Typhoon effects on litterfall in a subtropical forest

Kuo-Chuan Lin, Steven P. Hamburg, Sheng-lin Tang, Yue-Joe Hsia, and Teng-Chiu Lin

Abstract: The litterfall in a subtropical broadleaf forest within the Fushan Experimental Forest in northeastern Taiwan was monitored for 9 years. Mean annual litterfall was very sensitive to typhoon frequency and intensity, ranging from 3 to 11 Mg·ha^{-1}·year^{-1}. Litterfall was significantly higher in years with strong typhoons than in years without typhoons, and the number of strong typhoons explained 82% of interannual variation in litterfall. Nutrient-use efficiency (dry mass/nutrients in litterfall) was high for N, but low for P compared with other tropical forests. This result supports the idea that the study forest is P limited but not N limited. Nutrient loss via litterfall represents a large percentage of aboveground biomass, especially during years with strong typhoons (e.g., 19%–41%, 15%–40%, 5%–12%, for N, P, and K, respectively). Forests that experience infrequent wind disturbance (e.g., temperate or boreal forests) can gradually regain any lost nutrients prior to the next disturbance; this is different from the situation observed in the Fushan Experimental Forest. At Fu-shan the pattern of not responding to typhoons with a flush of new growth appears to be an adaptation to the frequency with which there are multiple typhoons affecting the forest in a single year. Nutrient loss in litterfall caused by frequent typhoon disturbances appears to limit tree growth and contributes to the very low canopy height of the Fushan Experimental Forest.

Résumé : La chute de litière dans une forêt décidue subtropicale située dans la forêt expérimentale de Fushan dans le Nord-Est de Taiwan a été suivie pendant 9 ans. La chute annuelle moyenne de litière était très sensible à l'intensité et la fréquence des typhons, variant de 3 à 11 Mg·ha^{-1}·an^{-1}. La chute de litière était significativement plus élevée lors des années avec de violents typhons que lors des années sans typhons. Le nombre de typhons violents expliquait 82 % de la variation inter annuelle dans la chute de litière. L'efficacité d'utilisation des nutriments (masse sèche/nutriments dans la chute de litière) était élevée pour N mais faible pour P comparativement à d'autres forêts tropicales. Ce résultat supporte l'idée que P est un facteur limitant dans la forêt sous étude mais que N ne l'est pas. La perte de nutriments via la chute de litière représente un important pourcentage de la biomasse épigée, particulièrement lors des années avec de violents typhons (p. ex. respectivement 19–41 %, 15–40 % et 5–12 % pour N, P et K). Les forêts qui ne sont pas fréquemment soumises à des perturbations par le vent (p. ex. les forêts tempérées ou boréales) peuvent graduellement retrouver les nutriments perdus avant que survienne une autre perturbation; cela est différent de la situation observée dans la forêt expérimentale de Fushan. À Fu-shan, le fait de ne pas produire de nouvelles pousses à la suite d'un typhon semble être une adaptation à la fréquence avec laquelle de multiples typhons affectent la forêt au cours d'une même année. La perte de nutriments causée par de fréquentes perturbations dues aux typhons semble limiter la croissance des arbres et contribue à la très faible hauteur du couvert à la forêt expérimentale de Fushan.

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Introduction

Litterfall plays an important role in nutrient cycling within forest ecosystems, with rates of litterfall and subsequent decomposition affecting nutrient availability to vegetation. In ecosystems where nutrients, e.g., N and P, limit primary productivity, the turnover rate of litter is a key determinant of nutrient uptake by plants (Jorgensen et al. 1975; Cole and Rapp 1981; Edwards 1982; Santa Regina and Gallardo 1989; Santa Regina and Tarazona 2001). One way to evaluate the efficiency with which nutrients such as N, P, and Ca cycle in low-nutrient-status forest ecosystems is to look at ratios of dry mass to nutrient flux in litterfall. Sites with low nutrient concentrations in living foliage tend to have high dry mass to nutrient ratios in litterfall (Vitousek 1984; Vitousek and Sanford 1986). In addition, rates of retranslocation of nutrients prior to leaf fall have been used as an indication of the efficiency of nutrient retention within forests (Nadkarni and Matelson 1992).

Litterfall rates vary widely among forest types, with boreal forests being at the low end with 2.4–3.5 Mg·ha^{-1}·year^{-1} (McInnes et al. 1992), and tropical forests being at the high

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end with >10 Mg·ha^{-1}·year^{-1} (Whitmore 1984; Rapp et al. 1999). This large range is the result of differences in growing season length, life form, and productivity (Welbourn et al. 1981; Klemmedson et al. 1990).

Disturbances, such as wind, can greatly affect annual or monthly litterfall rates (Lodge et al. 1991; Vitousek et al. 1995). Tropical cyclones in Central America (hurricanes) and East Asia (typhoons) impact forests with varying frequencies, from annually in Taiwan (Mabry et al. 1998), to two to three times a decade in Puerto Rico (Salivia 1972), to once a century in New England (Boose et al. 1994). When these storms impact a forest they often cause large amounts of litterfall (Lodge et al. 1991; Lu et al. 1988; Horng et al. 1995; Lin 1998). As plant material falls to the ground it is accompanied by nutrients. Although nutrients contained in litterfall eventually decompose, the shifting patterns of litter input change nutrient cycling patterns.

Several studies on subtropical humid forests in Puerto Rico indicate that the sudden increase in nutrient inputs to the soil caused by hurricane litterfall can significantly alter nutrient cycling patterns (Lodge et al. 1991). However, the role of frequent wind disturbances, such as those experienced in the East Asian subtropics, on nutrient cycling within forests could be very different from the impacts of less frequent hurricanes in the Caribbean. For example, litterfall is typically lower in the year following a major hurricane disturbance than in the year prior to the disturbance, which has been viewed as an indication of the forest undergoing a recovery process (Bellingham et al. 1996). However, in forests experiencing annual typhoons, year-to-year changes in litterfall mass are hard to interpret. Nutrients in litterfall represent a cost to a tree, as they have to be replaced to maintain primary productivity. For forests experiencing infrequent hurricanes or typhoons there is a long interval to regain nutrients lost as a result of a disturbance, but this is not the case for systems impacted on an annual basis. There are no data on the adaptation of species experiencing frequent disturbance to high nutrient loss, yet it is reasonable to expect that there has been some adaptation. In the study reported on here we examine patterns of litterfall in an East Asian subtropical forest impacted by 16 typhoons over a 9-year period (Lin et al. 2000, 2001). Special emphasis was placed on quantifying the patterns of nutrient flux and their association with typhoon events.

Study site

The study was carried out at Fushan Experimental Forest (Fu-shan) located in northeastern Taiwan (24°34′N, 121°34′E) with elevation ranging from 500 to 1200 m (Fig. 1). Since 1993 wind speed, wind direction, air temperature, relative humidity, precipitation, global solar radiation, net radiation, hemispherical total radiation, and quantum flux have been continuously monitored on two towers extending 5–10 m above the canopy on the east and west ridges of watershed-1 (Hsia and Hwong 1999). Between 1993 and 1999 annual precipitation varied from 2900 to 6000 mm·year^{-1}, with much of the variation attributable to the occurrence or absence of typhoons. Typhoons largely occur between July and September, with infrequent typhoons as early as May and as late as November (Chang 2001). The annual mean temperature was 18.6 °C, and the annual mean relative humidity was 96%. The forest is characterized as a moist subtropical mixed evergreen forest without an observable dormant season. Based on 2 years of data the phenological patterns could be summarized as follows: leaf out March to April; flower development in April; peak leaf density from April to May; flowering from April to June; fruiting from July to October; and leaf fall for deciduous tress October to the following February (Lin et al. 1997).

There are 515 plant species belonging to 329 genera and 124 families within Fu-shan (TFRI 1989). The dominant tree species are *Castanopsis carlesii* (Hemsl.) Hayata, *Machilus thunbergii* (Sieb. et Zucc.) Kostermans, *Engelhardtia raxburghiana* Wall., *Meliosma squamulata* Hance, *Litsea acuminata* (Blume) Kurata, *Diospyros morrisiana* Hance, *Helicia formosana* Hems, and *Pyrenaria shinkoensis* (Hayata) Keng. Shrubs were mostly *Ardisia quinquegona* Blume, *Blastus cochinchinensis* Lour, *Lasianthus fordii* Hance, and *Meliosma squamulata* (Wang et al. 2000). The forest is multistoried with scattered tree ferns and shrubs, and with an herbaceous ground cover of 22% on ridges, 71% on slopes, and 78% in the valleys (K.-C. Lin, unpublished data).

Materials and methods

Two 20 m × 20 m plots were established at the end of 1991, and two more were established at the end of 1994. The elevations of these plots ranged from 690 to 780 m, with slopes from 21° to 28°, facing south and southwest. The mean diameter at breast height (DBH) of the trees in the four sample plots ranged from 16.3 to 25.7 cm, tree height ranged from 9.4 to 11.6 m, and the number of trees ranged from 925 to 1500 trees·ha^{-1} (Table 1). There were no significant differences in DBH and tree height among the plots ($p > 0.05$), except that one plot had a higher mean DBH than the others. The dominant tree species in the plots were quite similar with six species (*Castanopsis carlesii*, *Meliosma squamulata*, *Diospyros morrisiana*, *Machilus thunbergii*, *Engelhardia roxburghiana*, *Pyrenaria shinkoensis*) accounting for 51%–60% of the trees in all four plots.

Ten 15 cm high, 50 cm × 50 cm horizontal litterfall traps were established in each plot 1 m off of the ground. The sides of the traps were made of wood beveled on the upper edge, while the bottoms were 1-mm mesh nylon netting. In addition, in each plot a 2 m × 5 m 1-mm mesh net was placed on the ground at the center of the plot to collect branches with diameters >2 cm. Litterfall was collected once a month and was brought back to the laboratory, dried at 40 °C for 24 h, and separated into foliage, large branches, small branches (all woody material other than large branches), flowers, and other material. After litterfall was classified it was dried at 65 °C to a constant mass. Litterfall was collected from January 1992 through December 2000 for the plots established in 1991 and from January 1995 through December 2000 for the plots established in 1994.

From 1992 through 1994 the samples of each component of the dried litterfall from five of the traps in each plot were combined, resulting in two composite samples per plot. All samples were ground using an intermediate Wiley mill (0.5-mm mesh screen), and 0.4-g subsamples were digested using a modi-

Fig. 1. Sampling site location.

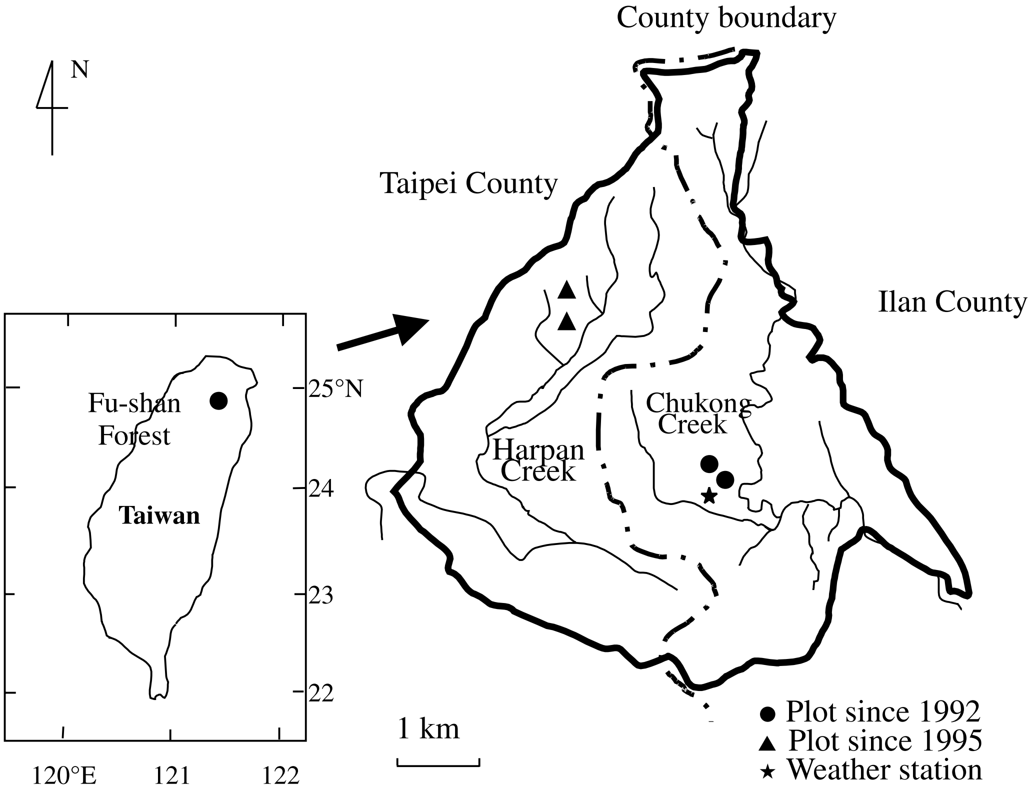

Table 1. Forest characteristics (mean ± standard error) of the four plots in which litterfall was collected within the Fushan Experimental Forest, in northeastern Taiwan.

	Plot A	Plot B	Plot C	Plot D
DBH (cm)	20.4±1.0	19.0±1.1	16.3±1.0	25.7±2.4
Tree height (m)	11±0.3	11±0.4	9±0.5	11±0.5
Tree density ($\text{trees}\cdot\text{ha}^{-1}$)	980	1500	925	975

Note: Litterfall was collected from January 1992 through December 2000 for plots A and B and from January 1995 through December 2000 for plots C and D.

fied Kjeldahl procedure, sulfuric acid with hydrogen peroxide and selenium as a catalyst. Nitrogen concentrations in the digests were analyzed using the molybdenum blue method and a spectrophotometer, and potassium, calcium, and magnesium were analyzed using an atomic absorption spectrophotometer (Allen et al. 1986). Duplicate analyses were carried out, and any replicate samples differing by >10% were rerun. Nutrient concentrations were calculated on a dry mass basis.

Nutrient concentrations were multiplied by the total biomass of each litterfall component for each month, and then the monthly fluxes were summed to get annual rates. Mean nutrient concentrations of litterfall were measured during the first 3 years of the study, and these data were utilized in the final 6 years of the study, as there was little temporal variation in concentrations for any of the macronutrients analyzed.

Litterfall mass in years with strong typhoons was compared with the mass in the preceding year without any typhoons using paired *t* test to examine if years with strong typhoons had significantly higher litterfall. Paired *t* tests were chosen because the amount of litterfall of any given year is directly affected by the preexisting conditions. Stepwise regression models were developed to predict litterfall using the number of strong (maximum wind speed $>51.0\ \text{m}\cdot\text{s}^{-1}$), medium ($>32.7$ and $<51.0\ \text{m}\cdot\text{s}^{-1}$), and light ($<32.7\ \text{m}\cdot\text{s}^{-1}$) typhoons (Taiwan Central Weather Bureau classification system) in a year as predictors. Predictors with probability of $F > 0.10$ are excluded from the models.

Results

Typhoons

There were 16 typhoons affecting Fu-shan in the 9-year study period; seven of them were classified as strong, six as medium, and three as light (Table 2). Using the Saffir–Simpson hurricane intensity scale (with a total of five categories, Simpson and Riehl 1981) seven of the 16 typhoons were category 3 (50–58 $\text{m}\cdot\text{s}^{-1}$), two were category 2 (43–49 $\text{m}\cdot\text{s}^{-1}$), four were category 1 (33–42 $\text{m}\cdot\text{s}^{-1}$), and three were tropical storms (17–32 $\text{m}\cdot\text{s}^{-1}$). The intensities of typhoons refer to wind velocities not amount of rainfall. The

Table 2. Characteristics of the typhoons that impacted the Fushan Experimental Forest from 1992 to 2000.

Year	Name of typhoon	Storm dates	Storm strength	Max. wind speed ($m \cdot s^{-1}$)	Total rainfall (mm)
1992	Polly	27–31 Aug.	Light	23	640
	Omar	3–5 Sept.	Medium	40	170
	Ted	20–23 Sept.	Light	30	83
1994	Tim	9–11 July	Strong	53	420
	Caitlin	3–4 Aug.	Light	25	160
	Doug	6–8 Aug.	Strong	58	380
	Fred	19–21 Aug.	Strong	55	340
	Gladys	31 Aug. – 1 Sept.	Medium	35	250
	Seth	7–10 Oct.	Strong	51	720
1996	Gloria	24–27 July	Medium	35	110
	Herb	29 July – 1 Aug.	Strong	53	780
1997	Winnie	17–18 Aug.	Medium	43	480
	Amber	27–29 Aug.	Medium	48	610
1998	Zeb	13–17 Oct.	Strong	55	420
2000	Bilis	21–23 Aug.	Strong	53	510
	Xangsane	31 Oct. – 1 Nov.	Medium	38	580

Note: Storm strength is characterized using the Taiwan Central Weather Bureau rating system. Rainfall and wind speed were recorded within the experimental forest.

Table 3. Annual litterfall (kilograms per hectare per year) of foliage, flowers, and small and large branches from 1992 through 2000 within the Fushan Experimental Forest.

Year	Foliage	Small branch	Large branch	Other	Total
1992	4300 (79)	720 (13)	50 (1)	390 (7)	5 460
1993	4340 (78)	790 (14)	60 (1)	410 (7)	5 600
1994	6400 (59)	2560 (24)	750 (7)	1090 (10)	10 800
1995	2190 (73)	340 (11)	250 (8)	240 (8)	3 020
1996	3030 (57)	1190 (23)	780 (15)	300 (6)	5 300
1997	3190 (70)	560 (12)	410 (9)	380 (9)	4 550
1998	3420 (74)	560 (12)	280 (6)	350 (8)	4 610
1999	3060 (81)	320 (8)	110 (3)	300 (8)	3 790
2000	4260 (66)	1110 (17)	560 (9)	490 (8)	6 410
Mean	3800 (69)	900 (16)	360 (7)	440 (8)	5 500

Note: Values in parentheses are the percentage of the annual contribution of each litterfall component.

quantity of rainfall associated with many light and medium typhoons is equal to or greater than the rainfall associated with strong typhoons. For example, typhoon Polly in 1992 had the lowest wind velocity but the second largest amount of rainfall of the 12 typhoons in the 9-year record. There were 3 years without any typhoons, but each of these was preceded and followed by years with typhoons. In 1994 there were six typhoons, with four of them classified as strong.

Litterfall mass

Annual litterfall flux ranged from 3.0 to 10.8 $Mg \cdot ha^{-1}$ with a mean of 5.5 $Mg \cdot ha^{-1}$ (Table 3). The mean annual flux rates of years with strong typhoons were significantly higher than those of the preceding years without typhoons (i.e., 1994, 1996, 2000 vs. 1993, 1995, 1999; one-tailed paired *t* test, $p = 0.034$).

Litterfall flux varied seasonally with two peak periods each year, one in spring (March to May) and the other in the typhoon season (July to September). In September 1992, there were two weak typhoons (Table 2), and the amount of litterfall was only 0.5–3.7 times higher than that in 1993, 1995, and 1999 when there were no typhoons. The litterfall between July to October 1994, the year with the strongest typhoon season, was 8.1–28 times higher than that seen in the 3 years when there were no typhoons. The lowest monthly litterfall fluxes were seen in December and January (90 to 310 $kg \cdot ha^{-1} \cdot month^{-1}$), with the lowest absolute fluxes following typhoon seasons with numerous storms, e.g., in December 1994 and January 1995.

On average, the foliage represented the largest component (69%) of litterfall mass, and the large branches the smallest (6%). The proportion of foliage in litterfall is highest in the spring (e.g., 690 $kg \cdot ha^{-1}$ or 91% in March 1992) and lowest during months with typhoons (e.g., 570 $kg \cdot ha^{-1}$ or 26% in July 1996). In contrast, the importance of large branches in litterfall was highest during typhoon months (e.g., 700 $kg \cdot ha^{-1}$ or 32% in July 1996) and lowest in the spring (e.g., 0 $kg \cdot ha^{-1}$ in 1992 and 1993). The changes in the proportional contribution of the various litterfall components are the result of differential increases among the components during typhoons. Compared with years without typhoons, the flux of large branches increased by more than an order of magnitude in years with strong typhoon(s). Small branches increased by not quite four times, while foliage increased by about 50% when there were strong typhoons.

The impact of typhoons on litterfall flux is closely related to the intensity of the typhoons. Typhoon Tim in 1994, which had a maximum wind velocity of 58 $m \cdot s^{-1}$, created 4500 $kg \cdot ha^{-1} \cdot month^{-1}$ litterfall, more than five times that seen in the spring. In contrast, typhoons with maximum winds speeds <40 $m \cdot s^{-1}$, such as those in 1992, resulted in small amounts of additional litterfall, and less than that seen in the spring of the same year. Strong typhoons following other strong typhoons can still produce large amounts of litter, e.g., in 1994 when Tim produced 4500 $kg \cdot ha^{-1} \cdot month^{-1}$ of litterfall, Doug and Fred, which struck later in the year, created an additional 1400 $kg \cdot ha^{-1} \cdot month^{-1}$ of litterfall. The results of a stepwise regression analysis indicate that only the number of strong typhoons is a significant predicator, explaining 82% of the annual variation in litterfall flux (litterfall ($kg \cdot ha^{-1} \cdot year^{-1}$) = 4301 ($kg \cdot ha^{-1} \cdot year^{-1}$) + 1549 ($kg \cdot ha^{-1} \cdot year^{-1}$) × (no. of strong typhoons), $R^2 = 0.82$, $p = 0.001$). Both the number of medium typhoons and the number of light typhoons are excluded from the model, as the p values for both predictor were >0.05 (0.36 for medium typhoon and 0.21 for light typhoons).

Litterfall nutrient concentration

Nutrient concentrations did not differ between foliar litter collected in months with and without typhoons ($P > 0.30$ for all nutrients analyzed, Table 4). Therefore, mean annual nutrient concentrations of each component (Table 5) were used to calculate annual nutrient litterfall flux. Nutrient content among the various litterfall components was highly variable; concentrations of foliage were highest, small branches intermediate, and large branches lowest. The nutrient concentrations of flowers, fruits, seeds, and insect bodies were comparable to that of foliage.

Litterfall nutrient flux

Litterfall nutrient flux ranged from 49 to 167 $kg \cdot ha^{-1} \cdot year^{-1}$ for N, 2.6 to 9.0 $kg \cdot ha^{-1} \cdot year^{-1}$ for P, 8.8 to 29 $kg \cdot ha^{-1} \cdot year^{-1}$ for K, 21 to 72 $kg \cdot ha^{-1} \cdot year^{-1}$ for Ca, and 4.2 to 14 $kg \cdot ha^{-1} \cdot year^{-1}$ for Mg. In years without typhoons (i.e., 1993, 1995, and 1999), the litterfall flux represented 8% to 17% of the N contained in aboveground living biomass, and the corresponding values were 4%–11% for P, 2%–4% for K, 4%–10% for Ca, and 2%–4% for Mg (Table 6). In years with strong typhoons (i.e., 1994, 1996, 1998, 2000), the corresponding values were 12%–26% for N, 9%–25% for P, 3%–7% for K, 6%–21% for Ca, and 5%–8% for Mg. The proportion of the canopy that was lost was greatest in 1994 when there were four typhoons with wind velocities >50 $m \cdot s^{-1}$, with litterfall flux representing 19%–41% for N, 15%–40% for P, 5%–12% for K, 9%–34% for Ca, and 8%–12% for Mg.

Annual nutrient transfer to the soil via litterfall (Table 6) relative to that via throughfall was 290%–1000% for N, 15%–50% for K, 46%–160% for Ca, and 26%–88% for Mg. The range in values represents the flux in 1994, the year with the strongest typhoons, and 1995, when there were no typhoons. The transfer of K, Ca, and Mg from the canopy to the soil via throughfall is greater than that via litterfall in years without strong typhoons, but is less in years when there are strong typhoons.

Table 4. Mean nutrient concentrations (milligrams/gram) of leaf litter collected in the Fushan Experimental Forest in typhoon and nontyphoon months from 1992 to 1994.

	Nutrient concentration ($mg \cdot g^{-1}$)		
Nutrient	Typhoon leaf litter ($n = 5$)	Nontyphoon leaf litter ($n = 39$)	p^a
N	1.83	1.81	0.90
P	0.9	0.9	0.33
K	0.35	0.33	0.60
Ca	0.67	0.57	0.67
Mg	0.15	0.16	0.60

[a] Probability values for typhoon concentrations vs. nontyphoon concentrations.

Discussion

Litterfall mass

In general, the annual litterfall of a mature forest will be relatively constant in the absence of disturbance (Brasell et al. 1980; Cuevas et al. 1991; Sampaio et al. 1993); however, natural disturbance such as typhoons (Horng et al. 1995), drought (Hegarty 1991), and avalanches (Arthur and Fahey 1992) have been shown to greatly increase litterfall rates and thus interannual variation (Lodge et al. 1991; Bellingham et al. 1996). Given that northern Taiwan is impacted by an average of 1.4 $typhoons \cdot year^{-1}$ (Mabry et al. 1998), it is not surprising that we found a threefold difference in annual litterfall flux over a 9-year period. The number of strong typhoons is key to the interannual variation in litterfall, as indicated by the high coefficient of determination of the regression model developed ($R^2 = 0.82$, $p = 0.001$). Although typhoons of medium and light intensities are accompanied by large amounts of precipitation, they seem to have much less impact on litterfall than do the stronger typhoons.

The annual litterfall in mature tropical rain forests has been reported to average 6.0–11.5 $Mg \cdot ha^{-1}$ (Whitmore 1984), with maximum values reaching 14 $Mg \cdot ha^{-1}$ (Proctor et al. 1983; Herbohn and Congdon 1993). At Fu-shan the flux rate (5.5 $Mg \cdot ha^{-1}$) is near the lower end of the reported range, but is consistent with that reported for subtropical forests in southwestern China (5.4–7.1 $Mg \cdot ha^{-1}$; Liu et al. 2002). Horng et al. (1995) reported slightly lower litterfall flux for Fu-shan, 3.8 $Mg \cdot ha^{-1} \cdot year^{-1}$ in 1992 and 1993, but well within the range of annual flux rates found in this study. Litterfall rates for two forests in central Taiwan were bracketed by the annual rates seen at Fu-shan, 7.2 $Mg \cdot ha^{-1} \cdot year^{-1}$ for a 32-year-old *Cryptomeria* plantation (Hsu 1981), and 8.5 $Mg \cdot ha^{-1} \cdot year^{-1}$ for a natural broadleaf forest (Lu et al. 1988). The low rates of litterfall flux observed at Fu-shan probably reflect the low aboveground biomass (197–290 $Mg \cdot ha^{-1}$, Lin et al. 1994) relative to other tropical rain

Table 5. Mean (±standard error) nutrient concentrations (milligrams/gram) of litterfall components in the Fushan Experimental Forest during 3 years, 1992–1994.

	Nutrient concentration ($mg \cdot g^{-1}$)			
Nutrient	Foliage	Small branches	Large branches	Other
N	17.9±0.31	9.5±0.29	7.1±0.69	18.8±0.60
P	0.92±0.01	0.63±0.01	0.51±0.03	0.91±0.03
K	3.30±0.08	1.2±0.08	1.0±0.20	3.7±0.22
Ca	7.3±0.11	4.7±0.14	4.8±0.43	7.9±0.26
Mg	1.5±0.02	0.95±0.03	0.63±0.10	1.3±0.05

Table 6. Nutrient content (kilograms per hectare) in aboveground biomass, throughfall (1994–1996), and litterfall in the Fushan Experimental Forest.

	Nutrient content ($kg \cdot ha^{-1}$)				
	N	P	K	Ca	Mg
Aboveground biomass[a]	410–870	23–60	250–560	220–780	120–180
Throughfall[b]	17	—	59	45	16
Litterfall					
1992	92	4.8	17	38	7.8
1993	93	4.9	17	39	8.0
1994	167	9.0	29	72	14
1995	49	2.6	8.8	21	4.2
1996	75	4.1	13	33	6.6
1997	73	3.9	13	31	6.2
1998	75	4.0	14	32	6.4
1999	64	3.3	12	27	5.5
2000	100	5.4	18	43	8.6

[a] Lin et al. (1996).
[b] Lin et al. (2000).

forests (>300 $Mg \cdot ha^{-1}$) and the subtropical forests in southeastern China (285–503 $Mg \cdot ha^{-1}$, Liu et al. 2002).

The pattern of two litterfall peaks seen in this study has been reported for other forests (Binkley et al. 1992; Herbohn and Congdon 1993), but was caused by a different natural disturbance, e.g., pronounced dry seasons. In our study the large amount of litterfall in the spring was caused by the senescence of the previous years' leaves, and the second peak was caused by the high winds that accompany typhoons. This typhoon-caused increase in litterfall is accompanied by a decrease in canopy leaf area index. In 1994 when the six typhoons resulted in 6300 $kg \cdot ha^{-1}$ of litterfall, canopy leaf area index decreased by as much as 66% on ridges (Lin et al. 1999).

Although the overall contribution of leaf litter to total litterfall is within the range seen in other forest types, typhoons decreased its relative importance, and its contribution dropped to as low as 26% in months with typhoons. The lower leaf litter contribution was also seen in a Taiwanese *Cryptomeria* plantation where during the typhoon season only 50% of litterfall was foliage (Hsu 1981). On the other hand, the contribution of large branches was as high as 32% in typhoon months. Because leaf litter has much higher nutrient concentrations than do branches, the changes in the composition of litterfall diminished the influence of typhoons on litterfall nutrient flux.

Litterfall nutrient concentration

The lack of significant differences in the nutrient concentrations between typhoon- and non-typhoon-induced litterfall (Table 4) is in contrast with the pattern reported for a subtropical rain forest in Puerto Rico. In that forest the concentrations of N and P in the hurricane leaf litter ranged from 1.1 to 1.5 and 1.7 to 3.3 times, respectively, the concentrations in nonhurricane leaf litter (Lodge et al. 1991). Forests in Puerto Rico experience hurricanes not more than two to three times a decade. Thus, the cost of losing a large amount of nutrient-rich foliage during a hurricane is less than that of reduced photosynthetic rates in nonhurricane years associated with reduced leaf nutrient concentrations. In other words, the cost of losing nutrient-rich leaves is compensated for prior to the next disturbance. Thus, it is advantageous for these forests to maintain high leaf nutrient levels, unlike the subtropical forests at Fu-shan, where maintaining lower concentrations of nutrients in limited supply provides a competitive advantage. This low leaf nutrient concentration may also contribute to the lack of a flush of new growth following typhoon disturbance at Fu-shan. Canopy leaf area index dropped more than 2.5 units as a result of the six typhoons of 1994 and recovered only 0.5 unit each of the following 3 years (Lin et al. 1999). By maintaining low leaf nutrient concentrations, with the exception of N, the trees at Fu-shan minimize the turnover of nutrients in short supply while optimizing photosynthetic rates, though not maximizing them.

Leaf litter N concentrations (18 $mg \cdot g^{-1}$) at Fu-shan were relatively high compared with most subtropical and tropical forests (Vitousek 1984; Veneklaas 1991; Swamy and Proctor 1994; Arunachalam et al. 1998; Haase 1999) and at the low end for temperate forests (Rapp et al. 1999; Gordon et al. 2000). Nitrogen-use efficiency (biomass/N on a dry mass basis, 56) at Fu-shan is lower than for other tropical and subtropical forests (Vitousek 1984) and near the lower range of the 95% confidence interval for temperate forests with the same amount of litterfall N flux. This low nutrient efficiency is most likely the result of the very high N deposition experienced at the site (18 $kg \cdot ha^{-1} \cdot year^{-1}$, Lin et al. 2000) for the past several decades. Phosphorous-use efficiency (biomass/P on a dry mass basis, 1087), on the other hand, is well within the range for tropical and subtropical forests and higher than in most temperate forests. This result is consistent with the results from a fertilization experiment that found that P fertilization of the forest at Fu-shan had a significant effect on tree growth, but the addition of N did not (Horng et al. 1994). Calcium-use efficiency at Fu-shan is lower than that for either tropical or subtropical forests with similar litterfall Ca flux. Soils at Fu-shan have very low levels of exchangeable cations, and the base saturation is <5% (Horng and Chang 1996), which would suggest high Ca-use efficiency. Although both precipitation and surface soils (<90 cm deep) at Fu-shan have a pH <4.5, streamflow has a pH of 7 (Wang et al. 1996; Lin et al. 2000). The deep bedrock is suspected of contributing Ca to stream water through primary weathering, and there may be tree roots tapping this same source of Ca, leading to the low Ca-use efficiency found in this study.

Litterfall nutrient flux

For a tree to grow, nutrients lost through litterfall in one year must be regained in following years. A study of a subtropical humid forest in southern China indicates that annual nutrient flux via litterfall considered as a percentage of that contained in aboveground living biomss is 5%, 3%, 2%, 2%, and 3% for N, P, K, Ca and Mg, respectively, much less than that found in the subtropical forest under study (Liu et al. 2002). Tree height at the subtropical humid forest in southern China was 24–25 m, and mean DBH was 30–58 cm; these values are much higher than those found at Fu-shan (tree height 9.4–11.0 m and DBH 16.3–25.7 cm). In contrast with our study forest, the subtropical humid forest in southwestern China is not impacted by typhoons. The difference in nutrient loss via litterfall between the two Asian subtropical forests that have been studied suggests that heavy nutrient loss due to typhoon disturbance at Fu-shan might contribute to the forest's low stature and small mean DBH, despite not having any history of direct human disturbance. Nutrient-poor soils, poor drainage, or other environmental factors may play an important role in nutrient turnover and canopy dynamics, but the fact that many hardwood forests in other parts of Taiwan, where typhoon frequency is much lower, have canopy heights well above 15 m (Lu and Tang 1995) suggests that typhoon disturbance is key to the low stature at Fu-shan.

Another study in an *Populus* hardwood forest in northern Wisconsin, U.S.A., indicates that annual nutrient flux via litterfall as a percentage of aboveground biomass was 10%, 10%, 4%, 7%, and <1% for N, P, K, Ca, and Mg, respectively (Pastor and Bockheim 1984). Although these temperate forest numbers are in the upper range of those found during nontyphoon years at Fu-shan, they are at the lower end of those found during typhoon years. These high rates represent a more important potential loss from the ecosystem at Fu-shan than in the temperate forests, where decomposition is much slower than the warm and humid subtropical forest we studied. In addition the high annual rainfall and the intense rains associated with typhoons increase the likelihood of leaching losses of the rapidly decomposing litter. Nutrient loss due to leaching is also influenced by uptake rates, which largely depend on the amount of foliage and evapotranspiration. Because foliage can be reduced by 66% as a result of typhoons, reduced nutrient uptake and increased leaching losses are likely. (Lin et al. 1999, 2003). This study indicates that litterfall is a more important source of N transfer from the canopy to the soil than throughfall (Lin et al. 2000). For K, Ca, and Mg the contribution of throughfall flux is more important than that of litterfall in years without strong typhoons, but less important in years when typhoons impacted the forest. Our results suggest that litterfall dominates the rapid cycling for most nutrients in years when typhoons impact Fu-shan.

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