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Throughfall Patterns in a Subtropical Rain Forest of Northeastern Taiwan

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ABSTRACT

Throughfall chemistry of a subtropical rain forest in Taiwan was examined for 3 yr to understand patterns of nutrient inputs to the forests of this region. Annual throughfall fluxes for NH_4^+, NO_3^-, and SO_4^{2-} (89, 28, and 83 mmol/m^2/yr, respectively) were close to the levels of the most polluted areas in the temperate region. The lack of major emission sources near the study site indicates that most of the pollutants were regional and/or international in origin. High rates of cation leaching from the forest canopy were evident and the pattern is similar to that seen in heavily polluted temperate forests. Typhoons played a central role in the hydrology of the study forest with eight typhoons contributing 26% of the total rainfall in 320 h over the three years monitored. This typhoon input represented 20% of the total precipitation flux of the ions found in seasalt aerosols but less than 10% of anthropogenically enriched ions. Canopy leaching was an important source of base cations in throughfall and NO_3^- was retained in the canopy. Using the Na-ratio method the contribution of dry deposition relative to precipitation input was estimated to be 40% in the summer and 10% in the winter. The contribution of dry deposition to total deposition is small relative to many temperate forests and might result from the lack of long dry periods between precipitation events. Net throughfall flux was negatively related to precipitation concentration for H^+, NH_4^+, NO_3^-, and SO_4^{2-}, suggesting that passive movement was important in characterizing throughfall dynamics.

During the past two decades throughfall analyses have become a routine method for estimating atmospheric input of pollutants in forest ecosystems. These studies have increased our understanding of the factors affecting throughfall chemistry, including forest type (evergreen vs. deciduous) (Cronan and Reiners, 1983), species (Norden, 1991), canopy components and position (Reiners and Olson, 1984), and elevation (Lovett and Kinsman, 1990). Yet, limited data are available for comparisons of throughfall dynamics of temperate forests with other types of forests. In particular, only a few studies examine throughfall dynamics within tropical and subtropical forests (Jordan et al., 1980; Vitousek and Sandford, 1986; Veneklaas and van Ek, 1990; Lin et al., 1997). Many tropical and subtropical regions experience deposition of anthropogenic N and S at rates much higher than the suggested critical loads for temperate forests (Schulze et al., 1989; Langan and Hornung, 1992; Lin et al., 1998). Therefore, if air pollution has a detrimental effect on the health of forest ecosystems, then forests in tropical and subtropical regions are likely to be negatively affected by current air pollution loads. In fact, the low soil base saturation of many tropical and subtropical forests could make them more susceptible to negative pollutant effects than many temperate forests (subtropical humid forests in Taiwan have a base saturation <15%; Chiang et al., 1994).

Numerous methods have been used to measure or estimate dry deposition on forest canopies (for review see Davidson and Wu, 1990), with multiple regression models (Lovett and Lindberg, 1984) and the Na-ratio approach (Mayer and Ulrich, 1974; Gosz, 1980) the most widely used. Both have been successfully applied to a variety of forests in the temperate region (Brown and Lund, 1994; Cappellato and Peters, 1995), but neither has been used in tropical or subtropical forests. The multiple regression method describes net throughfall flux (NTF) as linearly dependent on the amount of precipitation (P) and the length of the proceeding dry period (D). The Na-ratio method assumes that because Na concentration in foliage is very low, almost all (>90% Parker, 1983) of the throughfall Na^+ in excess of that in precipitation can be attributed to dry deposition. Dry deposition of other chemicals can be calculated on the basis of the Na to chemical ratios in atmospheric particles or more commonly in bulk precipitation. The contribution of canopy exchange to throughfall nutrient flux can be derived from the difference between throughfall flux and total atmospheric input (wet + dry). The two methods differ in their assumptions, but because no unique measurement needs to be made both are easy to apply.

In this study we examined throughfall dynamics within a subtropical rain forest in northeastern Taiwan. The area is characterized by frequent rainfall and is affected by air masses originating from mainland China during the winter. We examined the difference in volume, ion concentrations, and fluxes of throughfall among three forested plots, and examined the importance of typhoons on atmosphere–canopy interactions. We employed the Na-ratio method and multiple regression models in order to evaluate the contribution of dry deposition and canopy exchange to throughfall fluxes.

METHODS

Study Site

Measurements were made in Watershed 1 (37 ha) of the Fu-shan experimental forest in northeastern Taiwan (24°34′ N, 121°34′ E) (Fig. 1). The watershed varies in elevation from 670 to 1100 m. Between 1993 and 1998, annual precipitation ranged from 2900 to 6000 mm, annual mean temperature was 18.2°C with the lowest in January (11.8°C) and highest in July (24.1°C), and annual mean relative humidity was 96% with

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Abbreviations: NTF, net throughfall flux; P, precipitation; TF, throughfall.

the lowest in July (94%) and highest in February (98%). There is some elevational variation in precipitation patterns for individual storms but the variation in total annual precipitation across the watershed is <5% (Hsia, unpublished data). Heavy fog is common in the winter, but is usually accompanied by gentle precipitation, making collection of fog extremely difficult, if not impossible.

The watershed is drained by a first order stream that is a tributary of the Nan-she-chi River. The forest is characterized as a moist subtropical mixed evergreen forest without an observable dormant season. The dominant tree species are *Castanopsis carlesii* (Hemsl.) Hayata, *Litsea acuminata* (Bl.) Kurata, *Diospyros morrisiana* Hance, *Elaeocarpus japonicus* Turcz, *Persa thunbergii* (Sieb & Zucc) Kosterm, *Persea zuihonesis* (Hayata) Li, *Meliosma squimulata* Hance and *Pyrenaria shinkoensis* (Hayata) Keng. The forest is multistoried with scattered tree ferns (*Alsophila podophylla* Hook) and dense shrubs (mainly *Blastus cochinchinensis* Lour, *Helicia formosana* Hemsl. and *Lasianthus obliquinervis* Uerr.), with a herbaceous ground story. The soil is Typic Dystochrepts characterized as very acidic (pH 3.8–5.0) with low cation exchange capacity and very low base saturation (<5%) (Chiang et al., 1994).

Three 20- × 20-m plots were established on the lower one-eighth of the watershed (<700 m), and within each plot six throughfall collectors, consisting of three 20-cm diameter funnels, were located 0.5 m apart and 1.5 m above the ground arranged in a line and connected to a 30-L bucket using polypropylene tubing (Lin et al., 1997). Each funnel had a 6-cm vertical lip and a 45° slope to minimize splashing. To reduce the influence of plants directly over the collectors, all leaves and branches 1 m above the funnels were removed. To prevent leaves, small branches, and insects from falling into the funnels, each funnel was covered with 3-mm mesh plastic screening. Screening (0.5 mm) was also placed between the mouth of the funnel and the polypropylene tube.

Incident precipitation was collected using three collectors mounted on top of a 6-m tower in a forest clearing near the weir of Watershed 1. Each collector consisted of two funnels; the same type as used to collect throughfall, connected with polypropylene tubing to a 30-L plastic bucket on the ground. Rainfall volume and chemistry differed among the three precipitation collectors by less than 5% for the first 10 rainfall events. Therefore, samples from the three collectors were combined.

We explored using wet-only deposition employing Anderson wet–dry collectors (Anderson Sampler, Atlanta, GA), but they did not perform adequately during the frequent light rainfall events, when the rainfall intensity was close to the rate of evaporation. The difference in the chemical composition of wet-only deposition and bulk precipitation in the study area is minimal because of the high frequency of rain events, the low rates of dry deposition (Lin et al., 1993), and the low efficiency of funnels in collecting dry deposition.

Sample Collection and Laboratory Analysis

Precipitation and throughfall were collected after each rainfall event, which was defined as at least 5 mm of rain occurring between dry periods of at least 6 h. This minimum rainfall was selected in order to ensure sufficient water for chemical analysis. At our study site, canopy drip occurred for up to 6 h following cessation of rainfall.

The volume of all throughfall and precipitation samples was measured in the field and a 500-mL subsample was taken. The remainder of the samples was used to clean the collectors, tubing, and storage bucket. Every 90 d, collectors were washed with deionized water until the conductivity of the rinse water was less than 4 μohm/cm. Conductivity and pH were measured on all samples within 3 h of collection in our field laboratory, after which samples were transported to our main laboratory in Taipei for chemical analysis. Prior to analysis, samples were stored at 5°C without preservatives. Filtered samples (GN-6 grid 0.45-μm sterilized filter paper, Gelman Science, Ann Arbor, MI) were analyzed for both anions and cations including Cl^-, NO_3^-, SO_4^{2-}, Na^+, K^+, Ca^{2+}, Mg^{2+}, NH_4^+, and PO_4^{3-} using ion chromatography (Lin et al., 1997). The concentrations of PO_4^{3-} were below or near the detection limit and thus are not reported. Alkalinity was determined by titration with 0.005 *M* H_2SO_4 to pH 4.52 (Lin et al., 1997). Analysis of 10 split samples showed a variability of 8% for NH_4^+ and less than 5% for all other ions. Blind analysis of certified reference samples (SPEX Industries, Edison, NJ) yielded concentrations with less than 5% variation from the certified standard for all anions.

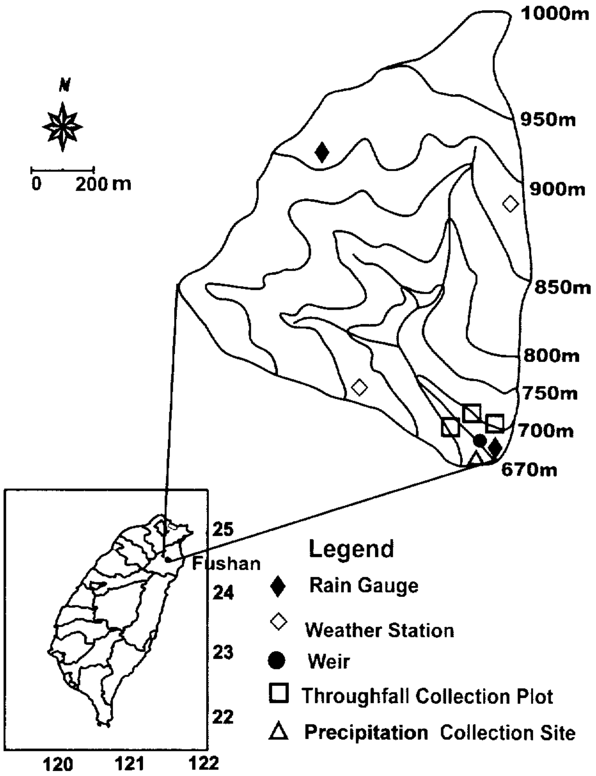

Fig. 1. Topographic map of Watershed 1 of Fu-shan experimental forest.

Data Analysis

The relationship between precipitation and throughfall quantity was examined using linear regression models. Both the multiple regression method (net throughfall flux [NTF] = $b_1P + b_2D$, where b_1 is the canopy exchange coefficient and b_2 is the dry deposition coefficient; Lovett and Lindberg, 1984) and the Na-ratio method (Mayer and Ulrich, 1974; Gosz, 1980) were applied to estimate dry deposition and canopy exchange effect. The relationship of net throughfall flux and concentration of a given ion in precipitation was examined using linear regression models (throughfall flux = $a + b$ concentration in precipitation). Differences in ion concentrations and fluxes between precipitation and throughfall and among the three forested plots were examined using analysis of variance (ANOVA; SPSS, 1992).

Table 1. Averaged monthly precipitation, rainy days, rainy hours, and frequency of daily maximum storm intensities (mm/hr) as measured at rain gauge by the weir between 1994 and 1996.

Statistic	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Storm intensity (mm/hr)												
≤1	12	12	14	6	4	4	3	5	5	9	11	13
1–2	5	6	2	5	3	3	1	3	5	3	3	4
2–5	5	3	3	7	4	4	5	1	2	4	4	3
5–10	0	1	1	1	4	4	2	2	3	3	2	1
10–20	0	0	2	1	1	1	2	1	2	1	1	0
20–30	0	0	0	0	2	2	0	2	0	0	0	0
>30	0	0	0	0	1	1	1	2	0	1	1	0
Rainy days	22	22	22	21	19	19	14	16	17	21	22	21
Rainy hours	198	189	145	120	124	67	75	110	153	188	209	178
Total mm	173	191	154	225	284	260	496	554	453	614	474	213

RESULTS

Precipitation and Interception

One hundred and sixty rain samples were collected from 1 Jan. 1994 to 31 Dec. 1996. Two periods, summer (April to September) and winter (October to March) were assigned to the 160 events with 100 during the summer and the remainder during the winter. Some samples contained more than one event, due to night-time events and very short periods between rainfall events, which did not allow for sample collection. Winter storms are typically of low intensity (<5 mm per h); whereas heavy storms with high intensities are common in the summer (Table 1).

The importance of intensive summer storms is seen in the contribution of typhoons to annual rainfall. Six typhoons in 1994 contributed 2270 mm rainfall in a 271-h period, representing 46% of the annual rainfall, and two typhoons in 1996 contributed 880 mm rainfall in a 49-h period, representing 20% of the annual rainfall.

No statistical difference in throughfall amount or chemical composition was found among the three plots. Therefore, the mean of the three plots was used in analyses. There was a strong linear relationship between the quantities of precipitation and throughfall (Throughfall [mm] = −0.24 [mm] + 0.90 precipitation [mm]; $R^2 = 0.98$), and throughfall represented a higher percentage of precipitation in summer (95%) than in winter (87%) (Table 2). Interception, the water not making it though the canopy, was assumed to be the difference between throughfall and precipitation (Table 2). Because previous research at the study site indicated that stemflow volume was <1% of throughfall volume (Wang, 1994), stemflow was not measured.

Precipitation and Throughfall Chemistry

The most abundant ions in precipitation were Cl^- and Na^+ followed by SO_4^{2-}. In addition to these three ions, HCO_3^- and base cations (K^+, Ca^{2+}, and Mg^{2+}) were also abundant in throughfall (Table 3). Charge balance for precipitation showed a slight anion deficiency in precipitation (summer 2.4%, winter 3.2%) and in throughfall (summer 6.3%, winter 8.0%) (Table 3).

Table 2. Mean precipitation, throughfall fluxes, and net throughfall fluxes (mmol/m²/period) and dry deposition and canopy exchange calculated using the Na-ratio method in WS1 of the Fu-shan Forest calculated on a seasonal (winter [October–March] and summer [April–September]) and annual basis.

		Ion flux									
Flux pathway	H_2O	H^+	Na^+	K^+	Ca^{2+}	Mg^{2+}	NH_4^+	Cl^-	NO_3	SO_4^{2-}	HCO_3^-
	mmol/m²/period										
						Summer					
Precipitation	2225	37.7	60.0	18.6	24.1	12.0	48.2	83.4	22.9	30.0	59.4
		*	*	*	*					*	
Throughfall	2117	2.5	86.0	87.4	53.3	32.6	53.4	114.7	17.2	34.7	152.3
Net throughfall	−108	−35.2	26.0	68.8	29.2	20.6	5.2	31.3	−5.7	4.8	92.9
Dry deposition		16.3	26.0	8.1	10.5	5.2	20.9	36.1	9.9	13.0	25.7
Canopy exchange		−51.5	0	60.7	18.8	15.5	−15.7	−4.9	−15.6	−8.2	67.1
						Winter					
Precipitation	1879	45.5	124.3	10.4	23.6	15.7	36.7	133.7	20.3	40.3	42.5
				*		*			*		*
Throughfall	1642	6.1	136.3	63.4	59.6	34.5	36.1	145.3	11.2	48.1	113.7
Net throughfall	−237	−39.4	12.0	53.0	36.0	18.8	−0.6	11.6	−9.1	7.8	71.2
Dry deposition		4.4	12.0	1.0	2.3	1.5	3.5	12.91	2.0	3.9	4.1
Canopy exchange		−43.8	0.0	52.0	33.8	17.3	−4.1	−1.3	−11.1	3.9	67.1
						Annual					
Precipitation	4104	83.2	184.3	29.0	47.7	27.7	84.9	217.1	43.2	70.3	101.9
		*	*	*	*	*			*		*
Throughfall	3759	8.6	222.3	150.8	122.9	67.1	89.5	259.9	28.4	82.8	265.9
Net throughfall	−345	−74.6	38.0	121.8	65.2	39.4	4.6	42.8	−14.8	12.6	164.0
Dry deposition		20.7	38.0	9.1	12.7	6.7	24.4	49.0	11.9	16.9	29.8
Canopy exchange		−95.3	0.0	112.7	52.5	32.7	−19.8	−6.2	−26.7	−4.4	134.2

* Significant difference ($p < 0.05$) between precipitation and throughfall fluxes (calculated on an event basis).

Table 3. Volume weighted concentrations of various chemicals (μmol/L) in precipitation (P) and throughfall (TF) on a seasonal (summer [April–September] and winter [October–March]) and annual basis.

Flow pathway	Ion concentration										
	H^+	Na^+	K^+	Ca^{2+}	Mg^{2+}	NH_4^+	Cl^-	NO_3^-	SO_4^{2-}	HCO_3^-	$\frac{(\Sigma+) - (\Sigma-)}{(\Sigma+) + (\Sigma-)}$
	μmol/L										%
							Summer				
P	16.9	27.0	8.4	10.9	5.4	21.7	37.5	10.3	13.5	26.7	2.4
	*	*	*	*	*		*			*	
TF	1.2	40.6	41.3	25.2	15.4	25.2	54.2	8.1	16.4	71.9	6.3
							Winter				
P	24.2	66.2	5.5	12.6	8.4	19.5	71.2	10.8	21.5	22.6	3.2
	*		*	*	*					*	
TF	3.7	83.0	38.6	36.6	21.0	22.0	88.5	6.8	29.3	69.2	8.0
							Annual				
P	20.3	44.9	7.1	11.7	6.8	20.7	52.9	10.5	17.1	24.4	2.8
	*		*	*	*					*	
TF	2.3	59.1	40.1	30.1	17.9	23.8	69.2	7.6	22.1	70.8	7.3

* Significant difference ($p < 0.05$) between precipitation and throughfall concentrations (calculated on a paired event basis using paired *t*-test).

All ions with the exception of H^+ and NO_3^- were enriched while passing through the forest canopy, though not necessarily significantly (Tables 2 and 3). The concentration and flux of H^+ and NO_3^- were significantly lower in throughfall than in precipitation, with the concentration of H^+ decreasing from 20 to 2 μmol/L while passing through the canopy and a corresponding increase in pH from 4.5 to 5.4. In contrast, alkalinity ($[HCO_3^-]$) increased from 25 to 71 μmol/L while passing through the canopy. Simple linear regression analysis using NTF as the dependent variable and precipitation concentration as the independent variable showed a highly significant negative relationship for all ions except Cl^- and HCO_3^- (Table 4). In other words, NTF tended to be more positive when the concentration of ion in precipitation was low, compared with when it was high.

All typhoon precipitation had high pH (>5.6) and high alkalinity. The eight typhoons that struck our study site during 1994–1996 contributed 40% of the total precipitation flux of HCO_3^- but only 2% of the total flux of H^+. Typhoon precipitation was rich in seasalt aerosols, contributing 21, 22, and 23% of the total flux of Na^+, Mg^{2+}, and Cl^-, respectively. For K^+ and Ca^{2+}, the corresponding loads were 15 and 24%. Yet, precipitation associated with typhoons had low fluxes of ions primarily derived from anthropogenic sources (i.e., <9% of the total flux of NH_4^+, NO_3^-, and SO_4^{2-}). Total throughfall flux of the eight typhoons contributed 27% of the annual throughfall flux of HCO_3^-; 15 to 25% of Na^+, K^+, Ca^{2+}, Mg^{2+}, Cl^-, and NO_3^-; 11% of NH_4^+ and SO_4^{2-}; and 9% of H^+.

Dry Deposition and Canopy Exchange

Periods of light rainfall (<0.5 mm/h) are very common in the winter, thus it is very hard to accurately determine periods without rain. For practical purposes we defined individual rainfall events as requiring at least 5 mm of total rain occurring between dry periods of at least 6 h duration; the result of this definition is that there was often light rain occurring during rainless periods. Consequently, dry periods, an essential component of the multiple regression models employed, were often not accurately reflected in the data (Lovett and Lindberg, 1984). During 1994 only 22 rainfall events had well-defined antecedent dry periods from which to estimate rates of dry deposition and canopy exchange using the multiple regression model. The multiple regression model yielded significant coefficients of determination (R^2) for H^+, Na^+, K^+, Ca^{2+}, and Mg^{2+}, but not for other ions (Table 5). The contribution of dry deposition relative to precipitation ranged from 14 to 130% for Na^{2+}, K^+, Ca^{2+}, and Mg^{2+} using the multiple regression model (Table 5). Based on the Na-ratio method the contribution of dry deposition relative to precipitation was about 30% for the 22 winter rainfall events used in the multiple regression analysis (Table 5).

The Na-ratio method indicated a negative canopy effect for H^+, NH_4^+, Cl^-, NO_3^-, and SO_4^{2-}, whereas the multiple regression model indicated that only H^+ and NO_3^- had a negative canopy exchange rate. Since well-defined antecedent dry periods were difficult to determine and the R^2 values were not significant for half of the ions analyzed, the multiple regression model was

Table 4. Linear regression coefficients for predicating net throughfall fluxes (mmol/m²) using precipitation concentrations (μmol/L) (NTF = A + B [concentration]; standard deviations are in parentheses; $n = 160$).

Coefficient	Variable									
	H^+	Na^+	K^+	Ca^{2+}	Mg^{2+}	NH_4^+	Cl^-	NO_3^-	SO_4^{2-}	HCO_3^-
A	0.51 (0.19)	1.03 (1.04)	2.56 (0.30)	1.26 (0.17)	0.72 (0.08)	0.20 (0.12)	1.35 (0.35)	0.12 (0.08)	1.34 (0.19)	1.42 (0.23)
B	−1.88 (0.44)	−0.51 (0.15)	−5.41 (2.23)	−0.99 (0.46)	−0.48 (0.40)	−0.84 (0.19)	−0.49 (0.31)	−1.65 (0.20)	−1.21 (0.20)	−0.56 (0.67)
R^2	0.10***	0.07***	0.04*	0.03*	0.008	0.11***	0.02	0.30***	0.20***	0.005

* $p < 0.05$, ** $0.01 < p < 0.05$, *** $p < 0.01$.

Table 5. Canopy exchange and dry deposition rate estimated by regression analysis of net throughfall and dry deposition estimated from Na ratio using subset (22 events) of all storms preceded by discrete dry period.

	Variable								
Parameter	H^+	Na^+	K^+	Ca^{2+}	Mg^{2+}	NH_4^+	Cl^-	NO_3^-	SO_4^{2-}
R^2	0.37*	0.50*	0.58*	0.67*	0.49*	0.09	0.08	0.00	0.09
Dry deposition rate (mmol/m²/h)	4.7*	4.5	8.5*	3.3*	3.0**	3.6	1.4	1.1	2.2
Dry deposition (mmol/m²)									
Multiple regression†	−7.2	6.8	13.0	5.0	4.6	5.5	2.1	1.6	3.3
Na-ratio	6.8	14.9	3.1	3.6	2.4	5.7	24.1	2.6	5.6
Canopy exchange rate (mmol/m²/rain)	−4.0	12.1**	10.2**	6.5***	2.1*	0.94	6.9	−0.27	0.55
Canopy exchange (mmol/m²)									
Multiple regression‡	−5.2	15.8	14.3	8.5	2.8	1.2	9.0	−0.35	0.75
Na-ratio	−24.8	0.0	31.9	12.3	7.2	−2.0	−12.3	−4.0	−2.8
Precipitation (mmol/m²)	22.2	49.0	10.0	11.8	7.9	18.7	79.1	8.6	18.2
Throughfall (mmol/m²)	4.1	63.9	45.0	27.6	17.4	22.4	98.9	7.3	21.0

* $p < 0.05$, **$0.01 < p < 0.05$, ***$p < 0.01$.

† Calculated by multiplying total dry period by the coefficient of dry deposition.

‡ Calculated by multiplying total precipitation by the coefficient of canopy exchange.

considered unreliable for use in the subtropical forest under study.

The Na-ratio method estimated that between 1994 and 1996, the contribution of dry deposition relative to precipitation input was approximately 40% in the summer and 10% in the winter. (Table 2). The canopy exchange effect in the summer was positive for HCO_3^- and base cations K^+, Ca^{2+}, and Mg^{2+} and negative for all other ions (Table 2). The pattern was the same in the winter, except that SO_4^{2-} had a positive canopy exchange (Table 2). Annual K^+ canopy exchange was approximately two times higher than dry deposition and precipitation combined, and canopy exchange was close to dry deposition and precipitation combined for Ca^{2+}, Mg^{2+}, and HCO_3^- (Table 2). Compared with base cations, canopy exchange was less prominent for SO_4^{2-} (−27% for the summer and 10% for the winter for dry deposition and precipitation combined) and was negligible for Cl^- (Table 2). Canopy retention (negative exchange) of NO_3^- exceeded dry deposition and resulted in a negative net throughfall flux. For NH_4^+, canopy retention exceeded dry deposition in the winter, but not in the summer; therefore, net throughfall flux was negative in the winter but positive in the summer.

DISCUSSION

The large amount of precipitation falling during typhoon events indicates the importance of rare events in the hydrology and biogeochemistry of the Fu-shan forest. Typhoons also have a major impact on the forest itself. During the 1994 typhoons there was more litterfall (5000 kg/ha) than during all of 1993 (4000 kg/ha), a year during which there were no typhoons (Horng et al., 1995). These high litterfall events were associated with a dramatic (60%) decrease in leaf area index (Lin et al., 1999). In the absence of these large storms the biogeochemistry of this forest is very different. In the Fu-shan forest typhoons are a regular occurrence, with an average return frequency of 1.5 per year (Mabry et al., 1998), thus, they are an integral part of the biogeochemical patterns of this forest.

Precipitation and Interception

The amount of interception measured at Fu-shan (10%) is similar to that reported for other moist hardwood forests in Taiwan (Pan, 1966; Hsia et al., 1982) and is lower than that reported for tropical rain forests in general (Nye, 1961; Edwards, 1982; Lloyd and Marques, 1988; San Jose and Montes, 1992). Some of the differences reported in the literature might be the result of intra-site spatial and temporal variability of throughfall, something which has not been effectively characterized in most studies (Kimmins, 1973; Kostelnik et al., 1989; Norden, 1991; Puckett, 1991; Forti and Neal, 1992; San Jose and Montes, 1992). When 20 or more throughfall collectors are employed for at least 1 yr, both spatial and temporal intra-site variability is usually incorporated in mean characteristics (Kostelnik et al., 1989; Puckett, 1991; Forti and Neal, 1992; Lawrence and Fernadez, 1993; Lin et al., 1997). In other words, if an insufficient number of collectors are used for too short a period of time, one can collect spurious data. In addition, differences in vegetation type and/or leaf area index are important in influencing inter-site variation and throughfall quantities (Jetten, 1996), yet most authors do not report leaf area indices of their study forests. Differences in storm characteristics also cause variation among sites. The proportion of interception is greater in small compared with large rainfall events. This may explain why our interception rates were lower than most reported in the literature for tropical forests, since our study site is dominated by typhoon events.

Another factor influencing interception capacity is the wetness of the canopy, because a dry tree canopy can potentially intercept more water than a wet tree canopy. In this regard, the drier leaf surfaces common during the summer relative to the winter (the result of higher average temperatures, lower relative humidity, and higher rates of evapotranspiration) could intercept more precipitation than in the winter. However, at our study site the lower proportion of interception in the summer suggests that seasonal differences in potential interception capacity were not the primary cause of seasonal differences in interception loss. Instead, evaporation during rainfall events, which include short periods of sunshine, is probably the key to the seasonal variation in interception observed at our study site. Although the rate of evaporation might be lower during rain events relative to rainless periods, evaporation does affect interception losses for rainfall events of long duration because additional retention of water in the canopy compensates for evaporation losses. During long rainfall events, which are common at our study site during the winter, interception losses may be closely related to the rate of evaporation during rain events (Ward, 1967). The inclusion of more than one rainfall event per collection could also be a factor in seasonal differences of canopy interception. Recall that because individual rainfall events are difficult to define in the winter, there are many more multi-storm collections in the winter than in the summer. A collection with more than one rainfall event will have a higher absolute and relative interception loss than a single rainfall event with the same precipitation amount. In general, the more wet and dry cycles in a collection period the higher the interception loss (Jackson, 1971). Finally, the lower rainfall interception in the summer relative to the winter may be partly the result of the overall higher rainfall intensities and associated higher momentums of raindrops preventing the retention of water by vegetation in the summer (Jetten, 1996).

The lack of significant differences in both throughfall quality and quantity among the three plots indicates that variation among plots was small. Many studies have suggested that spatial variability of throughfall chemistry is high for individual rainfall events and that the number of samples required to produce chemical estimates within 10% of the population mean could be as high as several hundred (Kimmins, 1973; Puckett, 1991). Our results suggest that over a longer period, such as a season or a year, variation may be considerably lower than that seen for individual rain events. This reduction in variation is because there is no consistent pattern of spatial variation over time, thus, any one sampling point may have higher concentrations during one event and lower concentrations during the next event and the annual mean among sampling points is less variable (Lin et al., 1997, also see Lawrence and Fernadez, 1993). At our study site individual rainfall events are seldom characteristic of seasonal or annual patterns.

Precipitation and Throughfall Chemistry

The abundance of Na^+, Cl^-, and Mg^{2+} in precipitation and throughfall indicates the strong oceanic influence. Because Taiwan is a small island (36 000 km^2), oceanic influences on precipitation and throughfall chemistry are common around the island. In comparison with temperate deciduous forests, the subtropical rain forest that we studied in northeastern Taiwan had higher throughfall fluxes for nutrients with potential pedogenic sources (Ca^{2+} and Mg^{2+}; Table 2) (Parker, 1983; Richter and Lindberg, 1988; Matzner, 1989; Hamburg and Lin, 1998), suggesting the possibility of a strong influence of soil-derived windblown materials. These cations may also be enriched as a result of high levels of industrial particulates or a combination of industrial and pedogenic sources. Throughfall fluxes for nutrients that are industrially and anthropogenically enriched (90, 28, and 83 mmol/m^2/yr for NH_4^+, NO_3^-, and SO_4^{2-}, respectively) are much higher than the suggested critical load (25 mmol/m^2/yr for SO_4^{2-}) for our study forest (Lin et al., 1998) and are close to the levels of the heavily polluted areas of Europe and North America (see Parker, 1983). At this point in time we do not know how rates of acidic deposition may be affecting the health of subtropical rain forests, but the high rates of cation leaching (Table 2) are no different than those observed in temperate forests.

Because there were no major emission sources in the vicinity of the study site, much of the anthropogenically enriched chemicals must have a regional (within the island) or international (outside the island) source. Based on seasonal variation in wind direction, and therefore the potential source area of the pollutants, the minimum contribution of long-range transport to the deposition of SO_4^{2-} and NO_3^- was estimated to be 20% in 1994 (Lin, 1995).

Unlike many temperate forests, where dry deposition contributes more than 50% of the total deposition of SO_4^{2-} and inorganic N, dry deposition contributed less than 25% of the total deposition of most ions to the subtropical forest we studied (Table 2). This lower rate of dry deposition on a percentage basis can be attributed to the frequent rainfall events at our study forest and the lack of pollution sources within 20 km of the site (Table 1). Because dry particles accumulate in the atmosphere and on leaves during rainless periods, the contribution of dry deposition will be less important in forests with shorter periods between rainfall events. At Fushan the higher dry deposition rates in the summer relative to the winter further illustrate that the importance of dry deposition is closely related to the length of rainless periods, as the winter had many more rainy days than did the summer (Table 1).

Although many temperate forests receive acid deposition comparable with the Taiwanese forest examined in this study, a considerable part of that deposition occurs during the dormant season (Lovett and Lindberg, 1984) or during rainless dry periods (Brown and Lund, 1995). In the subtropical forest we studied almost all of the acid deposition is deposited onto physiologically active leaves via precipitation. Since the stomata of forest trees are very sensitive to humidity, the humid subtropical forest trees under study can be expected to have their stomata open most of the time (Kozlowski, 1991). Open stomata will in turn intensify the interaction between acid deposition and plant tissues, making this subtropical forest potentially more sensitive to acid deposition and air pollution than its seasonal temperate counterparts.

Dry Deposition and Canopy Exchange

Multiple regression models were not very useful in estimating dry deposition and canopy exchange in the Fu-shan forest, because many of the R^2 values did not significantly differ from zero (Table 4). This lack of significance could be the result of a violation of the assumptions and limitations of the models (Neary and Gizyn, 1994) or low deposition rates (Shepard et al., 1989). The assumptions of the regression model, that rates of dry deposition and canopy exchange are constant over a season and that canopy leaching is proportional to the amount of water flowing across the canopy, are probably not valid for subtropical forests. For example, if the rates of canopy leaching are proportional to rainfall quantity, then canopy leaching during extremely heavy storms such as typhoon events would be extremely high, yet that is not evident in the data. The rates of dry deposition at Fu-shan forest were lower than those found in temperate forests where the regression models have been applied with success. The 22 rain events used in the regression analysis occurred during both the summer and the winter, but analyzing the data by season did not increase the significance of the models. Six types of precipitation events have been identified as occurring in Taiwan based on sources of air mass and time of year (Chen and Wang, 1996). Applying the models separately to each type of precipitation event might produce better results, but we do not have a large enough data set to conduct this analysis.

Since atmosphere–forest interactions have been studied more intensively in the temperate regions of the world, many, if not most, models were developed based on data from temperate ecosystems. Applying ecological methods and/or models to regions other than those for which they were developed requires caution. Our study indicates that the use of temperate forest models of throughfall dynamics in subtropical humid environments could lead to spurious results. The Na-ratio approach tends to overestimate dry deposition because canopy leaching of Na^+ is assumed to be zero, which is unlikely. In addition, using Na–chemical ratios in bulk precipitation to estimate dry deposition assumes that the chemical ratios in bulk precipitation are the same as in dry deposition. For this to be true raindrops would have to scavenge atmospheric materials in the same elemental ratios as those occuring on leaf surfaces, something which is unlikely, especially for elements with gaseous forms. To improve the estimation of dry deposition using the Na-ratio approach, the ratios in atmospheric particles, instead of in bulk precipitation, should be used whenever possible.

Most studies indicate that the ratio of canopy leaching to precipitation for K^+ is higher in the summer than the winter due to greater physiological activity. Yet, we found that as a proportion of precipitation canopy leaching was greater in the winter than the summer. This was also true for Ca^{2+}. Because the forest we studied is a subtropical humid forest without a true dormant season, physiological activity might not differ much between summer and winter. Winter is characterized by frequent rainfall, so the canopy is wet for a longer period than in the summer. Because canopy exchange occurs mainly when the canopy is wet, there is more time for canopy exchange in the winter than the summer.

In contrast to canopy leaching of base cations, canopy exchange for most anions was negative, suggesting that the forest canopy retained some of the anions in precipitation. Although canopy N retention is widely observed (Brown and Lund, 1994; Lin et al., 1998; Hamburg and Lin, 1998), the underlying mechanisms remain unclear and studies provide controversial explanations. Because N retention depends on the length of time the canopy remains wet, some believe that N retention is a biologically mediated process rather than simple chemical exchange or passive diffusion (Schaefer and Reiners, 1990; Brown and Lund, 1994). Yet, passive movement across a concentration gradient between the cytoplast and leaf surface has also been suggested as playing an important role in canopy retention of NH_4^+ (Wilson, 1992). The highly significant negative relationship between NH_4^+ and NO_3^- concentrations in precipitation and NTF indicates that when N concentrations were low in precipitation they increased while passing through the canopy and when N concentrations were high in precipitation they declined after passing through the canopy. This pattern supports the possibility that passive movement across a concentration gradient could play an important role in canopy N retention. If a passive, nonbiologically mediated process is important for ion movement into and out of the plant canopy, then it should also happen with ions other than NH_4^+ and NO_3^-. That all ions except Mg^{2+}, Cl^-, and HCO_3^- had a negative correlation between NTF and their concentration in precipitation supports the possibility that the nonbiologically mediated, passive movement across a concentration gradient is a common rather than rare process unique to inorganic N.

Although the regression models are highly significant, the low coefficient of determination (R^2) indicates that passive diffusion alone cannot explain the observed canopy exchange pattern. If passive diffusion is the dominant canopy process, we would expect to see less canopy leaching of Ca^{2+} and Mg^{2+} and more canopy retention of Cl^- and SO_4^{2-} in the winter when the average concentrations of these ions were high relative to summer concentrations. That these ions either had higher leaching rates or lower retention rates in the winter than the summer supports the idea that though possibly important, passive diffusion did not dominate canopy exchange.

Throughfall chemistry has been studied for more than three decades in the temperate region, yet the broad role of passive diffusion on canopy exchange, lower K^+ leaching in the summer relative to the winter, and the relatively limited role of dry deposition in high acid deposition environments has not been well addressed. This study illustrates the importance of comparing and contrasting what we know about temperate forests with forests from other regions in order to help expand our understanding of atmosphere–forest interactions.

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