400.520	810.639	290.510	2404.523 (100)
Belowground biomass nutrient						
Tree	97.880	26.804	90.747	171.215	92.762	479.406 (86.01)
Shrub	6.390	1.839	5.744	11.558	6.177	31.708 (5.69)
Herb	6.770	2.465	10.783	19.840	6.554	46.412 (8.32)
Total (B)	111.040	31.108	107.270	202.613	105.490	557.526 (100)
Total (A + B)						
Tree	706.060	267.470	459.430	913.770	363.820	2710.543 (91.51)
Shrub	13.587	4.415	9.786	20.859	11.772	60.419 (2.04)
Herb	45.353	8.128	38.796	78.623	20.612	191.512 (6.46)
Grand total	765.000	280.010	508.000	1013.250	396.200	2962.462 (100)

(continued)

(Table 2 - continued)

Component/nutrient	N	P	K	Ca	Mg	Total
Site III						
Aboveground biomass nutrient						
Tree	213.700	86.754	133.350	323.220	118.800	875.820 (87.04)
Shrub	16.652	4.913	9.985	20.327	11.160	63.040 (6.20)
Herb	17.715	2.459	13.026	25.745	8.417	67.360 (6.69)
Total (A)	248.070	94.126	156.360	369.292	138.380	1006.230 (100)
Belowground biomass nutrient						
Tree	57.599	13.996	52.625	89.184	50.964	264.368 (66.82)
Shrub	23.700	5.482	20.223	31.502	19.738	100.644 (25.44)
Herb	4.289	1.550	7.444	12.327	5.044	30.654 (7.75)
Total (B)	85.588	21.028	80.292	133.013	75.746	395.666 (100)
Total (A + B)						
Tree	271.300	100.750	185.980	412.463	169.780	1140.273 (81.33)
Shrub	40.352	10.394	30.208	51.829	30.897	163.680 (11.67)
Herb	22.044	4.009	20.470	38.072	13.461	98.056 (6.99)
Grand total	333.700	115.150	236.660	502.364	214.140	1402.01 (100)
Site IV (Plantation)						
Aboveground biomass nutrient						
Tree	274.630	112.440	177.300	519.282	307.670	1391.322 (95.10)
Shrub	2.697	0.8196	1.5126	3.661	1.9323	10.6225 (0.73)
Herb	16.800	2.024	11.762	25.350	4.206	60.142 (4.14)
Total (A)	294.130	115.280	190.580	548.293	313.810	1462.087 (100)
Belowground biomass nutrient						
Tree	99.572	21.845	90.850	140.212	84.110	436.589 (94.85)
Shrub	4.169	0.976	3.821	6.2402	3.636	18.8422 (4.09)
Herb	0.724	0.267	0.955	2.471	0.443	4.8597 (1.06)
Total (B)	104.470	23.088	95.626	148.923	88.189	460.291 (100)
Total (A + B)						
Tree	374.200	134.290	268.150	659.494	391.780	1827.914 (95.09)
Shrub	6.866	1.7956	5.3344	9.9012	5.5685	29.4657 (1.53)
Herb	17.524	2.291	12.717	27.821	4.6487	65.002 (3.39)
Grand total	398.590	138.380	286.200	697.216	402.000	1922.386 (100)

Note: Values in parentheses are per cent of the total uptake.

Allocation of nutrients in different tree components

Allocation of different nutrients in the biomass of different tree components is tabulated in Table 3. The allocation of nutrients was highest in bole followed by root, bark, twig and leaves. The allocation of nutrients (kg ha^{-1}) in bole was higher for sites I (1898.03) and site II (1707.93) and lower in the younger and less disturbed sites III (462.02) and IV (678.49). This is due to the maturity of stands. In contrast, allocation of nutrients in foliage was higher for young and less

Table 3 Allocation of different nutrients (kg ha^{-1}) in different tree components at different sites

Component/nutrient	N	P	K	Ca	Mg	Total
Site I						
Leaf	23.864	5.558	10.967	22.829	15.195	78.413
Twig	54.320	23.246	43.413	88.545	57.841	267.364
Bole	479.719	194.327	290.203	646.433	287.352	1898.033
Bark	30.164	30.681	42.661	195.108	70.387	369.001
Total AGN	588.067	253.812	387.244	952.915	430.773	2612.811
Roots	54.793	27.623	60.504	188.815	94.314	417.152
Grand total	642.860	281.435	447.748	1141.730	525.089	3029.903
Site II						
Leaf	17.275	5.999	5.516	18.710	9.390	56.890
Twig	39.512	16.656	28.659	65.994	35.755	186.575
Bole	526.687	194.170	301.395	502.041	183.638	1707.931
Bark	24.709	23.841	33.109	155.810	42.272	279.741
Total AGN	608.183	240.666	368.678	742.555	271.055	2231.137
Roots	97.878	26.804	90.747	171.215	92.762	479.406
Grand total	706.061	267.470	459.425	913.770	363.817	2710.543
Site III						
Leaf	26.916	6.779	12.774	30.722	17.410	94.601
Twig	22.800	8.353	16.148	38.097	19.579	104.977
Bole	144.539	53.816	79.682	134.789	49.191	462.017
Bark	19.448	17.806	24.749	119.671	32.640	214.314
Total AGN	213.703	86.754	133.352	323.279	118.820	875.909
Roots	57.579	13.996	52.625	89.184	50.964	264.368
Grand total	271.302	100.75	185.977	412.463	169.784	1140.277
Site IV (Plantation)						
Leaf	53.593	14.096	27.053	65.051	36.773	198.567
Twig	38.909	13.322	26.379	64.841	30.660	174.110
Bole	149.117	56.902	84.779	199.420	188.269	678.487
Bark	31.001	28.120	39.090	189.970	59.970	340.158
Total AGN	274.627	112.440	177.301	519.282	307.672	1391.322
Roots	99.572	21.845	90.85	140.212	84.110	436.589
Grand total	374.199	134.285	268.151	659.494	391.782	1827.911

Note: AGN = aboveground nutrients

disturbed sites IV (198.57) and III (94.60), but lower for mature and disturbed sites I (78.41) and II (56.89). It seems that younger stands require more nutrients in foliage as they are in aggregating phase of development. This view is further confirmed by the per cent allocation of nutrients in roots at the younger sites.

Allocation of nutrients in above- and belowground biomass

Tree, shrub and herb contributed 94.66, 1.87 and 3.47% nutrients respectively towards total aboveground biomass nutrients for site I (Table 2). These values were 92.79, 1.19 and 6.02% for site II, 87.04, 6.20 and 6.69% for site III and 95.10, 0.73 and 4.14% for site IV respectively. Site III showed relatively less contribution of tree nutrients due to less disturbances at the site, which improved absorption of nutrients by shrubs and herbs.

Belowground biomass nutrients in tree were 82.77, 86.01, 66.82 and 94.85% for sites I, II, III and IV respectively (Table 2). The contribution of belowground nutrients in tree was higher at disturbed site I and lower at less disturbed site III because of higher root biomass at the disturbed and mature site.

The values for contribution of above- and belowground biomass nutrients to total biomass nutrients were 84 and 16%, 81 and 19%, 72 and 28% and 76 and 24% for sites I, II, III and IV respectively. Aboveground biomass nutrients were higher for disturbed sites and lower for less disturbed sites. The higher belowground biomass nutrients for younger and less disturbed sites is related to higher activity and development of roots at the early stages of stand development.

Allocation of nutrients in major tree species

The allocation of nutrients in different tree species is given in Table 4. *Tectona grandis* (teak) contributed 62.66, 70.08, 84.60 and 99.92% of total tree biomass nutrients at sites I, II, III and IV respectively. Teak at the younger and less disturbed sites showed higher contribution towards total tree nutrients.

The contribution of *Lagerstroemia parviflora* (4.033%) ranked second to teak at site I. *Butea monosperma* contributed 1.53% and *Diospyros melanoxylon* and *Buchanania lanzen* each contributed 1.30% at site II. *Chloroxylon swietenia* and *L. parviflora* contributed 6.85 and 0.08% nutrients towards total tree biomass nutrients respectively at sites III and IV. The contribution of nutrients of species, except teak, towards the total tree biomass nutrients was higher for the mature and disturbed sites, i.e. 37.34% for site I and 29.92% for site II compared with the less disturbed sites III (15.74%) and IV (0.08%). Disturbance caused invasion of new species at disturbed sites and, as a result, these species contributed higher biomass and nutrients in biomass compared with species at the young and less disturbed sites (Table 4).

Table 4 Allocation of nutrients (kg ha^{-1}) in different tree species

Species/site	I	II	III	IV
Tectona grandis	1904.24 (62.66)	1899.44 (70.08)	1826.66 (84.60)	1826.66 (99.92)
Lagerstroemia parviflora	122.20 (4.033)	2.916 (0.07)	26.269 (2.30)	1.249 (0.08)
Cassia fistula	6.567 (0.217)	-	-	-
Chloroxylon swietenia	-	-	78.204 (6.85)	-
Diospyros melanoxylon	-	35.70 (1.30)	27.364 (1.30)	-
Milusa tomentosa	-	9.169 (0.31)	19.645 (1.72)	-
Butea monosperma	-	41.61 (1.53)	9.928 (0.87)	-
Buchanania lanzen	-	33.143 (1.30)	-	-
Zizyphus xylocarpus	-	10.191 (0.38)	16.518 (1.45)	-
Exora aerborea	-	13.880 (0.51)	-	-
Sterculia urens	-	-	1.555 (0.136)	-
Miscellaneous	996.896 (32.902)	664.491 (24.52)	-	-
Total	3038.86(100)	2710.54 (100)	1140.28 (100)	1827.99 (100)

Note: Values in parentheses are per cent values.

Nutrient uptake

Nutrient uptake by tree, shrub and herb at different sites is given in Table 5. Tree species contributed 40.44, 43.46, 40.69 and 50.89% towards total uptake by all life forms respectively at sites I, II, III and IV. The uptake of nutrients by tree species was higher for less disturbed and young sites. The per cent contribution of nutrients of shrub species at the various sites was 9.09 (I), 4.13 (II), 17.44 (III) and 5% (IV) towards total uptake while herbs contributed 50.46 (I), 52.40 (II), 41.87 (III) and 44.11% (IV) nutrient uptake towards total nutrient uptake. Herbs have maximum share in total uptake except at site IV, where tree showed highest values. Site IV is a high density plantation inside the forest and leave less chance for the establishment of herbs and, thus, less uptake of herbs at this site.

Nutrient use efficiency

The nutrient use efficiency for per unit biomass was higher for herb followed by shrub and tree, irrespective of sites (Table 5). Herb biomass has higher concentration of nutrients compared with trees. The disturbed sites showed less nutrient use efficiency than the less disturbed younger sites for trees. The herbs and shrubs showed a reverse trend. This showed that less nutrient use efficiency of tree is compensated by shrub and herb species to minimise nutrient loss from the system at disturbed sites. Per cent nutrient use efficiency per unit biomass was also higher for less disturbed and younger sites III (4.36) and IV (4.52) compared with mature sites I (2.02) and II (4.17). The demand for more nutrients by roots of the trees at younger sites is indicative of their higher vitality and activity.

Nutrient return through litterfall

Annual monthly mean nutrient returns by litter are tabulated in Table 6. The highest mean annual nutrient return was recorded for Ca followed by N, Mg, K and P, irrespective of sites. Site II registered highest mean nutrient return compared with other sites. This might be the impact of insect pest attack at the site (Pande *et al.* 2002). The high Ca return is due to its high concentration in leaf litter (Table 3). Twig litter showed fewer variations in nutrients than that of leaf litter. Total annual nutrient return (kg ha^{-1}) for different sites followed the order: II (191.5) > I (1280.0) > III (114.8). The order of importance for annual N, P, K and Mg return for different sites was II > III > I, while for Ca, the order was II > I > III. The higher nutrient return at site II was associated with higher litterfall and litter nutrient concentrations. The order of importance in terms of magnitude of nutrient return was Ca > N > Mg > K > P.

Table 5 Nutrients uptake (kg ha^{-1} $year^{-1}$) by different life forms at different sites

Site/nutrient	N	P	K	Ca	Mg	Total	% of total	NUE (%)
I								
Tree	23.10	10.11	17.16	41.02	18.87	110.27	40.44	3.18
Shrub	9.24	1.40	3.66	6.56	3.92	24.79	9.09	5.13
Herb	30.63	5.45	28.08	54.82	18.62	137.59	50.46	5.95
Total	62.97	16.96	48.90	102.4	41.41	272.65	100	-
Nutrient retained	37.25	10.11	39.44	32.48	25.34	144.58	53.03	-
II								
Tree	41.37	15.67	26.92	53.53	21.32	158.81	43.46	3.20
Shrub	3.40	1.10	2.45	5.21	2.94	15.10	4.13	3.99
Herb	45.35	8.12	38.80	78.62	20.61	191.50	52.41	8.83
Total	90.12	24.89	68.17	137.46	44.87	365.41	100	-
Nutrient retained	34.44	9.96	50.95	0.37	18.15	173.86	47.58	-
III								
Tree	22.67	0.42	15.54	34.46	14.19	95.28	40.69	3.60
Shrub	10.09	2.60	7.56	12.97	7.63	40.85	17.44	4.33
Herb	22.04	4.01	20.47	38.07	13.46	98.05	41.87	5.77
Total	54.80	15.03	43.57	85.50	35.28	234.18	100	-
Nutrient retained	28.63	7.73	33.39	32.98	16.62	119.35	50.97	-
IV								
Tree	15.35	5.51	11.00	27.05	16.07	74.98	50.89	4.03
Shrub	1.72	0.45	1.33	2.48	1.39	7.37	5.00	4.03
Herb	17.52	2.29	12.72	27.82	4.65	65.00	44.11	5.99
Total	34.59	8.25	25.05	57.35	22.11	147.35	100	-

NUE = nutrient use efficiency

Table 6 Annual nutrient return (kg ha^{-1}) through litter components at different sites

Site/nutrient		N	P	K	Ca	Mg	Total
I	Leaves	23.423	6.0699	8.7808	61.662	8.8938	108.838
	Twigs	2.293	0.7839	0.6742	8.254	7.1800	19.185
	Total	25.716	6.8538	9.4550	69.916	16.0738	128.02
II	Leaves	52.882	14.539	16.558	69.906	25.0804	178.965
	Twigs	2.801	0.3873	0.662	7.086	1.6420	12.578
	Total	55.683	14.9263	17.220	76.992	26.7224	191.540
III	Leaves	21.264	5.9810	8.967	39.445	15.1270	90.784
	Twigs	4.901	1.3180	1.211	13.080	3.5310	24.041
	Total	26.165	7.2990	10.178	52.525	18.6580	114.825

Nutrient cycling

Nutrient return as percentage of uptake was calculated from Tables 5 and 6. The nutrient return was higher for younger sites III (49.03%) and IV (86.90%). Lower per cent nutrient return was achieved at mature sites I (46.96%) and II (52.42%). The higher value of nutrient return at site II compared with site III may be related to the bimodal leaf fall caused by heavy attack of insect pest (Pande *et al.* 2002). Lower nutrient return at the mature sites may also be related to retranslocation of nutrient to the plants prior to the formation of abscission layer in order to minimise nutrient loss. Biochemical cycle is also a strategy of mature stands to minimise nutrients loss from trees via retranslocation (Sharma & Pande 1989). The per cent retention of N, P and K were 59, 59 and 80% for site I; 34, 10 and 76% for site II; 51, 52 and 76% for site III and 25,17 and 62% for site IV. The retention of nutrients was also generally higher for disturbed and mature sites. Comparing the nutrients retained at mature sites I and II, it is clear that site II (48%) was more efficient in recycling nutrients by way of retaining smaller quantities and returning greater quantities of nutrients compared with site I (53%). Site II is relatively less disturbed between the two mature sites. In the same way, site III and IV, the younger and less disturbed sites, also showed more efficient nutrient cycling than the mature and disturbed sites I and II.

Conclusions

The lower uptake and higher retention of nutrients at the disturbed sites in this study are part of an inefficient nutrient cycling. High nutrient retention checks the nutrient flow to the forest floor, whereas lower uptake may cause nutrient loss from the system by leaching and other physical processes. Therefore, artificial regeneration is suggested inside the blanks of disturbed forest sites to minimise nutrient losses.

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