Research paper

Nutrient Accumulation and Distribution of the Aboveground Biomassin a Secondary Subtropical Forest in Central Taiwan

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【Summary】

The nutrient accumulation and distribution of the aboveground biomass were measured using a stratified harvest method in a secondary hardwood forest in the Guandaushi Long Term Ecological Research site, central Taiwan. Nutrient contents of C, N, P, K, Ca, and Mg in the aboveground biomass were 169,030.71, 2799.77, 52.24, 715.70, 918.72, and 216.41 kg ha^{-1}, respectively. Most nutrients in the understory were concentrated below 3.3 m, but in the overstory, they were evenly distributed in each layer below 13.3 m. Although most nutrients accumulated in the stems, the accumulation of N, P, and Ca in the litter layer was higher than in the shrub and herb layer. This result suggested that the litter layer plays an important role in nutrient cycling in Guandaushi secondary hardwood forests. The N content at our research site was quite high compared to that at the Fushan Experimental Forest in northern Taiwan. Factors affecting the nutrient accumulation and allocation in this Guandaushi secondary hardwood forest need to be studied in the future.

Key words: mineral nutrient, secondary hardwood, carbon.

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研究報告

關刀溪次生林地上部養分的聚積和分配

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摘　要

本試驗於惠蓀林場第三林班內之關刀溪長期生態研究試區的次生闊葉林，選定一處20×20 m樣區，以分層收穫法進行闊葉樹林養分累積和分配的研究。養分聚積量的估算方面，地上部碳蓄積量為169,030.71 kg ha^{-1}、氮為2799.77 kg ha^{-1}、磷為52.24 kg ha^{-1}、鉀為715.70 kg ha^{-1}、鈣為918.72 kg ha^{-1}、以及鎂為216.41 kg ha^{-1}。在灌木與地被層中，養分分佈主要集中在3.3 m以下，喬木層則均勻分佈在13.3 m以下的各層中。雖然大部分養分累積分配在樹幹，但枯枝落葉層較灌木層及草本層累積更多的氮、磷、和鈣，顯示枯枝落葉層對關刀溪次生林養分循環的重要性。關刀溪次生林地上部N含量遠高於台灣東北部的福山試驗林。未來應延伸研究關刀溪次生林地上部養分的聚積和分配的影響原因。

關鍵詞：礦質養分、次生林、碳。

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INTRODUCTION

Biomass can generally be defined as the amount of accumulated organic matter found in an area at a given time. Therefore, biomass has a strong relationship with net primary production, and it is well known that studying the biomass of forest vegetation is very important for understanding the structure and function of forest ecosystems (Anderson 1970, Swank and Schreuder 1974, Melillo et al. 1993, Peng and Fang 1995, Fang et al. 1998). Furthermore, forest biomass accounts for approximately 90% of all living terrestrial biomass on the earth (Olson et al. 1983, Dixon et al. 1994).

Biomass estimates and nutrient contents of different tree components (e.g., foliage, branches, stems, and stem bark) were previously used as a function of biomass removal (Hendrickson et al. 1987) to describe temporal patterns of biomass and nutrient accumulation in chronosequences of paper birch stands on good, medium, and poor sites (Wang et al. 1996), compare carbon and nutrient storage in the aboveground vegetation and soil between a primary forest fragment and secondary forest stands (which were 10, 20, and 40 years old) (Johnson et al. 2001), report amounts of biomass, C, and nutrients in both the above- and below-ground pools (Hart et al. 2003), highlight implications for sustainable management at practically achievable production levels (Embaye et al. 2005), and quantify changes in C and nutrients in aboveground biomass along a vegetation gradient that represents stages in a transition from forest to savanna induced by fire (Dezzeo and Chacón 2005).

It was hypothesized that stand dynamics would differ from those of other forests, and that nutrient accumulation patterns may be unique in different forest ecosystems. Compared to temperate and tropical forests reported in the literature, little is known about nutrient patterns in subtropical forests. In this study, we used a stratified harvest method in a secondary hardwood forest to quantify the vertical distributions of nutrient storage in a Guandaushi subtropical forest. We hope this study will be a basis for discussing nutrient cycling and energy flows in this type of forests.

MATERIALS AND METHODS

Study area

This study was carried out in the Guandaushi Experimental Forest, central Taiwan (Fig. 1). The site is located within a 47-ha watershed with elevations ranging 1100~1700 m. The mean annual temperature is 20℃, and the annual rainfall is 2700 mm with distinct rainy and dry seasons (data from the nearest weather station at Huisun Experimental Forest station). Typhoons occasionally affect the area between June and September and bring intense precipitation and disturbances to the site. The site is a typical mid-elevation subtropical mixed-hardwood forests of central Taiwan, which is characterized by steep topography, abundant riparian ferns, virgin hardwood forests, and abundant epiphytes. The hardwood forests are composed of the typical Lauro-Fagaceae association of Taiwan. The Lauraceae (15 species) and Fagaceae (14 species) are the major families in the study area, and they respectively account for 4.60

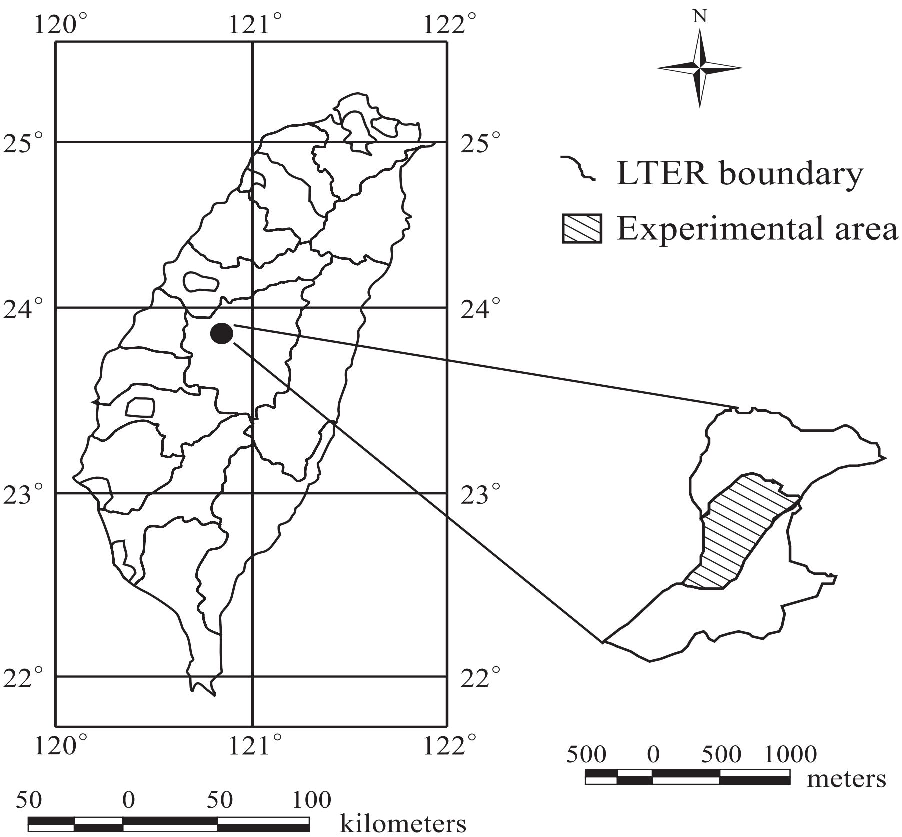

Fig. 1. Location of the study site at the Guandaushi Experimental Forest in central Taiwan.

and 4.29% of the total forest composition (Lu and Ou 1996).

Biomass determination (Hsiue and Sheu 2003)

A sample plot 20×20 m was established at the site. This large plot was subdivided into 16 subplots of 5×5 m to survey shrub and herb distributions. On each subplot, the diameters at 1.3-m height (DBH) of all trees of > 10 cm were measured, and then those trees were felled. Each felled tree was individually divided into sections according to its height (0~1.3, 1.3~3.3, 3.3~5.3, 5.3~7.3, 7.3~9.3, 9.3~11.3, and 11.3~13.3 m, respectively), and from each section, different parts, i.e., the stems, branches (no leaves), branchlets (leaves on), leaves, and necromass, of the tree were weighed in the field. A subsample was packed up and brought to the laboratory for oven drying and nutrient analyses. These subsamples were oven-dried to a constant weight at 70℃ for 48 h to calculate the water content of each sample and for the nutrient analyses. Biomass components of the shrub layer (< 10 cm in DBH) were separated and measured as described for the trees. In terms of the herb layer, we weighed all of the herbs collected and took subsamples. The litter layer was also collected in each subplot to estimate the biomass and conduct nutrient analyses.

Plant nutrient analyses

All biomass samples were oven-dried at 70℃ for 48 h, and ground in a Wiley mill to pass through a 0.149-mm mesh. Total C and N contents were analyzed by dry combustion using an elemental analyzer (elemental analyzer Vario EL, Elementar Analysensysteme GmbH, Hanau, Germany). Total P, K, Ca, and Mg contents of the plant parts were analyzed, after acidic (HNO_3/H_2SO_4) digestion, by inductive coupled plasma atomic emission spectroscopy (ICP-AES) (LeemanLabs, Inc., Hudson, NH, USA).

RESULTS

Stand characteristics of the overstory and understory were studied by Hsiu and Sheu (2003). Tree numbers, mean DBH, basal area, biomass, and the leaf area index (LAI) of each tree species and understory were obtained. These data showed that approximately 43% of tree numbers, 55% of the biomass, and 40% of the LAI were concentrated in 2 tree species, *Engelhardtia roxburghiana* and *Castanopsis fargesii*.

The aboveground biomass included the overstory biomass of 311.70 Mg ha^{-1}, the understory biomass of 23.03 Mg ha^{-1}, the necromass biomass of 3.39 Mg ha^{-1}, and an LAI of 9.52. The major distribution of biomass in the overstory was concentrated below 13.3 m in height, while that in the understory was below 7.3 m; the major distribution of the LAI in the overstory was concentrated at 5.3~15.3 m, while that in the understory was below 7.3 m.

Nutrient contents

Concentrations of C, N, and Ca increased with increasing height of the shrubs and herbs. Concentrations of P, K, and Mg tended to decrease with height in branches and leaves, but showed no differences in stems (Table 1). Table 1 also shows that most nutrients were generally concentrated in leaves, followed by branches and stems. Nutrient concentrations considerably varied among tree components and species. For example, concentrations of Ca varied by > 11-fold among branchlets (Table 2).

Concentrations of N, P, K, and Mg in trees increased with increasing height in the stem, but C and Ca concentrations changed little with height. Generally, the nutrient con-

Table 1. Mean concentration (mg g^{-1}) of nutrients of shrubs and herbs with respect to height and components in Guandaushi secondary hardwood forests

Height (m)	C			N			P		
	Stems	Branches	Leaves	Stems	Branches	Leaves	Stems	Branches	Leaves
0~1.3	468.49	466.02	456.54	7.05	9.15	21.82	0.11	0.29	0.76
1.3~3.3	468.11	467.47	476.44	6.76	9.12	19.70	0.14	0.25	0.64
3.3~5.3	469.22	473.23	495.52	5.68	9.59	21.99	0.12	0.26	0.74
5.3~7.3	472.37	478.15	495.30	5.74	8.04	19.01	0.12	0.17	0.67
7.3~9.3	474.19	475.77	501.31	7.12	10.23	22.25	0.10	0.31	0.69
9.3~11.3	478.40	470.11	503.06	7.95	10.52	24.51	0.15	0.18	0.44
11.3~13.3	476.52	476.66	502.70	7.05	9.93	24.78	0.13	0.18	0.62
Mean	472.47	472.49	490.12	6.76	9.51	22.01	0.12	0.23	0.65
Litter layer		487.62			16.12			0.49	
Height (m)	K			Ca			Mg		
	Stems	Branches	Leaves	Stems	Branches	Leaves	Stems	Branches	Leaves
0~1.3	2.01	4.28	11.82	2.05	2.48	5.03	0.49	1.60	3.75
1.3~3.3	1.91	3.65	8.33	2.59	4.10	5.70	0.52	1.19	2.63
3.3~5.3	1.76	3.82	8.41	1.91	2.66	3.49	0.40	0.90	1.71
5.3~7.3	1.71	2.03	6.03	1.84	2.35	3.50	0.40	0.69	1.65
7.3~9.3	1.59	2.60	8.67	2.14	3.18	4.11	0.45	0.84	1.50
9.3~11.3	2.92	3.93	6.43	3.51	3.65	4.20	1.00	1.50	1.70
11.3~13.3	1.95	2.44	6.64	3.00	4.00	5.29	0.59	0.92	1.81
Mean	1.98	3.25	8.05	2.43	3.20	4.47	0.55	1.09	2.11
Litter layer		1.44			5.01			1.19	

Table 2. Range of mean concentrations (mg g^{-1}) of nutrients of each tree species with respect to components in Guandaushi secondary hardwood forests

Component	C	N	P	K	Ca	Mg
Stems	469.57~513.39	4.77~8.58	0.01~0.25	0.74~3.02	0.84~7.57	0.15~0.98
Branches	467.02~510.79	6.11~13.15	0.09~0.76	1.10~7.19	1.00~6.55	0.21~1.89
Branchlets	461.66~515.77	8.20~20.40	0.10~1.04	1.89~14.91	1.26~14.45	0.50~3.49
Leaves	480.24~542.01	14.47~27.27	0.34~1.30	3.62~15.72	1.21~8.35	0.68~2.93
Necromass	466.64~511.06	6.94~21.79	0.05~0.65	0.21~5.55	1.99~10.30	0.32~2.52

centrations of trees were allocated as follows: leaves > branchlets > branches > stems (Table 3). With respect to height, the concentration of Mg in branchlets was generally higher than that in leaves with increasing height.

Nutrient accumulation and distribution

Total nutrient contents of the aboveground biomass were calculated by multiplying the nutrient concentrations by the dry weight of each tree component with respect to different heights. Those nutrient distribution patterns did not show the same trend as the patterns of biomass, except for C, especially in branches and leaves (Fig. 2). The aboveground biomass of shrubs and herbs was concentrated at 5.3~7.3 m, however, the contents of K and Mg were highest at 0~1.3

Table 3. Mean concentrations (mg g^{-1}) of nutrients of trees with respect to height and components in Guandaushi secondary hardwood forests

Height (m)	C					N					P				
	Stems	Branches	Branchlets	Leaves	Necromass	Stems	Branches	Branchlets	Leaves	Necromass	Stems	Branches	Branchlets	Leaves	Necromass
0.3~1.3	482.96	489.00	475.65	482.40	506.10	6.77	10.68	12.97	22.77	21.79	0.09	0.59	0.53	1.08	0.65
1.3~3.3	481.03	480.57	487.35	491.44	-	6.41	8.83	18.02	25.18	-	0.08	0.16	0.68	1.01	-
3.3~5.3	481.63	483.13	485.98	501.78	491.40	6.48	9.60	13.20	20.53	10.02	0.09	0.24	0.55	0.57	0.27
5.3~7.3	483.60	483.78	486.25	502.83	493.86	6.63	9.28	12.91	21.52	11.73	0.10	0.23	0.46	0.71	0.20
7.3~9.3	481.65	486.24	494.99	507.35	479.83	6.50	9.39	13.51	22.20	8.68	0.11	0.26	0.52	0.70	0.09
9.3~11.3	481.28	487.00	494.07	510.27	490.14	6.87	9.18	13.05	21.77	8.98	0.11	0.22	0.45	0.72	0.15
11.3~13.3	481.69	485.42	491.66	510.82	486.47	6.84	9.31	13.32	22.34	8.78	0.12	0.24	0.47	0.62	0.14
13.3~15.3	482.41	485.73	487.02	514.04	487.35	6.62	9.13	12.43	22.68	9.40	0.13	0.23	0.38	0.58	0.18
15.3~17.3	480.23	483.72	482.10	517.89	-	7.50	9.69	14.37	26.44	-	0.15	0.27	0.57	0.69	-
Mean	481.83	484.95	487.23	504.31	490.74	6.74	9.45	13.75	22.83	11.34	0.11	0.27	0.51	0.74	0.24

Height (m)	K					Ca					Mg				
	Stems	Branches	Branchlets	Leaves	Necromass	Stems	Branches	Branchlets	Leaves	Necromass	Stems	Branches	Branchlets	Leaves	Necromass
0.3~1.3	1.54	1.63	8.99	13.82	1.85	2.43	3.95	3.40	3.41	6.24	0.36	0.41	1.05	1.54	1.31
1.3~3.3	1.38	2.73	9.43	11.75	-	1.93	2.37	3.40	2.88	-	0.34	0.44	1.07	1.53	-
3.3~5.3	1.46	2.68	5.08	6.66	1.30	2.32	3.08	5.34	3.63	4.20	0.39	0.74	1.54	1.53	0.68
5.3~7.3	1.46	3.06	6.20	8.36	2.20	2.50	3.40	5.18	4.07	4.80	0.39	0.86	1.63	1.74	1.17
7.3~9.3	1.68	3.04	6.20	7.54	2.38	2.00	3.00	4.35	3.17	4.00	0.42	0.79	1.50	1.53	1.20
9.3~11.3	1.75	2.71	5.82	6.87	1.50	2.29	2.93	4.85	3.19	2.82	0.52	0.85	1.78	1.53	0.75
11.3~13.3	1.73	2.80	5.95	6.50	1.33	1.96	3.34	5.82	3.13	4.24	0.45	0.99	2.01	1.74	1.05
13.3~15.3	2.06	2.53	5.62	5.95	1.85	2.18	3.52	6.96	2.99	5.51	0.54	0.98	2.12	1.58	1.32
15.3~17.3	2.17	2.65	5.38	5.83	-	5.01	6.05	9.55	3.07	-	0.65	1.36	2.59	1.53	-
Mean	1.69	2.65	6.52	8.14	1.77	2.51	3.52	5.43	3.28	4.54	0.45	0.82	1.70	1.58	1.07

m. On the other hand, the greatest percentage on a weight basis of all nutrients accumulated in leaves, except for C. The total nutrient content was concentrated below 7.3 m, and the relative abundances of the different components in C and Ca had the same trend as biomass of stems > branches > leaves, while for other nutrients, the trend was stems > leaves > branches.

Nutrient contents of different components of trees were distributed with respect to height, and among total nutrient contents of different trees, only C had the same pattern as the biomass. P and Ca were concentrated at 5.3~7.3 m, however, K and Mg were concentrated at 11.3~13.3 m (Fig. 3).

Nutrient contents of different components of trees were allocated as follows: stems > branches > leaves > branchlets. Stem N, P, K, Ca, and Mg contents respectively comprised 65.59, 51.92, 56.15, 68.63, and 52.39% of the total aboveground nutrient contents. However, there was a greater stem C content (75.78%) than other nutrients, and the percentage was similar to that of biomass (75.77%). This resulted in branches, branchlets, and leaves accumulating higher percentages of N, P, K, Ca, and Mg on a weight basis. The leaf P content accounted for 13% of the total aboveground P contents, and the branch P, K, and Mg contents were also > 30% of the total aboveground nutrient contents (Table 4).

Table 5 shows that nutrient contents of major tree species. The C content had the same trend of percentage as the biomass (Hsiue and Sheu 2003) in these different tree species. *Glochidion lanceolatum*, *Elaeocarpus japonicus*, *Cinnamomum subavenium*, *Engelhardtia roxburghiana*, and *Castanopsis fargesii* (the tree numbers of which accounted for 75% in this stand plot) accounted for 80.08% of the N, 78.18% of the P, 81.03% of the K, 79.58% of the Ca, and 81.27% of the Mg of the aboveground biomass. *Schima superba*, *Elaeocarpus japonicus*, *Cinnamomum subavenium*,

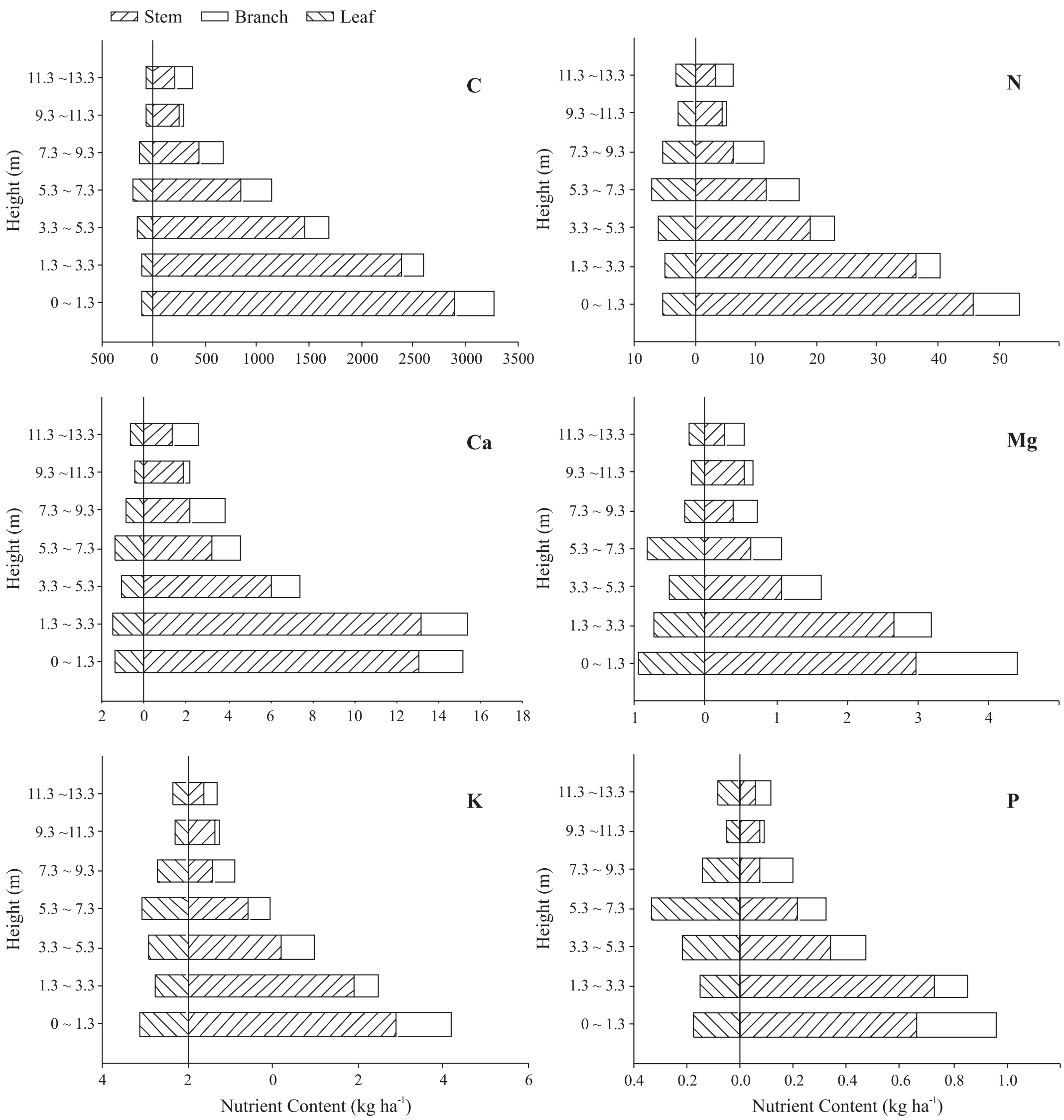

Fig. 2. Nutrient contents of different components of the shrub and herb distributed with respect to height in Guandaushi secondary hardwood forests.

Engelhardtia roxburghiana, and *Castanopsis fargesii* (the biomass of which accounted for 75% of the total aboveground biomass) accounted for 79.61% of the N, 77.44% of the P, 79.63% of the K, 80.61% of the Ca, and 80.95% of the Mg. Regardless of whether from a tree number or biomass point of point, these dominant trees accounted for about 80% of the nutrient contents in the stand.

In terms of the nutrient content distribution with respect to the 4 strata (Table 6), 169,030.71 kg ha^{-1} of C had accumulated in the aboveground biomass which accounted for about half of the total biomass. Aboveground biomass values of N, P, K, Ca, and Mg were respectively 2799.77, 52.24, 715.70, 918.72, and 216.41 kg ha^{-1}. Generally, trees accumulated the greatest percentage (about

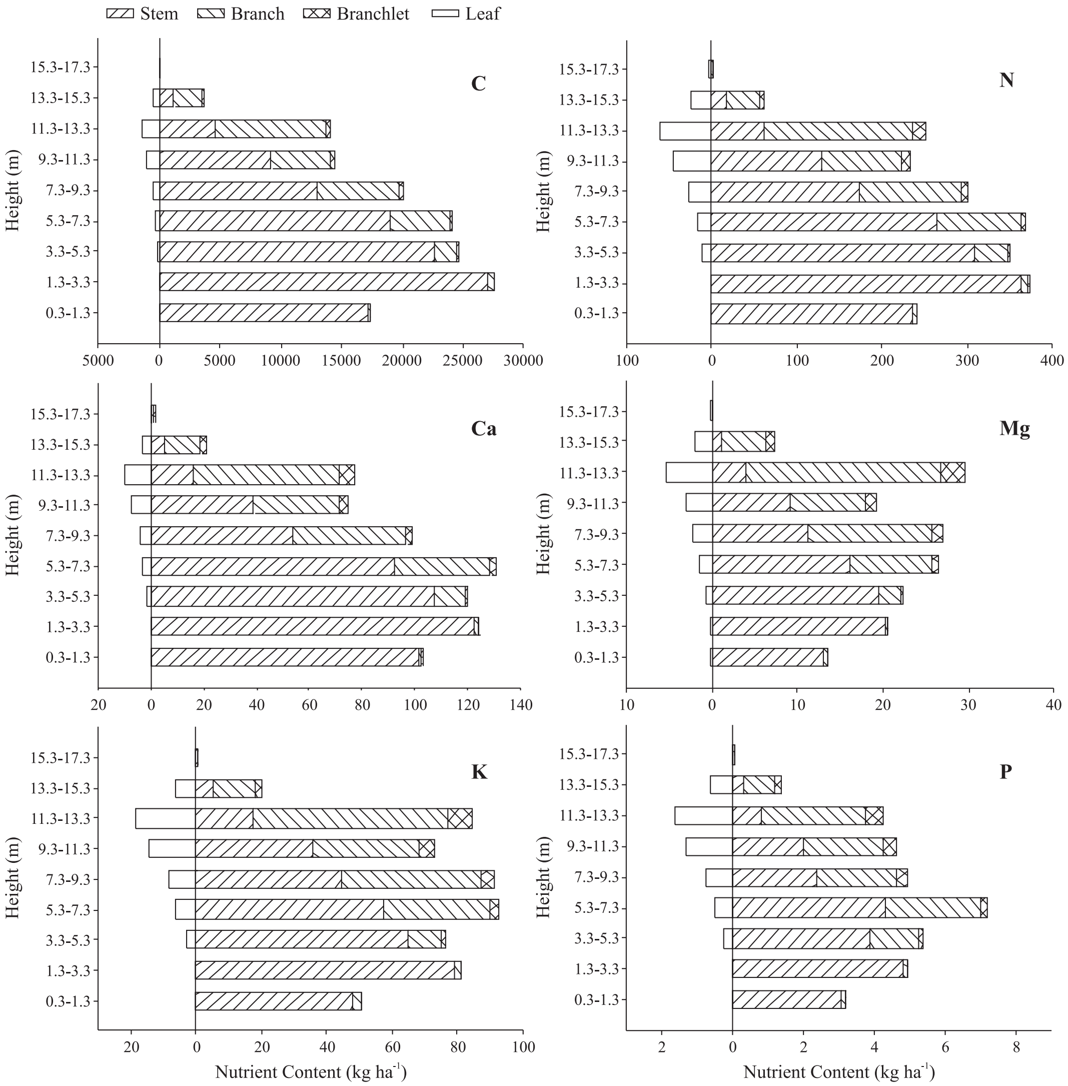

Fig. 3. Nutrient contents of different components of trees distributed with respect to height in Guandaushi secondary hardwood forests.

80%) on a weight basis of all nutrients. On the other hand, although the litter biomass represented 3.64% of the total aboveground biomass (Hsiue and Sheu 2003), the N, P, Ca, and Mg content accounted for 7.32, 12.42, 6.95, and 6.86%, respectively. The relative contributions of shrubs and herbs to the total aboveground nutrient contents were 6.84% of N, 7.96% of P, 6.38% of Ca, and 7.40% of Mg.

DISCUSSION

There were large differences in nutrient accumulation and distribution patterns in trees and shrubs, except carbon which had a similar pattern as biomass (Hsiue and Sheu 2003). This observation can mainly be explained by nutrient concentrations of different components (Johnson 1974, Uhl and Jordan 1984, Lin et al. 1996), due to the different

Table 4. Nutrient contents (kg ha^{-1}) of trees distributed with respect to height and component in Guandaushi secondary hardwood forests

Height (m)	C					N					P				
	Stems	Branches	Branchlets	Leaves	Necromass	Stems	Branches	Branchlets	Leaves	Necromass	Stems	Branches	Branchlets	Leaves	Necromass
0.3~1.3	17,129.64	277.79	7.03	15.46	13.31	236.86	5.07	0.23	0.69	0.20	3.05	0.13	0.01	0.02	0.00
1.3~3.3	27,084.82	436.90	8.44	21.59	70.10	362.64	9.01	0.34	1.18	1.37	4.80	0.10	0.01	0.04	0.01
3.3~5.3	22,636.45	1906.90	124.48	226.31	168.99	309.08	38.14	3.26	10.08	3.33	3.84	1.38	0.14	0.30	0.05
5.3~7.3	19,070.83	4778.86	196.02	384.89	154.16	263.05	100.63	5.33	16.73	3.66	4.30	2.70	0.18	0.53	0.05
7.3~9.3	12,949.26	6800.42	272.81	589.28	276.37	172.46	121.22	7.46	26.31	5.24	2.33	2.29	0.26	0.78	0.06
9.3~11.3	9243.79	4865.18	411.15	1042.45	504.73	129.73	92.23	11.25	44.74	10.21	1.96	2.24	0.39	1.31	0.14
11.3~13.3	4514.14	9119.97	518.26	1351.96	421.11	62.95	173.80	14.61	60.67	8.48	0.77	2.95	0.53	1.67	0.16
13.3~15.3	1222.46	2197.48	202.47	528.53	26.82	17.07	40.43	5.26	23.32	0.54	0.27	0.90	0.16	0.64	0.01
15.3~17.3	45.70	60.66	11.73	38.58	--	0.71	1.32	0.37	1.97	--	0.02	0.02	0.01	0.05	--
Total	113,897.08	30,444.17	1752.39	4199.05	1635.60	1554.54	581.84	48.11	185.70	33.02	21.35	12.72	1.69	5.34	0.48

Height (m)	K					Ca					Mg				
	Stems	Branches	Branchlets	Leaves	Necromass	Stems	Branches	Branchlets	Leaves	Necromass	Stems	Branches	Branchlets	Leaves	Necromass
0.3~1.3	48.29	2.26	0.11	0.19	0.01	101.37	1.53	0.08	0.15	0.08	13.16	0.49	0.03	0.08	0.01
1.3~3.3	79.01	2.19	0.17	0.50	0.35	122.39	2.09	0.06	0.10	0.49	20.20	0.41	0.01	0.04	0.18
3.3~5.3	64.92	10.26	1.24	3.25	0.69	107.47	11.51	1.12	1.45	1.25	19.47	2.54	0.30	0.64	0.37
5.3~7.3	57.55	32.59	2.39	6.13	0.80	92.29	36.55	1.95	3.15	1.28	16.10	9.73	0.69	1.31	0.35
7.3~9.3	44.86	42.83	3.52	8.35	1.21	53.42	43.43	2.56	4.08	2.93	11.26	14.46	1.15	2.09	0.79
9.3~11.3	36.02	32.14	5.18	14.69	3.19	38.97	32.10	3.81	7.30	3.99	9.28	8.60	1.39	2.94	1.66
11.3~13.3	17.39	59.89	7.26	18.53	3.53	15.83	55.62	5.57	9.98	3.49	3.90	22.73	2.90	5.20	1.45
13.3~15.3	5.03	12.78	2.46	6.15	0.18	4.90	14.02	2.47	3.64	0.22	1.22	4.99	1.04	1.95	0.08
15.3~17.3	0.21	0.33	0.13	0.42	--	0.39	0.74	0.21	0.21	--	0.06	0.13	0.06	0.10	--
Total	353.28	195.26	22.45	58.20	9.97	537.03	197.58	17.83	30.05	13.75	94.65	64.08	7.57	14.34	4.90

Table 5. Nutrient contents (kg ha^{-1}) of major tree species in Guandaushi secondary hardwood forests

	C	N	P	K	Ca	Mg
Neolitsea variabllima	743.25 (0.49)*	10.23 (0.43)	0.20 (0.48)	2.76 (0.44)	4.03 (0.51)	0.37 (0.21)
Litsea acuminata	1890.91 (1.26)	31.21 (1.32)	0.78 (1.91)	9.04 (1.44)	10.17 (1.30)	1.46 (0.81)
Cunninghamia lanceolata	1885.92 (1.25)	28.37 (1.20)	0.60 (1.45)	4.92 (0.78)	9.70 (1.24)	1.20 (0.66)
Lithocarpus nantoensis	3593.27 (2.39)	59.66 (2.52)	1.48 (3.59)	13.40 (2.13)	14.70 (1.88)	3.81 (2.11)
Cyclobalanopsis glauca	3827.46 (2.55)	60.05 (2.53)	0.91 (2.22)	13.47 (2.14)	21.28 (2.72)	4.16 (2.30)
Castanopsis kawakamii	4276.40 (2.85)	67.54 (2.85)	0.84 (2.05)	12.08 (1.92)	19.91 (2.54)	4.37 (2.42)
Diospyros morrisiana	6517.23 (4.34)	110.69 (4.67)	1.92 (4.67)	33.67 (5.35)	43.39 (5.54)	8.71 (4.82)
Glochidion lanceolatum	6719.60 (4.47)	115.39 (4.87)	2.55 (6.20)	38.79 (6.17)	28.58 (3.65)	10.35 (5.73)
Schima superba	8216.84 (5.47)	104.38 (4.40)	2.24 (5.46)	29.99 (4.77)	36.64 (4.68)	9.77 (5.41)
Elaeocarpus japonicus	10,289.57 (6.85)	171.55 (7.24)	2.83 (6.89)	40.75 (6.48)	52.55 (6.72)	9.98 (5.53)
Cinnamomum subavenium	13,358.61 (8.89)	201.60 (8.50)	3.14 (7.65)	55.27 (8.78)	47.57 (6.08)	10.49 (5.81)
Engelhardtia roxburghiana	32,337.26 (21.51)	576.34 (24.31)	11.84 (28.80)	158.16 (25.13)	235.85 (30.14)	39.83 (22.05)
Castanopsis fargesii	56,649.43 (37.69)	833.40 (35.16)	11.78 (28.64)	216.93 (34.47)	258.18 (32.99)	76.15 (42.15)

* Numbers in parentheses are percentage of nutrient contents for the different species.

patterns between nutrient and biomass accumulation resulting from large differences in concentrations of nutrient in different components. Sander and Ericsson (1998) studied the vertical distribution of elements in the woody biomass of 2 willow stands and found that concentrations of P, K, Ca, Mg, S, Mn, Zn, Cu, Ni, and Cd significantly increased with height, which was assumed to mainly be a consequence of increasing bark proportions. Concentrations of plant nutrients are generally higher in bark than in wood, indicating a difference in the concentration gradient between elements being ascribed in part to their

Table 6. Nutrient contents (kg ha^{-1}) distributed with respect to 4 strata in Guandaushi secondary hardwood forests

Stratum	Biomass	C	N	P	K	Ca	Mg
Tree	311,769 (88.83)*	150,292.69 (88.91)*	2370.19 (84.66)	41.11 (78.69)	629.20 (87.91)	782.49 (85.17)	180.65 (83.48)
Shrub and Herb	23,030 (6.56)	10,868.40 (6.43)	191.53 (6.84)	4.16 (7.96)	58.31 (8.15)	58.59 (6.38)	16.01 (7.40)
Litter layer	12,776 (3.64)	6234.02 (3.69)	205.03 (7.32)	6.49 (12.42)	18.22 (2.55)	63.89 (6.95)	14.85 (6.86)
Necromass	3390 (0.97)	1635.60 (0.97)	33.02 (1.18)	0.48 (0.92)	9.97 (1.39)	13.75 (1.50)	4.90 (2.26)
Total	350,965	169,030.71	2799.77	52.24	715.70	918.72	216.41

* Numbers in parentheses are percentages of the total content.

differential redistributions in tissues. Similar trends were found for the concentrations of N, P, K, Ca, and Mg from most tree stems in our study.

In terms of leaf nutrient accumulation and distribution, the concentration of Mg was much higher in shrubs and herbs than in trees, indicating that understory plants had higher levels of chlorophyll to catch more light in the darker environment.

As Vogt et al. (1986) reported, there can be considerable variability in forest floor detritus, and this appears to be the case for the few Taiwanese studies. The amount of material in the litter layer (12.78 Mg ha^{-1}) at the Guandaushi secondary hardwood was much higher than the 6.85 Mg ha^{-1} measured by Horng et al. (1986) at Lienhuachih and 4.58~5.10 Mg ha^{-1} measured by Lin et al. (1994) at Fushan. Our measurements showed that the litter layer had accumulated 6.86~12.42% of total nutrients, except for K which was 2.55%; moreover, the accumulation of N, P, and Ca in the litter layer was higher than in shrubs and herbs, and it was apparent that there was a strong effect of stand composition on forest ecosystem biomass and nutrient accumulation (Cannell 1982).

The nitrogen content in this stand was far higher than those in other studies. In our research, ranges of nitrogen concentrations in stems, branches, branchlets, and leaves were 4.77~8.58, 6.11~13.15, 8.20~20.40, and 14.47~27.27 mg g^{-1}, respectively. Results showed that the nitrogen concentration in woody components was quite high compared to that of the Fushan Experimental Forest in northern Taiwan (Lin et al. 1996). We suggest that this difference may have been due to environmental factors (for example, precipitation) and different analytical methods (i.e., a combustion method was used in this study, and a Kjeldahl method was used at Fushan). Alavoine and Nicolardot (2000) compared results obtained between a high-temperature catalytic oxidation method (HTCO) and a Kjeldahl digestion method for total N measurement and found that both methods were in good agreement, while the HTCO method was more efficient.

CONCLUSIONS

In terms of nutrient content distributions with respect to the 4 strata, 169,030.71 kg ha^{-1} C accumulated in the aboveground portion and represented about half of the biomass. N, P, K, Ca, and Mg respectively accumulated at 2799.77 kg ha^{-1}, 52.24 kg ha^{-1}, 715.70 kg ha^{-1}, 918.72 kg ha^{-1}, and 216.41 kg ha^{-1} of the aboveground biomass. Nutrient contents of different components of trees were allocated as follows: stems > branches > leaves > branchlets. Stem N, P, K, Ca, and Mg contents respectively comprised 65.59, 51.92, 56.15, 68.63, and 52.39% of the total aboveground nutrient contents. Although most nutrients accumulated in stems, the accumulation of N, P, and Ca in the litter layer was higher than that in the shrub and herb layer. This result suggests that the litter layer plays an important role in nutrient cycling in Guandaushi secondary hardwood forests. Further investigations are needed to determine the factors affecting variations in nutrient concentrations and flux in Guandaushi secondary hardwood forests.

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