# Base cation leaching from the canopy of a subtropical rainforest in northeastern Taiwan[1]

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**Abstract**: We examined base cation leaching from the canopy of a subtropical rainforest in northeastern Taiwan. The forest is characterized by extremely low levels of base cations in both canopy vegetation and in the soils. The rates of canopy leaching of $K^+$, $Ca^{2+}$, and $Mg^{2+}$ were very high, representing up to 30, 35, and 190%, respectively, of the amount stored in leaves. The rate of $H^+$ retention in the canopy was close to the rate of base cation leaching, suggesting that cation leaching is neutralizing acid precipitation. The subtropical forest studied leached cations from the canopy throughout the year, unlike temperate deciduous forests, which are physiologically inert in the winter. The forest canopy of the subtropical forest we studied is impacted by acid deposition and fog throughout the winter because of frequent rainfall and high relative humidity. This continuous exposure to acid precipitation could cause more intense negative effects on the canopy of subtropical forests as compared with temperate forests exposed to similar pollution loads. We suggest that the low base status of subtropical forests growing on low base status soils may make them very vulnerable to the negative effects of air pollution.

**Résumé** : Nous avons étudié le lessivage des cations basiques dans le couvert d'une forêt subtropicale ombrophile du nord-est de Taiwan. Cette forêt est caractérisée par des niveaux extrêmement faibles de cations basiques tant dans le couvert végétal que dans le sol. Les taux de lessivage de $K^+$, $Ca^{2+}$ et $Mg^{2+}$ sont très élevés dans le couvert; ce qui représente respectivement jusqu'à 30, 35 et 190% de la quantité emmagasinée dans les feuilles. Le taux de rétention de $H^+$ dans le couvert se rapproche du taux de lessivage des cations basiques; ce qui indique que le lessivage des cations neutralise les précipitations acides. Dans la forêt subtropicale sous étude, les cations dans le couvert sont lessivés pendant toute l'année, contrairement aux forêts décidues tempérées qui ne sont pas physiologiquement actives durant l'hiver. Le couvert de la forêt subtropicale que nous avons étudiée subit l'effet du brouillard et des dépôts acides pendant tout l'hiver à cause des précipitations fréquentes et de l'humidité relative élevée. Cette exposition continue aux précipitations acides pourrait entraîner des effets néfastes plus intenses dans le couvert des forêts subtropicales comparativement aux forêts tempérées exposées à des quantités similaires de pollution. Nous croyons que la faible quantité de cations basiques dans les forêts subtropicales qui croissent sur des sols pauvres en cations basiques peut les rendre très vulnérables aux effets néfastes de la pollution.

[Traduit par la Rédaction]

## Introduction

There has been increasing concern about the linkage between declining health of many forest ecosystems and atmospheric deposition. Several pathways by which atmospheric deposition can damage forests have been proposed: (*i*) soil acidification, cation depletion, and $Al^{3+}$ toxicity (van Breemen et al. 1982; Ulrich and Pankrath 1983; Schulze 1989; Likens et al. 1996; Lawrence et al. 1999); (*ii*) direct and indirect influence of pollutants on the physiological status of the trees (Unworth and Ormrod 1982; Eamus and Murray 1991; DeHayes et al. 1999); (*iii*) excess N deposition and subsequent soil acidification or physiological injury (Nihlgard 1985; Aber et al. 1989, 1998; Nilsson and Wiklund 1992).

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In the early 1980s, several researchers hypothesized that acid deposition could lead to soil cation depletion and subsequent soil acidification thereby affecting the health of forest ecosystems (van Breemen et al. 1982; Ulrich and Pankrath 1983). Recently, using long-term data from temperate deciduous forests, Likens et al. (1996) and Lawrence et al. (1999) proposed that atmospheric deposition induced base cation depletion has a major detrimental effect on nutrient cycling and forest health.

Base cations are not just essential to plant growth but are also critical components for buffering acid deposition in the soil and canopy. Cation leaching from the forest canopy could affect physiological processes, damage flowering and dormancy patterns, and make plants more vulnerable to diseases and the effects of freezing (Tukey 1970; DeHayes et al. 1999). In the soil, exchange of base cations with $H^+$ helps to keep soil pH >4.2 (Fernandez 1989; Fasth et al. 1991). If acid deposition exceeds the buffering capacity of the available base cations, then soil pH will drop to <4.2, and $Al^{3+}$ will be released.

Although base-cation leaching from forest canopies is well documented for temperate forests (Reiners and Olson 1984; Fahey et al. 1988; Carleton and Kavanagh 1990; Turner and van Broekhuizen 1992; Cappellato et al. 1993; Lovett et al. 1996; Hamburg and Lin 1998), little is known about what is happening in tropical and subtropical forests (Lin et al. 1997, 1998, 2000). Because nutrient cycling patterns differ among forests of different regions (Vitousek and Sanford 1986; Bruijnzeel 1991), impacts of acidic deposition on base-cation leaching cannot be easily extrapolated from temperate forests to subtropical forests. In fact, the typically low base saturation of subtropical forests in Taiwan, especially humid subtropical forests (Chiang et al. 1994), could make them more vulnerable to base-cation leaching than temperate forests. Evergreen hardwood forests occupy a majority (62%) of the forested area of Taiwan (Goan and Chen 1995), and thus, a thorough examination of the interactions between atmospheric deposition and the forest canopies of evergreen hardwood forests is of particular importance.

Our previous work demonstrates that there are high rates of deposition of acidic pollutants, predominately through wet deposition, and canopy leaching of base cations is substantial (Lin et al. 1998, 2000). Studies at other forests of Taiwan also indicate strong canopy leaching of base cations (Liu and Sheu 1997). However, patterns of base cation leaching have not been described, and the role of cation leaching on forest nutrient cycling and forest health is unclear.

We present a 2-year study of the relationship between atmospheric deposition and base-cation leaching in a subtropical rainforest in northeastern Taiwan. The objectives were to (*i*) quantify base-cation leaching from the canopy relative to the canopy's nutrient content, (*ii*) identify seasonal variation in base-cation leaching from the forest canopy, and (*iii*) develop a conceptual model of the influence of cation leaching on the forest canopy of the Fu-shan Experimental Forest.

## Materials and methods

### Study site

The study was conducted on 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, mean annual temperature was 18°C with the lowest monthly mean temperatures in January (12°C) and highest in July (24°C), and mean annual relative humidity was 96% (July, 94%; February, 98%). Extremely high humidity (97%) and frequent light precipitation (1100 h of rain/winter) characterize the winters (October to April).

Watershed 1 is drained by a first-order stream that is a tributary of the Nan-she-chi River. The soil is coarse-loamy Typic Dystochrepts with the top 30 cm characterized as very acidic (pH 3.8–5.0) with extremely low bulk density (0.5–0.8 $Mg/m^3$) and very low base saturation (2–5%) (Horng and Chang 1996; Liang et al. 1997).

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* Sieb & Zucc, *Persa thunbergii* Sieb & Zucc, *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* Lour, and *Lasianthus obliquinervis* Uerr.), and herbaceous cover. Total leaf area index (LAI) of the forest varies from 6 to 8, with canopy trees having a LAIs of 3–6 (Lin 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. Because rainfall volume and chemistry differed among the three precipitation collectors by less than 5%, samples from the three collectors were combined (Lin et al. 1997).

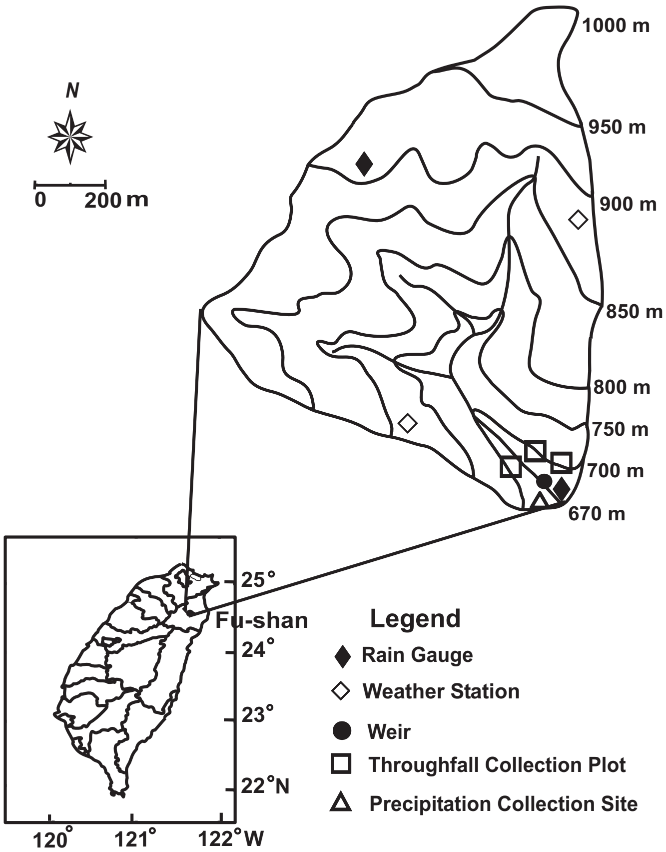
### Sample collection and laboratory analysis

Precipitation and throughfall were collected once a week. If it was raining during the routine collection time, the collection was postponed until the rain stopped. The volume of all throughfall and precipitation samples was measured in the field and a 500 mL subsample collected. The remainder of each sample was used to clean the collectors, tubing, and storage bucket. Every 3 months, collectors were washed with deionized water until the conductivity of the rinse water was less than 6 μmhos/cm. Conductivity and pH were measured on all samples within 3 h of collection, after which samples were transported to our laboratory in Taipei for chemical analysis. Prior to analysis samples were stored at 5°C. Cations were analyzed on filtered samples (Gelman Science GN-6 grid 0.45 μm sterilized filter paper) using ion chromatography (Lin et al. 1997). Analysis of 10 split samples showed a variability of less 5% for base cations.

### Data analysis

Differences in ion concentrations and fluxes between precipitation and throughfall and among the three-forested plots were examined using one-way analysis of variance (ANOVA). The effect of acidity ($[H^+]$) and quantity ($P$) of precipitation on net canopy effect

**Fig. 1.** Topographic map of watershed 1 of Fu-shan Experimental Forest.




(NCE) was examined using simple linear regression (NCE = $a$[$H^+$] + $bP$). There is no intercept in the regression models, because there should be no canopy effect when there is no precipitation to wash off dry-deposited materials and to move materials in and out of the canopy.

A Na-ratio method (Mayer and Ulrich 1974; Gosz 1980; Lin et al. 2000) was applied to estimate dry deposition and canopy exchange effect. The Na-ratio method assumes that because $Na^+$ concentrations in foliage are very low, almost all (>90%) of the throughfall $Na^+$ in excess of that in precipitation can be attributed to dry deposition (Parker 1983). Dry deposition of other chemicals can be calculated on the basis of the $Na^+$ to other ion 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 net throughfall flux and dry deposition estimated from the Na-ratio method.

Three factors may affect the accuracy of the Na-ratio method in estimating dry deposition in the Fu-shan Experimental Forest. The first potential limitation is that the source areas of the ions in the atmosphere may differ, and their ratios can vary considerably through space and time. Since we collected precipitation and throughfall weekly within the same watershed, the differences in temporal and spatial variation should be minimal and should not affect the validity of the Na-ratio method at our study site. Secondly, the use of ion ratios in bulk precipitation instead of in air particles could affect the estimation of dry-deposition rates. If there is error associated with the use of ion ratios in bulk precipitation it could lead to either an underestimate or overestimate of dry-deposition rates, which would then affect estimates of cation leaching rates. Gaseous and particulate concentrations of $HNO_2$, $HNO_3$, $SO_2$, $SO_4^{2-}$, and $NH_3$ were measured at Fu-shan Experimental Forest using annular denuder tubes and micro-orifice uniform deposit impactors in 1993 and 1994. Using the atmospheric turbulence and diffusion division (ATDD) model approximately 11–42, 9–31, and 7–14% of $NH_4^+$, $SO_4^{2-}$, and $NO_3^-$, respectively, was deposited through dry deposition (Lin 1996). The Na ratio resulted in an estimate of dry deposition that was was approximately 22% for $NH_4^+$, $NO_3^-$, and $SO_4^{2-}$ between 1994 and 1996 (Lin et al. 1998). The use of the ion ratios in bulk precipitation lead to reasonable estimates. Thirdly, some of the $Na^+$ in throughfall may come from canopy leaching, resulting in an overestimate of the dry deposition of $Na^+$ and, in turn, the dry deposition of other base cations. Our study site is very close to the ocean (22 km), and thus, $Na^+$ is abundant in aerosols. Yet, foliar $Na^+$ content in the leaves of the dominant tree species is low (0.03–0.08% in contrast to 0.7–1.6% for $K^+$, $Ca^{2+}$, and $Mg^{2+}$) and the foliar storage of $Na^+$ is less than 1 kg/ha (F.W. Horng, unpublished data). Though overestimation of dry deposition is theoretically possible, as a result of the low foliar concentrations, any overestimation due to the leaching of $Na^+$ from the canopy should be minimal.

**Table 1.** Mean precipitation and throughfall concentrations of $H^+$ and base cations (µequiv.·$L^{-1}$) in watershed 1 of the Fu-shan Experimental Forest (1997–1998).

| | | $H^+$ | $Na^+$ | $K^+$ | $Ca^{2+}$ | $Mg^{2+}$ |
|---|---|---|---|---|---|---|
| Summer | Precipitation | 21.1 | 24.0 | 3.8 | 14.1 | 7.6 |
| | Throughfall | 2.3 | 39.3 | 30.2 | 22.3 | 19.7 |
| Winter | Precipitation | 17.8 | 27.5 | 3.2 | 12.2 | 8.2 |
| | Throughfall | 3.7 | 45.2 | 23.1 | 26.9 | 18.7 |
| Annual | Precipitation | 19.4 | 25.9 | 3.5 | 13.1 | 7.9 |
| | Throughfall | 3.0 | 42.4 | 26.5 | 24.7 | 19.2 |

**Note:** Differences between precipitation and throughfall concentrations are significant for all cations seasonally and annually ($p$ < 0.0001, calculated on a paired event basis using paired $t$ test).

## Results and discussion

No statistical difference in throughfall cation composition was found among the three plots ($p$ > 0.05). Therefore, the means of the three plots was used in all analyses.

### Precipitation and throughfall chemical composition

On an equivalent basis, $Na^+$ was the most abundant cation in precipitation followed by $H^+$, $Ca^{2+}$, $Mg^{2+}$, and $K^+$ (Table 1). The high $Na^+$ content in precipitation can be attributed to oceanic influence, as the study forest is only 22 km west of the east coast of Taiwan. The high $H^+$ content, though, is directly attributable to the heavy acid deposition at Fu-shan Experimental Forest. Annual deposition of S and inorganic N at the study forest (23 and 20 kg·$ha^{-1}$·$year^{-1}$, respectively, between 1994 and 1996; Lin et al. 2000) was similar to that of heavily polluted forests in North America and Europe (Richter et al. 1983; Lindberg et al. 1986; Matzner and Prenzel 1991; Lindberg and Lovett 1992; MacDonald et al. 1993). The high $Na^+$ (from the ocean) and $H^+$ (from air pollution) content of precipitation indicates that both natural and anthropogenic sources of nutrient inputs are important in patterns of nutrient cycling at Fu-shan Experimental Forest.

Chemical composition of precipitation significantly changes as it passes through the forest canopy (Tables 1 and 2). Sodium was still the most abundant cation in throughfall followed by $K^+$ (which was the least abundant ion in precipitation) $Ca^{2+}$, $Mg^{2+}$, and $H^+$ (Tables 1 and 2). The large differences in pre-

**Table 2.** Seasonal and annual nutrient flux of precipitation, throughfall, net throughfall, and dry deposition input of $H^+$ and base cations (mequiv.·m$^{-2}$) in watershed 1 of the Fu-shan Experimental Forest.

| | | $H_2O$ (mm) | Ion flux (mequiv.·m$^{-2}$) | | | | |
|---|---|---|---|---|---|---|---|
| | | | $H^+$ | $Na^+$ | $K^+$ | $Ca^{2+}$ | $Mg^{2+}$ |
| Summer | Precipitation | 2200 | 47.2 | 53.7 | 8.5 | 31.5 | 17.0 |
| | Throughfall | 2100 | 4.9 | 82.7 | 63.5 | 46.9 | 41.3 |
| | Net throughfall | | –42.3 | 29.0 | 55.0 | 15.4 | 24.3 |
| | Dry deposition | | 25.5 | 29.0 | 4.6 | 17.0 | 9.2 |
| | Canopy exchange | | –67.8 | 0.0 | 50.4 | –1.6 | 15.1 |
| Winter | Precipitation | 2600 | 46.6 | 71.9 | 8.3 | 31.9 | 21.3 |
| | Throughfall | 2300 | 8.3 | 103.0 | 52.7 | 61.2 | 42.6 |
| | Net throughfall | | –38.3 | 31.1 | 44.4 | 29.3 | 21.3 |
| | Dry deposition | | 20.2 | 31.1 | 3.6 | 13.8 | 9.2 |
| | Canopy exchange | | –58.5 | 0.0 | 40.8 | 15.5 | 12.1 |
| Annual | Precipitation | 4800 | 93.8 | 125.6 | 16.8 | 63.4 | 38.3 |
| | Throughfall | 4400 | 13.2 | 185.7 | 116.2 | 108.1 | 83.9 |
| | Net throughfall | | –80.6 | 60.1 | 99.4 | 44.7 | 45.6 |
| | Dry deposition | | 45.6 | 60.1 | 8.2 | 30.8 | 18.4 |
| | Canopy exchange | | –126.2 | 0.0 | 91.2 | 13.9 | 27.2 |

**Note:** Differences between precipitation and throughfall flux are significant for all cations seasonally and annually ($p < 0.0001$ calculated on a paired event basis using paired $t$ test).

cipitation and throughfall chemistry indicate that the brief contact between precipitation and the forest canopy significantly influences throughfall chemistry (Schaefer and Reiners 1990; Lin et al. 2000). Therefore, understanding of canopy processes is critical to our understanding of forest nutrient cycling.

Base cations, $Na^+$, $K^+$, $Ca^{2+}$, and $Mg^{2+}$, were enriched in throughfall relative to that in precipitation (Table 1). On the other hand, the average $H^+$ deposition rate dropped from 94 to 13 mequiv.·m$^{-2}$·year$^{-1}$ indicating substantial canopy retention (87%; Table 2). This corresponded with an increase in pH from 4.7 in precipitation to 5.5 in throughfall. It seems that the canopy of the evergreen hardwood forest we studied effectively neutralized acidic precipitation.

## Canopy processes

Canopy neutralization involves processes both external and internal to the canopy (Lindberg et al. 1986; Puckett 1990; Potter et al. 1991). External processes include wash-off of dry deposited base cations from the canopy. Internal processes consist of an exchange of $H^+$ with other cations (Tukey 1970; Lovett et al. 1996) and (or) leaching of weak bases from leaves in the canopy (Cronan and Reiners 1983). After subtracting dry deposition (estimated using the Na-ratio method), all base cations had a positive annual canopy exchange, indicating canopy leaching (Table 2). Among the base cations, $K^+$ leached out of the canopy at the highest rate. This observation is consistent with other throughfall studies and is related to the concentration and mobility of $K^+$ in precipitation and plant tissues (Tukey 1970; Parker 1983; Arthur and Fahey 1993). Potassium is the least abundant ion, on an equivalent basis, in precipitation (Table 2) but xylem is rich in $K^+$ and is known to efflux to outer surfaces of leaves (Cronan 1980; Reiners and Olson 1984; Turner and van Broekhuizen 1992). The great concentration gradient of $K^+$ between leaf xylem tissues and precipitation would enhance the diffusive movement of $K^+$ through leaf surfaces. Annually, the contribution of canopy leaching was five times the precipitation flux for $K^+$ (Table 2).

For $Mg^{2+}$ and $Ca^{2+}$, canopy leaching was about 71 and 22%, respectively, of precipitation flux (Table 2). Compared with many temperate hardwood forests, the rate of base cation leaching from the canopy relative to atmospheric deposition is low at our study forest (Table 3). Yet, the importance of base cation losses from the canopy can only be understood in the context of the nutrient demands of the vegetation and the pool of available cations in the soil. Few throughfall studies have addressed canopy-cation leaching from this perspective (Henderson et al. 1977; Potter et al. 1991; Cappellato et al. 1993). The observed annual rate of $K^+$, $Ca^{2+}$, and $Mg^{2+}$ leaching from the canopy represents a large percentage of the stock of these nutrients in the leaves of the subtropical forest we studied ($K^+$, 69–189%; $Ca^{2+}$, 11–35%; $Mg^{2+}$, 19–30%: the ranges represent the variation in estimates of nutrient stores within the vegetation of the watershed; Table 4). This relative leaching rate is much higher than seen in the few throughfall studies that have addressed canopy-cation leaching in relation to the foliage pool ($K^+$, 13–40%; $Ca^{2+}$, 4–26%; $Mg^{2+}$, 6–7%; Table 3).

Ions dissolved in soil solution are the most readily available nutrients for root uptake. Annual rates of $K^+$, $Ca^{2+}$, and $Mg^{2+}$ leaching from the canopy are more than two times greater than the stock of soluble cations in the top 30 cm of soil (Table 4). The Fu-shan soils have a low clay content and are very porous, as indicated by their very low bulk density (0.5–0.8 Mg/m$^3$; Horng and Chang 1996), and as a result they have a limited capacity to hold the cations leached from the canopy. Given the high rates of precipitation in this forest, the residence time of soil water is very short. For large storms in which substantial canopy leaching may occur, precipitation reaches the stream in less than 30 min (Wang 1994). Output of base cations in stream water during ty-

**Table 3.** Canopy leaching (kg·ha$^{-1}$·year$^{-1}$) and foliar base cation content (kg·ha$^{-1}$) of selected forests.

| Location | Forest type | | K | Ca | Mg |
|---|---|---|---|---|---|
| Northeastern Taiwan | Evergreen and broadleaf | Atmospheric deposition | 6.6 | 12.7 | 4.7 |
| | | Canopy leaching | 36 | 2.8 | 3.3 |
| | | Foliar content[a] | 19–52 | 8–25 | 11–17 |
| Tennessee, U.S.A. | Mixed | Atmospheric deposition[b] | 1.0 | 8.9 | 1.0 |
| | | Canopy leaching[b] | 11–22 | 3.6–18 | na |
| | | Foliar content[c] | 35–55 | 45–69 | 12–21 |
| Northern California, U.S.A. | Deciduous | Atmospheric deposition | na | na | na |
| | | Canopy leaching[d] | 2.6 | 1.4 | 0.4 |
| | | Foliar content[d] | 20 | 38 | 6.4 |
| Georgia, U.S.A. | Deciduous | Atmospheric deposition[e] | 1.1 | 3.3 | 0.69 |
| | | Canopy leaching[e] | 24 | 5.6 | 2.2 |
| | | Foliar content[f] | 58 | 73 | 30 |

[a]Lin et al. (1996).
[b]Lovett and Lindberg (1984).
[c]Henderson et al. (1977).
[d]Potter et al. (1991).
[e]Cappellato and Peters (1995).
[f]Cappellato et al. (1993).

**Table 4.** Base cations leached from the canopy and base cation contents in foliage, and soils in WS1 of the Fu-shan Experimental Forest.

| | K | Ca | Mg | CEC[a] | BS[b] |
|---|---|---|---|---|---|
| Canopy leaching (kg·ha$^{-1}$·year$^{-1}$) | 36 | 2.8 | 3.3 | | |
| Foliage (kg·ha$^{-1}$)[c] | 19–52 | 8–25 | 11–17 | | |
| Soil[d] | | | | | |
| Exchangable (cmol·kg soil$^{-1}$)[e] | 0.17 | 0.09 | 0.14 | 23.4 | 1.8 |
| Extractable (kg·ha$^{-1}$)[e] | 115 | 30.7 | 30.0 | | |
| Soluble (kg·ha$^{-1}$)[e] | 18.8 | 10.8 | 9.8 | | |
| Total (kg·ha$^{-1}$)[e] | 35.2 | 517 | 8500 | | |

[a]CEC, cation exchange capacity (cmol·kg soil$^{-1}$).
[b]BS, percentage of base saturation.
[c]Adapted from Lin et al. (1996).
[d]Modified From Horng and Chang (1996).
[e]Data are for the top 30 cm of soil.

phoon events represents more than 30% of the annual output of $Ca^{2+}$ and $Mg^{2+}$ (L.-J. Wang, unpublished data). Therefore, the loss of base cations through canopy leaching and rapid loss in stream water represents a substantial annual loss (input from precipitation – output through stream flow) of $Ca^{2+}$ and $Mg^{2+}$ from the forest ecosystem (100 and 25 kg·ha$^{-1}$ for $Ca^{2+}$ and $Mg^{2+}$; T.-C. Lin and L.-J. Wang, unpublished data). The rate of cation loss is much greater than that seen in temperate forests where the base status of the vegetation and soil is usually higher.

The mean annual canopy retention of $H^+$ (126 mequiv.·m$^{-2}$) was very close to canopy leaching of base cations, $K^+$, $Ca^{2+}$, and $Mg^{2+}$ (Table 2). The $H^+$ is transferred from water films on leaf surfaces to exchange sites on the surfaces (Wood and Bormann 1975). Although canopy neutralization through canopy leaching of Bronsted bases as proposed by Cronan and Reiners (1983) cannot be ruled out, the potentiometric titration method they used may underestimate cation exchange because it misses a metabolism linked exchange capacity (Ighe and Pettersson 1974; Turner and van Broekhuizen 1992). Our results indicated that base-cation exchange could explain much of the observed canopy neutralization.

### Quantity and acidity of precipitation versus base cation leaching

The two predictors of the regression model NCE = $a[H^+] + bP$ ($[H^+]$ and $P$) were positive and significant for all base cations indicating that both quantity and acidity of precipitation have positive effect on canopy base cation leaching (Table 5). In contrast to many temperate forests, which experience lower precipitation rates, high annual precipitation is inherent to the study site. During heavy storms, i.e., typhoon events that bring several hundred millimetres of precipitation in several days, as much as 80% of the streamflow comes from near surface flow (Wang et al. 1998). Therefore, most of the canopy-leached cations are likely to be lost from the soils and could represent permanent loss of these base cations from the ecosystem.

The study forest has experienced high precipitation since its original development. Canopy leaching of base cations associated with heavy precipitation does not seem to affect the integrity of the forest (Mabry et al. 1998). Possibly, the forest has been able to compensate for canopy leaching of base cations through high rates of soil weathering and root uptake; however, recent increases in acidity may have changed

**Table 5.** Linear regression coefficients for predicating net canopy effect (NCE) using quantity ($P$) and acidity ([$H^+$]) of precipitation concentrations (NCE = $a[H^+] + bP$; SDs are given in parentheses; $n$ = 74).

| Coefficient | Variable | | |
|---|---|---|---|
| | $K^+$ | $Ca^{2+}$ | $Mg^{2+}$ |
| *a* | 25.1 (4.38)*** | 10.3 (4.88)* | 11.9 (2.79)*** |
| *b* | 0.011 (0.0011)*** | 0.0049 (0.0012)*** | 0.0050 (0.0070)*** |

**Note:** *, $p < 0.05$; ***, $p < 0.0001$.

the situation. The positive effect of precipitation acidity on canopy leaching of base cations suggests that a portion of the high rates of base cation leaching from the canopy may be the result of the higher acidity in precipitation during the past several decades. Laboratory experiments have demonstrated that acid deposition intensifies canopy leaching of base cations (Potter et al. 1991; Cappellato et al. 1993). Since the acidity of precipitation is closely linked to air pollution, the dramatic rise in air pollution in Taiwan during the past 40 years may be responsible for changing the base status of the study forest and community-level responses to this new stress may not yet have occurred. Although acidic precipitation could increase weathering rates and therefore the release of cations, the low base saturation of the soils of the Fu-shan Experimental Forest (Table 4) suggests this is not likely to influence the availability of base cations. In fact acidic precipitation may intensify base-cation leaching and lead to soil acidification (Ulrich and Pankrath 1983; Schulze 1989).

### Seasonal variation

Patterns of net throughfall flux were similar between summer and winter except for $Ca^{2+}$ (Table 2), suggesting internal and (or) external canopy processes were active in the winter. Studies of temperate hardwood forest ecosystems indicate that canopy processes are much more active during the growing season (Puckett 1990; Hamburg and Lin 1998). Because leaves are the first and the major interface between forests and atmospheric deposition, canopy interaction is closely related to leaf area index (Carleton and Kavanagh 1990; Hamburg and Lin 1998). In the winter dormant season, trees of temperate deciduous forests drop their leaves. As a result there is a limited canopy surface to intercept external dry deposition and interact with deposited chemicals. In addition, because physiological activity is low in the winter, internal canopy processes are also reduced. The study forest, by contrast, experienced dry deposition and canopy exchange in the winter as well as the summer. Canopy leaf area index at the study forest is very similar in July and in February in years in which there are no late summer typhoons (Lin et al. 1999). The significant canopy exchange of cations in our study forest suggests that the trees actively interact with atmospheric deposition in the winter.

The high humidity, low temperature (and therefore low evapotranspiration), together with the frequent rainfall immerses the forest canopy in acid precipitation for much of the winter. Studies using simulated acid rain found that canopy leaching of base cations $K^+$, $Ca^{2+}$, and $Mg^{2+}$ is positively correlated with the duration of the exposure of leaves to contact with acid deposition (Turner and van Broekhuizen 1992). Thus, base cation leaching from the forest canopy at Fu-shan can be expected to be high.

Several researchers have classified moist tropical forests based on nutrient cycling patterns (Jordan and Herrera 1981; Vitousek and Sandford 1986). According to these descriptions, the forest we studied is oligotrophic and is susceptible to leaching loss of nutrients as the result of rapid decomposition and heavy, frequent rains. Superimposed on this naturally stressed forest is the increased rate of base-cation leaching due to heavy acid deposition. In southwestern China a growth decline in subtropical forests has been reported (Zhao and Seip 1991), and acid deposition induced base-cation depletion is suspected to be the cause (Liu and Li 1991; Feng 1993). To date, the Fu-shan Experimental Forest has not shown any indication of a decline in productivity, despite the substantial loss of base cations described in this paper. Since the effects of air pollution are likely to be additive it may take decades before symptoms of decline are observed (Bormann 1985).

## Conclusions

The observed annual leaching of base cations, $K^+$ (69–189%), $Ca^{2+}$ (11–35%), and $Mg^{2+}$ (19–30%) was very high relative to the cations stored in canopy leaves. Unlike temperate deciduous forests that typically have large stores of nutrients in the soils, the soils of the subtropical rainforest we investigated have an extremely low base-cation status. Thus, canopy storage of cations represents a large proportion of the available nutrient capital at the Fu-shan Experimental Forest. The warm and humid climate speeds decomposition and the large amount of precipitation removes many of the nutrients leached from the forest canopy, released by decomposition, or released through weathering. Therefore, pollution induced increases in canopy leaching of base cations could lead to a permanent and detrimental loss of base cations. These forests may have adapted to low levels of soil base cations and the limited capacity of the soils they grow on to retain base cations. However, increases in acid deposition over the past 40 years may be overwhelming the ability of these forests to retain sufficient amounts of base cations to thrive. Because of the lack of a dormant season and extremely high humidity and frequent rainfall, particularly in the winter, the forest canopy is exposed to acid precipitation for prolonged periods of time. The subtropical rainforest we studied is probably more susceptible to acid deposition than are the temperate forests that have similar loadings of acidic pollutants.

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