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Nitrogen availability in disturbed, rehabilitated and mature forests of tropical China

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Abstract

To investigate the impact of human disturbance and subsequent recovery on soil nitrogen processes, nitrogen availability during different seasons and at two soil depths in disturbed, rehabilitated and mature forests in tropical China was estimated using the ion exchange resin (IER) bag method. Soil total mineral N ($\text{NH}_4^+\text{-N} + \text{NO}_3^-\text{-N}$) varied significantly depending on forest and season. Overall, total mineral N concentrations ranked as follows: rehabilitated > mature > disturbed (forest); and spring > fall > winter > summer (season). Of the total mineral N, $\text{NH}_4^+\text{-N}$ was the major form in all forests (about 50–95%) with its proportion varying depending on forest and season. The correlation between $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ was strongest in the mature forest, followed by the rehabilitated forest and by the disturbed forest. Harvesting understory and litter had significant effects on soil N—mineral N was higher in treatment plots (more disturbed) than in control plots (relatively less disturbed). Although mineral nitrogen is produced, fewer plants and low microbial activity lead to low uptake and low immobilization resulting in greater N leaching losses in treatment plots. The results of this study suggest that over the period of 50 year or so, successful rehabilitation of soil N availability on severely degraded lands is possible, however, as long as harvesting of understory and litter continues in the degraded forest, this rate and level of recovery is unlikely to be realized.

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1. Introduction

Conversion to non-forest use is considered to be one of the largest threats to tropical forests worldwide. Currently, tropical deforestation is estimated to be on the order of 10 million hectare per year during the 1990s (FAO, 2001). However, of equal concern, but yet poorly quantified, is degradation of tropical forests, including reductions in biomass, fragmentation,

and loss in biodiversity (FAO, 1996). Degradation is generally the culprit when a forest has a significantly lower biomass than would be expected given the climate conditions and the soil type (Brown et al., 1991). Factors behind degradation include: intensive harvesting for timber and fuelwood, unsustainable agriculture, fires, and overgrazing by domestic animals. Removal of biomass causes nutrient losses and changes in soil physical and chemical characteristics (Allen, 1985; Montagnini and Buschbacher, 1989; Hornbeck et al., 1990; Lederle and Mroz, 1991; Steudler et al., 1991; Wang et al., 1991). The amount of nutrient loss depends on the intensity of

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the activities, environmental factors, and type and successional state of the forest. If nutrient losses cannot be recovered during regrowth, forests often become degraded through time (Jordan et al., 1983; Vitousek, 1983). Thus, it is important that nutrient dynamics of human-impacted forests be well understood to develop sustainable forest management plans. However, disturbed ecosystems are among the least studied in the tropics (Brown and Lugo, 1990).

Most of the land originally covered with primary forests in southern China has been degraded by human activities during the past several hundred years (Wang et al., 1982). In extreme cases, the land became completely non-vegetated (He and Yu, 1984). Attempts to reverse this process of land degradation have been initiated in the southern region of China. Over the last few decades, large areas have been reforested with a native pine species, *Pinus massoniana*, to prevent further degradation of the landscape. Cutting of the trees is now prohibited, but harvesting of understory and litter is allowed to satisfy human fuel needs. Compared with whole-tree harvest, this practice removes less biomass from the forests, however, as understory and litter are relatively nutrient-rich, this practice may prevent the recovery of soil fertility and productivity of these forest ecosystems. Compared with remnant mature forests of the region and rehabilitated forests (reforested but no harvesting), the disturbed forest appears to have lower productivity and lower nutrient levels (Ehleringer et al., 1986; Peng et al., 1989), but definitive data are lacking.

We have previously reported on the organic matter and nutrient cycling dynamics in reforested pine forests in southern China (Brown et al., 1995 and Mo et al., 1995). We found that harvesting understory and litter removed substantial quantities of nutrients, 44–73% of the amount in litter and understory production (depending on the element), a rate that appeared to exceed most nutrient inputs from atmospheric deposition (Mo et al., 1995). The current low site productivity appears to be mainly caused by this practice (Brown et al., 1995).

The goals of the present study were to: (1) measure the effects of harvesting understory and litter in the reforested pine forest on soil nitrogen availability during different seasons; (2) test the hypothesis that the soil nitrogen availability increases with restoration

of degraded forests; and (3) compare soil nitrogen availability among different stages of forest succession, season, and depth. Results from such studies will provide insight into the mechanisms underlying the low productivity, low biomass, and low nutrient availability observed previously in the degraded site (Brown et al., 1995; Mo et al., 1995); and the rate of rehabilitation for the degraded forest.

2. Methods

2.1. Site description

This study was conducted in three forest types in the UNESCO/MAB Dinghushan biosphere reserve (DHSBR) in southern China: pine (disturbed), pine-broadleaf mixed (rehabilitated), and monsoon evergreen broadleaf forests (MEBF-mature). In 1956, the area became the first nature reserve in China and was affiliated with the Academia Sinica. In 1978, a Forest Ecosystem Experimental Station was established in the reserve. One year later, the reserve was placed in the UNESCO/MAB network of reserves for the humid tropics. The biosphere reserve lies in the middle part of Guangdong Province (112°10'E longitude and 23°10'N latitude).

The DHSBR occupies an area of approximately 1200 ha. The monsoon evergreen broadleaf forest, at about 250–300 m above sea level (ASL) occupies 20% of the reserve area, the mixed pine and broadleaf forest, at about 200 m ASL occupies 50%, and the pine forest, at about 50–200 m ASL occupies 20% (Zhou et al., 1986). The monsoon evergreen broadleaf has been protected from human impacts for more than 400 years by monks in the temples. (There are three temples in DHSBR: Baiyun (established in A.D. 678), Yunrong monastery (A.D. 678) and Qingyun temple (A.D. 1633).) The pine-broadleaf mixed forest originated from a planted pine forest that was naturally invaded and colonized by broadleaf species and is a transitional forest from pine to monsoon evergreen broadleaf forest. The age of this mixed forest is about 65 years (Wang et al., 1982). It is relatively inaccessible to the rural population, and litter and understory harvesting have been minimal to absent. The pine forest was planted in about 1930. It has been under constant human pressures most of the time since it

was planted (generally the harvesting of understory and litter). Thus, these forests vary both in level of human impacts as well as stages of succession, site conditions, and species assemblages (Wang et al., 1982).

The reserve has a monsoon climate and is located in a subtropical moist forest life zone (*sensu*, Holdridge, 1967). The mean annual rainfall of 1927 mm has a distinct seasonal pattern, with 75% of it falling from March to August and only 6% from December to February (Huang and Fan, 1982). Annual average relative humidity is 80%. Mean annual temperature is 21.0 °C, with an average temperature of the coldest (January) and hottest (July) month of 12.6 and 28.0 °C, respectively.

The soil in the three study sites is lateritic red earth formed from sandstone, but the soil depths vary in each site. In the monsoon evergreen broadleaf forest the soil is deeper than 60 cm. In the mixed forest, depth ranges from 30 to 60 cm, and in the pine forest the depth is generally less than 30 cm to bedrock. The major species in the MEBF (mature) are *Castanopsis chinensis*, *Schima superba*, *Cryptocarya chinensis*, *C. concinna*, *Machilus chinensis* in the tree layer and *Calamus rhabdioladus*, *Ardisia quinquegona* and *Hemigramma decurrens* in the understory layers (Wang et al., 1982). Tree heights range from 4 to 30 m and diameters from 5 to 163 cm (Wang et al., 1982).

The major species in the mixed pine broadleaf forest (rehabilitated) are *P. massoniana*, *S. superba*, *C. chinensis*, *Craibiodendron kwangtungense*, *Lindera metcalifiana*, *C. concinna* in the tree layer and *Rhodomyrtus tomentosa*, *Evodia leptota*, *Dicranopteris linearis* var. *dichotoma* in the understory (Wang et al., 1982). Tree heights range from 4 to 12 m and diameters from 4 to 48 cm (Wang et al., 1982).

The pine forest (disturbed) is dominated by *P. massoniana*. Pine trees range from 100 to 1000 trees ha⁻¹, with diameters of 4–32 cm and heights of 3–11 m (Brown et al., 1995). Age of pine trees range from 12 to 69 years, with a mean value of 30 years. In addition to pine trees, there were a few eucalyptus trees (*Eucalyptus robusta*). Understory species included grasses, ferns, vines and shrubs for a total of 43 species (Brown et al., 1995).

To investigate the impact of harvesting understory and litter in the pine forest (disturbed) on nitrogen

availability we used a paired-plot design, with 20 replicates (Brown et al., 1995). Each pair consisted of a treatment (continued harvest) and control (no harvest) plot, 10 m × 10 m in size, and surrounded by a 10 m wide buffer strip. In the treatment plots, local people continued to harvest litter and understory according to their practice (about 2–3 times a year) from the beginning of the experiment in May 1990. Control plots were protected from any harvesting. Each plot of a pair was similar in soil, slope, aspect, and elevation to its matched plot.

2.2. Field sampling and sample analyses

The ion exchange resin (IER) bag method was used to evaluate nitrification (production of NO₃⁻-N) and nitrogen mineralization (production of NH₄⁺-N+NO₃⁻-N) (Binkley and Matson, 1983, Binkley, 1986, Anderson and Ingram, 1989; Mark et al., 1989). Because IER bags were in contact with the soil solution and exposed to approximately the same soil environmental conditions as tree roots, analysis of IER extracts provided a measure of the relative concentration of NH₄⁺-N and NO₃⁻-N in the soil solution during the incubation period. The concentration of NH₄⁺-N and NO₃⁻-N in the resin bags represents the net difference between two processes: nitrogen mineralization and nitrogen uptake by plants and microbes. We refer to the concentration of NH₄⁺-N and NO₃⁻-N in the resin bags as an index of N availability.

At the beginning of the study, 120 IER bags were prepared by placing about 12 g of mixed cation + anion resin (about 5 g dry weight, 105 °C for 24 h) in bags made from nylon hose, which were then stapled shut (Binkley and Matson, 1983, Anderson and Ingram, 1989). Because there were three study sites, these 120 bags were randomly divided into three sets (40 bags per set) and then buried in randomly chosen locations (20 locations per site). At each location, one bag was buried at 2–7 cm and one at 12–17 cm, below the forest floor/mineral soil interface. The first 120 bags were placed in the field on 15 September 1992, and picked up 3 months later (15 December 1992). The bags were placed in an ice chest for transportation and then stored in a refrigerator until extraction. This experiment was repeated three times: from 14 December 1992 to 14 March 1993; 15 March to 14 June 1993, and 15 June to 14 September 1993.

For the experiment on the impact of harvesting understory and litter on nitrogen availability, 100 IER bags were prepared by placing about 10 g of mixed cation + anion resin in nylon hose. Five of the paired plots were randomly selected, and 20 bags (10 for control and 10 for treatment plot) were buried 2–7 cm below the forest floor/mineral soil interface on 30 May 1990. Bags were retrieved on 14 August 1990, placed in an ice box for transportation and then stored in a refrigerator until extraction. The experiment was repeated from 14 August 1990 to 7 March 1991, 7 March 1991 to 21 May 1991, and 23 December 1991 to 16 May 1992.

Soil and roots attached to the resin bags were carefully removed by hand prior to extraction. The resin bags were extracted with 100 ml of 1N KCL by shaking in a shaker for 1 h (Binkley and Matson, 1983). Ammonium ($\text{NH}_4^+\text{-N}$) was determined with an autoanalyzer and nitrate ($\text{NO}_3^-\text{-N}$) with colorimetric determination (Anderson and Ingram, 1989) in the South China Institute of Botany (SCIB), Academia Sinica.

Samples for measuring soil properties were collected on 15 September 1992. Ten locations were randomly chosen in each study site and two cores of soil were collected from each location, one from a depth of 0–10 cm and one from 10 to 20 cm. Soils were dried to a constant weight at 40 °C immediately after collection. Soil samples were ground to pass through a 2 mm mesh sieve. Subsamples of soil materials were dried to 105 °C, and all results were reported on 105 °C basis (Nanjing Soil Institute,

1978). All soil analyses were done according to standard methods (Nanjing Soil Institute, 1978).

Main effects of site (forest), soil depth, and season, and their interaction on nitrogen availability were determined in a three-way analysis of variance (ANOVA). Least square regression analysis was used to determine the relationship between ammonium and nitrate values. A paired *t*-test was used to test the difference in values of $\text{NH}_4^+\text{-N}$ and of $\text{NO}_3^-\text{-N}$ between treatment (understory and litter removal) and control plots. Differences for all tests were considered to be significant at the 0.05 level.

3. Results

3.1. Soil properties

The concentration of organic matter, total N, and water content in soil of the study sites were ranked in the order: mature > rehabilitated > disturbed forest, and decreased with soil depth (Table 1). In contrast, pH and bulk density values in soil were lowest in mature, second in rehabilitated and highest in disturbed forest, and both increased with soil depth (Table 1).

3.2. Patterns in $\text{NH}_4^+\text{-N} + \text{NO}_3^-\text{-N}$ concentrations

Significant main effects were observed in concentrations of total mineral N ($\text{NH}_4^+\text{-N} + \text{NO}_3^-\text{-N}$) depending on forest and season (Figs. 1–2 and Table 2; $P < 0.001$). Concentrations of total mineral

Table 1
Soil properties in disturbed, rehabilitated and mature forests in tropical China (mean S.E. in parenthesis; $n = 10$ for all samples).

Forest type	Soil depth (cm)	Organic matter (%)	Total N (%)	C/N	pH	Bulk density (g cm^{-3})	Moisture content (%)
Disturbed (pine)	0–10	3.67 (0.14)	0.11 (0.01)	19.01 (0.80)	3.99 (0.02)	1.34 (0.04)	27.83 (1.22)
	10–20	1.79 (0.19)	0.07 (0.01)	14.57 (1.08)	4.07 (0.01)	1.47 (0.04)	21.97 (0.98)
	Mean	2.73 (0.17)	0.09 (0.01)	16.79 (0.94)	4.03 (0.02)	1.41 (0.04)	24.90 (1.10)
Rehabilitated (mixed)	0–10	4.87 (0.58)	0.13 (0.02)	21.35 (1.05)	3.79 (0.03)	1.24 (0.03)	28.39 (1.04)
	10–20	2.02 (0.11)	0.07 (0.00)	16.45 (0.89)	3.92 (0.01)	1.36 (0.04)	23.55 (0.77)
	Mean	3.45 (0.35)	0.10 (0.01)	18.90 (0.97)	3.86 (0.02)	1.30 (0.04)	25.97 (0.91)
Mature ^a	0–10	7.24 (0.74)	0.25 (0.02)	16.81 (0.70)	3.76 (0.07)	1.06 (0.02)	43.91 (1.70)
	10–20	3.46 (0.41)	0.13 (0.01)	15.02 (1.02)	3.81 (0.05)	1.37 (0.03)	33.23 (0.67)
	Mean	5.35 (0.58)	0.19 (0.01)	15.91 (0.86)	3.79 (0.06)	1.21 (0.03)	38.57 (1.19)

^a Monsoon evergreen broadleaf forest.

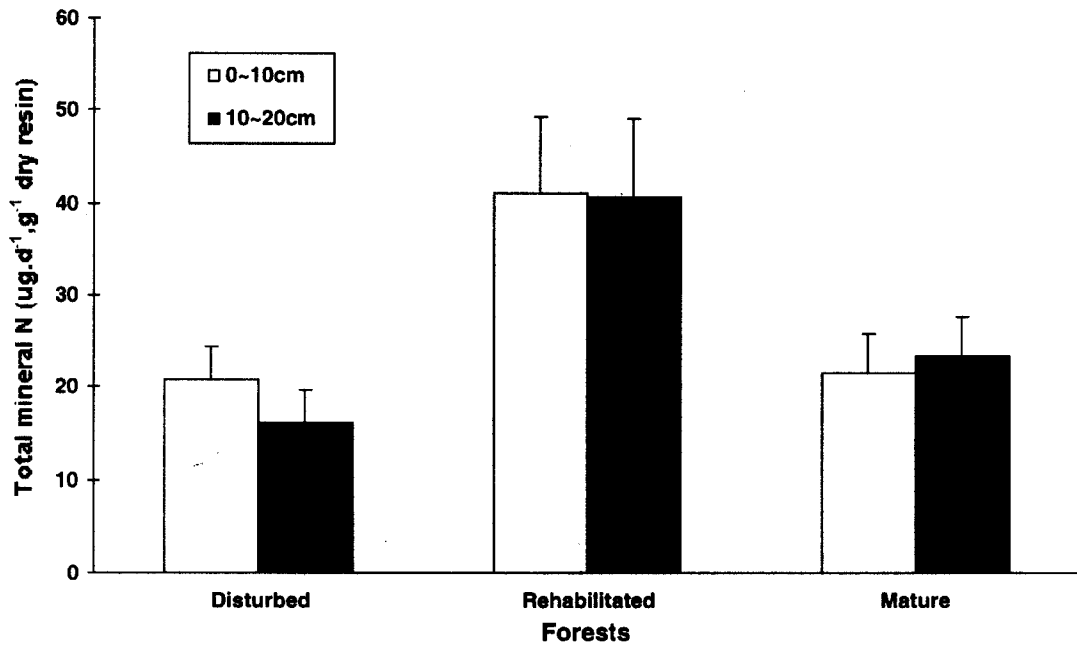


Fig. 1. A comparison of $\text{NH}_4^+-\text{N}+\text{NO}_3^--\text{N}$ concentrations among different forests in Dinghushan biosphere reserve, southern China.

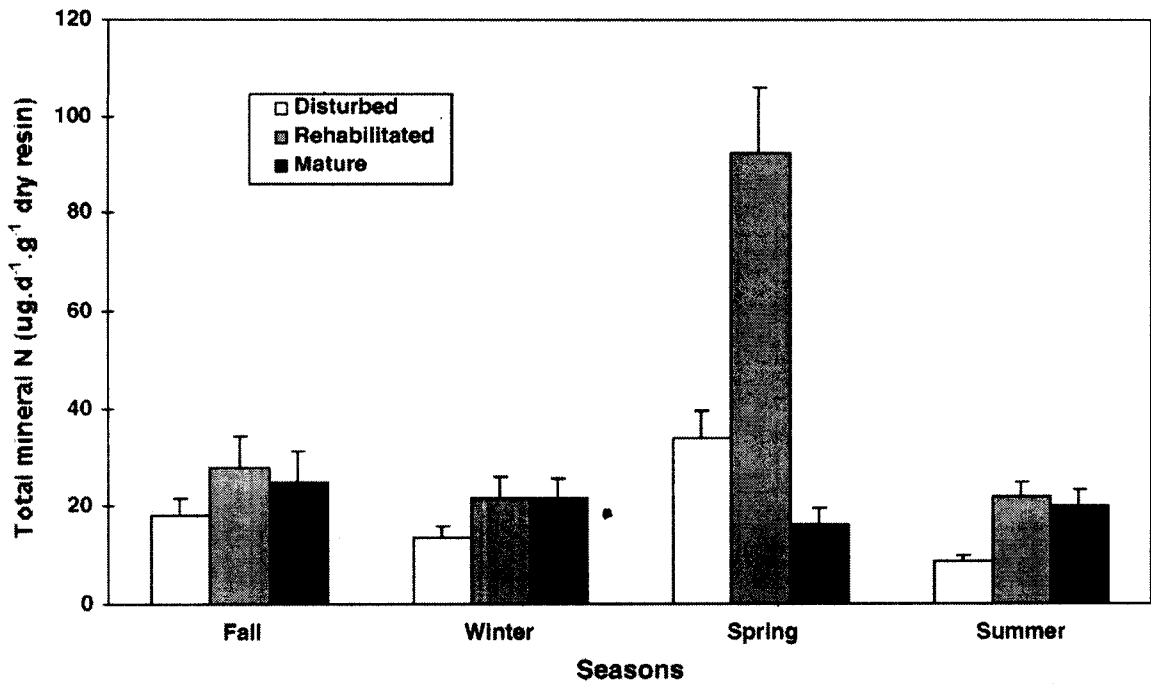


Fig. 2. A comparison of seasonal variations of $\text{NH}_4^+-\text{N}+\text{NO}_3^--\text{N}$ concentrations among different forests in Dinghushan biosphere reserve, southern China.

Table 2

F-statistic and probability of significant difference by analysis of variance for the main effects and their interactions on $\text{NH}_4^+\text{-N} + \text{NO}_3^-\text{-N}$ values in disturbed, rehabilitated, and mature forests in a MAB biosphere reserve of subtropical China

	Forest		Depth		Season		Forest × season		Forest × depth		Depth × season	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
All forests	13.794	<0.001	0.001	0.972	36.232	<0.001	11.445	<0.001	0.067	0.935	0.314	0.815
Pine			0.010	0.920	10.945	<0.001					0.561	0.642
Mixed			0.003	0.960	27.961	<0.001					0.082	0.970
Mature			0.419	0.526	1.014	0.389					1.966	0.122

N varied significantly among different forests. Overall, rehabilitated forest was highest in total mineral N concentrations (Fig. 1; 41.04 ± 8.33 and $40.77 \pm 7.09 \mu\text{g per day g}^{-1}$ dry resin in depth of 0–10 cm and 10–20 cm, respectively), followed by mature forest (21.57 ± 4.38 and $23.45 \pm 5.12 \mu\text{g per day g}^{-1}$ dry resin in depth of 0–10 cm and 10–20 cm, respectively) and by disturbed forest (20.86 ± 3.47 and $16.13 \pm 2.94 \mu\text{g per day g}^{-1}$ dry resin in depth of 0–10 cm and 10–20 cm, respectively). The values of $\text{NH}_4^+\text{-N} + \text{NO}_3^-\text{-N}$ also exhibited significant seasonal variations (Fig. 2 and Table 2; $P < 0.001$) and generally showed the following order: spring (total mean value: $47.64 \pm 14.67 \mu\text{g per day g}^{-1}$ dry resin) > fall ($23.51 \pm 2.30 \mu\text{g per day g}^{-1}$ dry resin) > winter ($18.76 \pm 2.06 \mu\text{g per day g}^{-1}$ dry resin) > summer ($16.81 \pm 3.29 \mu\text{g per day g}^{-1}$ dry resin). However, when analyzed by separate forest type, mature forest, unlike the other forests, had no significant seasonal variation (Table 2; $P < 0.001$ for disturbed and rehabilitated forest; $P > 0.389$ for mature forest).

Although no significant main effects were found with soil depths (Fig. 1 and Table 2), variations with depth were found depending on forest. The concentrations of total mineral N in the top soil was 1.3 times that in deeper soil in disturbed forest, similar to each other in rehabilitated forest, and 0.9 times that in deeper soil in mature forest.

In addition to significant main effects, interactions of forest and season for total mineral N concentrations were also significant (Fig. 2 and Table 2; $P < 0.001$). These results indicate that (1) the effect of forest type on N availability significantly differed depending on season or (2) the effect of season on N availability significantly differed depending on forest. For example, in spring the mineral N concentrations exhibited the following order: rehabilitated (mean total mineral

N: $92.57 \pm 13.45 \mu\text{g per day g}^{-1}$ dry resin) > disturbed ($34.03 \pm 5.52 \mu\text{g per day g}^{-1}$ dry resin) > mature ($16.32 \pm 3.16 \mu\text{g per day g}^{-1}$ dry resin). However, in summer the order was rehabilitated ($23.01 \pm 3.41 \mu\text{g per day g}^{-1}$ dry resin) > mature ($12.63 \pm 2.32 \mu\text{g per day g}^{-1}$ dry resin) > disturbed ($9.72 \pm 1.47 \mu\text{g per day g}^{-1}$ dry resin; forest × season). In disturbed forest, the mineral N concentrations were highest in spring season ($35.49 \pm 5.89 \mu\text{g per day g}^{-1}$ dry resin) and lowest in summer ($9.72 \pm 1.47 \mu\text{g per day g}^{-1}$ dry resin). In rehabilitated forest, the highest concentrations were also found in spring season ($93.20 \pm 13.28 \mu\text{g per day g}^{-1}$ dry resin), but the lowest were generally in winter ($18.87 \pm 3.90 \mu\text{g per day g}^{-1}$ dry resin; forest × season).

3.3. Relationship of ammonium and nitrate

Of the total mineral N, ammonium was the major form in both soil depths and in all forests (Fig. 3). However, the percentages of total mineral N as NH_4^+ varied significantly depending on forest and on season, but not on depth ($P < 0.001$ for the main effect and interaction of forest × season; data not shown in Table). The percentages of NH_4^+ in both soil depths in disturbed forest were similar to those in rehabilitated forest (Fig. 3; disturbed forest: 86.58–93.41%, rehabilitated forest: 86.48–94.61%), but the percentages of NH_4^+ in these two forests were significantly higher than those in mature forest (49.61–84.71%). A comparison by season shows that the percentages of NH_4^+ in mature forest were highest in fall season, but, in disturbed forest the highest percentages were found in spring season (forest × season).

Ammonium supply is a factor regulating nitrification in these forests, but the supply varied depending on season and forest (Table 3). In fall and winter

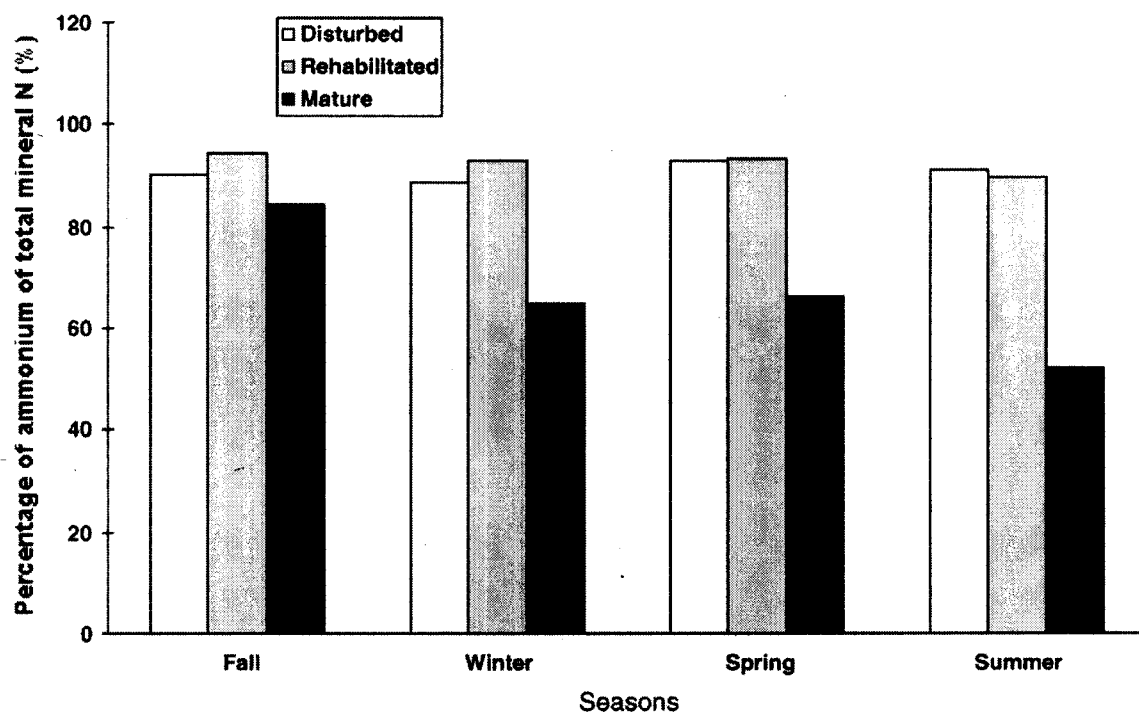


Fig. 3. A comparison of percentage of ammonium of total mineral N among different forests in Dinghushan biosphere reserve, southern China.

seasons, NO_3^- values were highly positively correlated with NH_4^+ values at both soil depths in all forests ($P < 0.05$, Table 3). In summer season, this relationship was only found in the deeper soil in mature forest. A comparison of the different forests showed that the correlation between NO_3^- and NH_4^+ was strongest in the mature forest, followed by rehabilitated forest and by disturbed forest.

Table 3

Correlation coefficients of NH_4^+ -N and NO_3^- -N in disturbed, rehabilitated and mature subtropical forests in China ($n = 20$ for all seasons and depths)

Forest	Soil depth (cm)	Fall	Winter	Spring	Summer
Disturbed	0–10	0.625*	0.554*	0.382	0.148
	10–20	0.672*	0.573*	0.438	0.117
Rehabilitated	0–10	0.753*	0.609*	0.480	0.130
	10–20	0.699*	0.751*	0.704*	0.022
Mature	0–10	0.835*	0.905*	0.616*	0.426
	10–20	0.79*	0.832*	0.877*	0.903*

* Significant at ($P < 0.05$).

3.4. Effects of organic matter removal

Harvesting understory and litter had a significant impact on NH_4^+ and NO_3^- concentrations in the resin bags (Fig. 4). During the first 3 months of the experiment, there was no significant difference in NH_4^+ between treatment and control plots. From the third month to the end of this experiment, concentration of NH_4^+ was significantly higher in treatment plots than in control plots ($P < 0.05$). Nitrate values responded in similar way to NH_4^+ , but with more pronounced differences in the last two time periods.

4. Discussion

4.1. Impacts of organic matter harvesting on nitrogen availability in the disturbed forest

Relatively little information is available about N mineralization in tropical forest soils, especially in disturbed ecosystems, although it is well accepted that

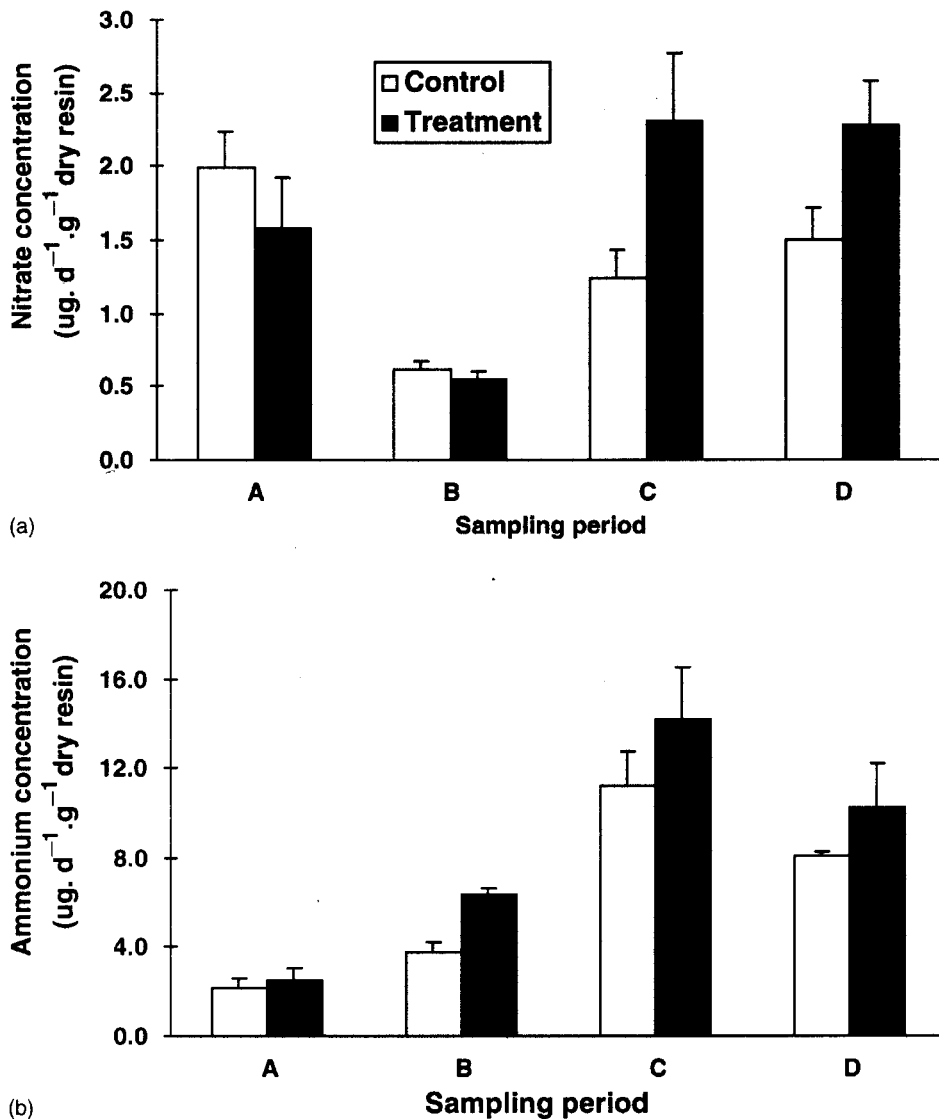


Fig. 4. A comparison of (a) nitrate and (b) ammonium concentrations in control and treatment plots in different sampling period in a disturbed pine forest in tropical China. (A): 30 May 1990–14 August 1990 (76 days); (B): 14 August 1990–7 March 1991 (204 days); (C): 7 March 1991–21 May 1991 (74 days); and (D): 23 December 1991–16 May 1992 (145 days).

there is a close relationship between forest productivity and N supply from the soil. Compared to the complete harvesting of the forest, harvesting of litter and understory removes fewer nutrients from the forest sites. Our previous results indicated that this practice still removed substantial quantities of nutrients, 44–73% of the total litter and understory pool, a

rate that appeared to exceed most nutrient inputs from atmospheric deposition (Mo et al., 1995).

However, another effect of organic matter removal is not so obvious. This is the impact on mineral nitrogen leaching losses. It is reported that disturbances in forest ecosystems transform considerable amounts of organic N to more mobile forms and

therefore, increase the potential for leaching losses of nitrogen (Bonilla and Roda, 1990; Adams and Attiwill, 1991). When perturbation is less severe, nitrate-leaching losses are reduced (Jordan et al., 1979). That mineral N was higher in treatment plots (more disturbed) than in control plots (relatively less disturbed), especially for NO_3^- , suggests that leaching losses were higher, a trend consistent with these previous findings.

There are three possible explanations for the variations of mineral N level caused by the practice of organic matter removal.

- (1) This practice changed the cycles of soil drying and wetting. Removal of understory and litter increased the exposure of the soil surface to sunlight and rainfall. This results in higher fluctuation of soil temperature and moisture, or more stress for microorganism. Cycles of wetting and drying greatly affect decomposition of organic matter and the turnover of biomass (Van Veen et al., 1984) and cause flushes in net mineral nitrogen level (Marrs et al., 1991).
- (2) This practice decreased the uptake of mineral nitrogen by plants. Plants influence mineral nitrogen concentrations mainly through uptake. The faster plants grow and the more biomass they contain, the more inorganic nitrogen is taken up (after the practice of understory harvesting was stopped, biomass production and N concentration in the understory increased; unpublished data from related studies at this site). It can be inferred that because of the ongoing removal of understory in treatment plots, the uptake of mineral nitrogen by plants is less there than in control plots (Mo et al., 1995).
- (3) This practice changed the quantity and quality of the standing litter. Fresh materials decompose faster than older materials (Berg and Soderstrom, 1979). In control plots, the substrate is continually renewed by litterfall, while the substrate in treatment plots is largely removed and the remainder becomes progressively enriched in substances more resistant to decomposition. We inferred that there would be more microorganisms in control plots than in treatment plots after a certain period because of the higher quantity and quality of organic matter. More microorganisms mean more available nitrogen would be

immobilized (N was the only element immobilized in decomposing litter in control sites; Mo et al., 1995).

Harvesting understory and litter not only removes the nutrients therein, but it also removes organic matter and thus, substrate for microbial activity. Although mineral nitrogen is produced, fewer plants and low microbial activity lead to low uptake and low immobilization resulting in greater leaching losses in treatment plots and thus, higher concentrations in the resin bags. We propose that this mechanism is one of the major reasons that the nutrient standing stocks, forest biomass, rates of biomass production, and decomposition rates of the disturbed pine forest are low for its age as shown in our previous work (Brown et al., 1995, Mo et al., 1995).

4.2. Does soil nitrogen availability increase with restoration of the degraded forest?

We have demonstrated that harvesting understory and litter resulted in direct and indirect loss of soil N in disturbed forest. As humans have disturbed the pine forest site for a long time, the land has become severely degraded. This is also reflected in the difference in soil N concentrations between the pine forest and mature forest (Table 1). Soil N concentration in mature forest was twice that of the disturbed forest. Then, the question is whether the soil N availability increases with restoration of the degraded forest and if so how long would this process take? In order to answer this question, we compared data for disturbed forest with that for rehabilitated forest and mature forest (Figs. 1 and 2). Although we assume that a comparison along this successional gradient will reflect the expected changes in soil N availability over time, we must recognize that each forest type has a different complement of species, with pine dominating the degraded site, co-dominant in the rehabilitated site, and completely absent from the mature site. The differences in species assemblages affect many aspects of the N cycle (e.g. stocks and rate of cycling). Of relevance to the discussion here on soil N availability is the potential differences in the C/N ratio of the foliage, litter and soil in the different forest sites as these factors influence the rate of nitrogen mineralization by decomposers. Such data exist for the degraded

and mature forest sites (Mo et al., 1995; Ding et al., 2001; Table 1). The C/N ratios for fresh leaves, litter, and soil of the degraded forest are 37, 83, and 16.8, respectively; for the mature forest the corresponding values are 32, 36, and 15.9. Only the litter for the mature forest site is lower than for the degraded site, the other values are practically the same. The high C/N ratio for the litter of the degraded forest is due to significant retranslocation of N from foliage resulting in low N concentration in litter, a common observation in N-poor sites (Mo et al., 1995).

Even though the rehabilitated forest is only about 10 year older than the disturbed forest, on average, and is growing on the same soil type, its mineral N availability values were up to 2.0–2.5 times higher than those of the disturbed forest. The mineral N values in the rehabilitated forest were 1.7–1.9 times higher than those of the mature forest. The reason for the lower mineral N values in mature forest compared to those of the rehabilitated forest was likely caused by the higher plant N uptake in the mature forest than in the rehabilitated forest (higher total and leaf biomass in the mature forest; Ding et al., 2001). A comparison of the results between disturbed and rehabilitated forests suggests that over the period of 50 year or so, successful rehabilitation of nutrient availability on severely degraded lands is possible. This is similar to the results we obtained for the rehabilitation of forest biomass and primary productivity (Brown et al., 1995, Mo et al., 1995). However, as long as harvesting of understory and litter continues in the degraded forest, this rate and level of recovery is unlikely to be realized.

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References

- Adams, M.A., Attiwill, P.M., 1991. Nutrient balance in forests of northern Tasmania. Alteration of nutrient availability and soil water chemistry as a result of logging. *For. Ecol. Manage.* 44, 115–131.
- Allen, J.C., 1985. Soil response to forest clearing in the United States and the tropics: geological and biological factors. *Biotropica* 17, 15–27.
- Anderson, J.M., Ingram, J.S.I., 1989. *Tropical Soil Biology and Fertility: A Handbook of Methods*. CAB International, Wallingford, Oxford, UK.
- Berg, B., Soderstrom, B., 1979. Fungal biomass and nitrogen in decomposing scots pine needle litter. *Soil Biol. Biochem.* 11, 339–341.
- Binkley, D., Matson, P., 1983. Iron exchange resin bag method for assessing forest soil nitrogen availability. *Soil Sci. Soc. Am. J.* 47, 1050–1052.
- Binkley, D., 1986. Nitrogen availability in some Wisconsin forests: comparisons of resin bags and on-site incubations. *Biol. Fertil. Soils* 2, 77–82.
- Bonilla, D., Roda, F., 1990. Nitrogen cycling responses to disturbance: trenching experiments in an evergreen oak forest. In: Harrison, A. F., Ineson P., Heal O. W. (Eds.), *Nutrient Cycling in Terrestrial Ecosystems*. Elsevier Applied Science, London, pp. 179–189.
- Brown, S., Lugo, A.E., 1990. Tropical secondary forests. *J. Trop. Ecol.* 6, 1–32.
- Brown, S., Gillespie, A.J.R., Lugo, A.E., 1991. Biomass of tropical forests in South and Southeast Asia. *Can. J. For. Res.* 21, 111–117.
- Brown, S., Lenart, M.T., Mo, J.M., Kong, G.H., 1995. Structure and organic matter dynamics of a human-impacted pine forest in a MAB reserve of subtropical China. *Biotropica* 27, 276–289.
- Ding, M.M., Brown, S., Lugo, A.E., 2001. A continental subtropical forest in China compared with an insular subtropical forest in the Caribbean. USDA Forest Service General Technical Report IITF-17, Rio Piedras, Puerto Rico.
- Ehleringer, R.J., Field, C.B., Lin, Z., Kuo, C., 1986. Physiological responses in subtropical plants subject to different disturbance levels. *Trop. Subtrop. For. Ecosys.* 4, 23–34.
- FAO, 1996. Forest resources assessment 1990: survey of tropical forest cover and study of change processes. FAO Forestry Paper 130, Rome, Italy.
- FAO, 2001. Global forest resources assessment 2000 SP (FRA 2000), Results as of 10 April 2001. Available from www.fao.org/forestry/fo/fra/index.jsp.
- He, S., Yu, Z., 1984. The studies on the reconstruction of vegetation in tropical coastal eroded land in Guangdong. *Trop. Subtrop. For. Ecosys.* 2, 87–90.
- Holdridge, L.R., 1967. Life zone ecology. Tropical Science Center, San Jose, Costa Rica.
- Hornbeck, J.W., Smith, C.T., Martin, Q.W., Tritton, L.M., Pierce, R.S., 1990. Effects of intensive harvesting on nutrient capitals of three forest types in new England. *For. Ecol. Manage.* 30, 55–64.
- Huang, Z.F., Fan, Z.G., 1982. The climate of Ding Hu Shan. *Trop. Subtrop. For. Ecosys.* 1, 11–23.
- Jordan, C.F., Todd, R.L., Escalante, G., 1979. Nitrogen conservation in a tropical rainforest. *Oecologia* 39, 123–129.

- Jordan, C., Caskey, W., Escalante, G., Herrera, R., Montagnini, F., Todd, R., Uhl, C., 1983. Nitrogen dynamics during conversion of primary Amazonian rain forest to slash and burn agriculture. *Oikos* 40, 131–139.
- Lederle, K., Mroz, G.D., 1991. Nutrient status of bracken (*Pteridium aquilinum*) following whole-tree harvesting in upper Michigan. *For. Ecol. Manage.* 40, 119–130.
- Mark, W.P., Dawson, J.O., David, M.B., 1989. Soil nitrogen mineralization in plantations of *Juglans nigra* interplanted with actinorhizal *Elaeagnus umbellata* or *Alnus glutinosa*. *Plant Soil* 118, 32–42.
- Marrs, R.H., Thompson, J., Scott, D., Proctor, J., 1991. Nitrogen mineralization and nitrification in terra firme forest and savanna soils on Ilha de Maraca, Roraima, Brazil. *J. Trop. Ecol.* 7, 123–137.
- Mo, J.M., Brown, S., Lenart, M., Kong, G.H., 1995. Nutrient dynamics of a human-impacted pine forest in a MAB Reserve of subtropical China. *Biotropica* 27, 290–304.
- Montagnini, F., Buschbacher, R., 1989. Nitrification rates in two undisturbed tropical rain forest and three slash-and-burn sites of the Venezuelan Amazon. *Biotropica* 21, 9–14.
- Nanjing Soil Institute, Academia Sinica. 1978. Analysis of Soil Properties. Shanghai Science Press, Shanghai China.
- Peng, S., Li, M., Lu, Y., 1989. A primary study on the biomass and productivity of *Pinus massoniana* population in Ding Hu Shan biosphere reserve. *Trop. Subtrop. For. Ecosys.* 5, 75–82.
- Stuedler, P.A., Melillo, J.M., Bowden, R.D., Castro, M.S., Lugo, A.E., 1991. The effects of natural and human disturbances on soil nitrogen dynamics and trace gas fluxes in a Puerto Rican wet forest. *Biotropica* 23 (4a), 356–363.
- Van Veen, J.A., Ladd, J.N., Fressel, M.J., 1984. Modelling C and N turnover through the microbial biomass in soil. *Plant Soil* 76, 257–274.
- Vitousek, P.M., 1983. The effects of deforestation on air, soil, and water. In: Bolin, B., Cook, R.B., (Eds.), *The Major Biogeochemical Cycles and Their Interactions*. Wiley, New York, pp. 223–245.
- Wang, D., Bormann, F.H., Lugo, A.E., Bowden, R.D., 1991. Comparison of nutrient-use efficiency and biomass production in five tropical tree taxa. *For. Ecol. Manage.* 46, 1–21.
- Wang, Z., He, D., Song, S., Chen, S., Chen, D., Tu, M., 1982. The vegetation of Ding Hu Shan biosphere reserve. *Trop. Subtrop. For. Ecosys.* 1, 77–141.
- Zhou, H., Li, M., Zhou, Y., He, D., Huang, Y., 1986. The vegetation map of Ding Hu Shan biosphere reserve with reference to its illustration. *Trop. Subtrop. For. Ecosys.* 4, 43–49.