10-2011

Effects of experimental nitrogen additions on plant diversity in tropical forests of contrasting disturbance regimes in southern China

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Recommended Citation

Lu X, J Mo, FS Gilliam, G Yu, W Zhang, Y Fang, and J Huang. 2011. Effects of experimental nitrogen additions on plant diversity in tropical forests of contrasting disturbance regimes in Southern China. Environmental Pollution 159:2228-2235.

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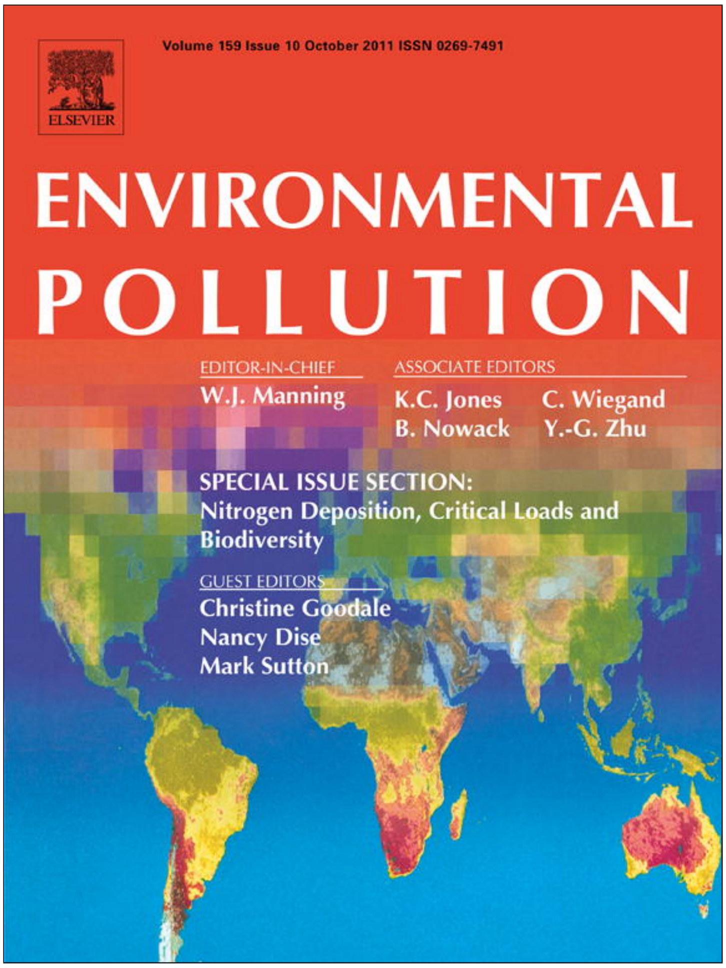
Volume 159 Issue 10 October 2011 ISSN 0269-7491
ELSEVIER
ENVIRONMENTAL POLLUTION
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Environmental Pollution 159 (2011) 2228–2235

Contents lists available at ScienceDirect

Environmental Pollution

journal homepage: www.elsevier.com/locate/envpol

Effects of experimental nitrogen additions on plant diversity in tropical forests of contrasting disturbance regimes in southern China

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ARTICLE INFO

Article history:
Received 7 July 2010
Received in revised form
26 October 2010
Accepted 31 October 2010

Keywords:
Nitrogen deposition
Biodiversity
Tropical reforestation
Land-use history
Light limitation

ABSTRACT

Responses of understory plant diversity to nitrogen (N) additions were investigated in reforested forests of contrasting disturbance regimes in southern China from 2003 to 2008: disturbed forest (with harvesting of understory vegetation and litter) and rehabilitated forest (without harvesting). Experimental additions of N were administered as the following treatments: Control, 50 kg N ha^{-1} yr^{-1}, and 100 kg N ha^{-1} yr^{-1}. Nitrogen additions did not significantly affect understory plant richness, density, and cover in the disturbed forest. Similarly, no significant response was found for canopy closure in this forest. In the rehabilitated forest, species richness and density showed no significant response to N additions; however, understory cover decreased significantly in the N-treated plots, largely a function of a significant increase in canopy closure. Our results suggest that responses of plant diversity to N deposition may vary with different land-use history, and rehabilitated forests may be more sensitive to N deposition.

1. Introduction

Responses of plant biodiversity to nitrogen (N) deposition have been studied primarily in temperate/boreal zones, where ecosystems are commonly N-limited. It is well known that increased N deposition typically decreases plant biodiversity in the affected ecosystems (see a review of Bobbink et al., 2010), although a few studies have reported no significant change (e.g., Gilliam et al., 2006). In contrast, less is known regarding the impact of N deposition on plant diversity of tropical/subtropical areas (Bobbink et al., 2010), which are typically N rich and more likely to be phosphorus (P) limited (Vitousek, 1984; Matson et al., 1999). Extensive work in tropical forests of the Hawai'i archipelago (see Vitousek, 2004) has shown that much of this arises from loss of available P through the long-term pedogenic processes of tropical soil formation. A limited number of studies (e.g., Lu et al., 2008, 2010) on the effects of N deposition on tropical forest plant diversity in natural ecosystems have shown that there are regional differences on this response. Lu et al. (2010) found that high levels of N additions (e.g., 150 kg N ha^{-1} yr^{-1}) significantly reduced understory plant diversity in an N-saturated mature forest of tropical China. They concluded that the mechanism for this decline was N deposition-mediated soil acidification, rather than competition-based mechanisms commonly found in studies of temperate ecosystems (Gilliam, 2006).

Forest ecosystems at various stages of reforestation following a variety of land-use practices are quite common in tropical regions, and are indeed becoming the dominant forest cover type in the tropics (Brown and Lugo, 1990; Houghton, 1994). Plant community composition and structure of reforested ecosystems often differs from mature forest ecosystems (Lugo, 1992; Marin-Spiotta et al., 2007). To our knowledge, dynamics of plant diversity in these reforested ecosystems are poorly understood. Gardner et al. (2009) suggested that both spatial and temporal patterns of biodiversity are the dynamic product of interacting historical and contemporary human and ecological processes. Considering the central role of tropical forests in protecting and maintaining terrestrial biodiversity, it is important to clarify the responses of biodiversity in these ecosystems to interactions of typical anthropogenic legacies (e.g., land-use practices) and contemporary anthropogenic influences (especially for N deposition).

Many primary forests in China have been deforested during the past several centuries (Wang et al., 1982; Liu et al., 2000; Li, 2004), with only 2% the nation's total forest resources remaining intact (Liu, 2006). More intensive disturbances result in minimal remnant vegetation cover (He and Yu, 1984). Attempts to reverse land

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doi:10.1016/j.envpol.2010.10.037

degradation have been made in many subtropical and tropical regions of China, with extensive areas having been reforested with native pine species (e.g., *Pinus massoniana* Lamb) to prevent further degradation of the landscape (Brown et al., 1995; Mo et al., 2004). Although cutting of the trees is usually prohibited, harvesting of understory vegetation and litter is often allowed to satisfy fuel needs of local people (Brown et al., 1995; Mo et al., 1995, 2003). These reforested stands are often referred to as *disturbed forests* (having experienced understory vegetation and litter removal) and *rehabilitated forests* (reforested without such removal) (Mo et al., 2003). Secondary forests now cover more than half of the total forested area in subtropical and tropical China (Brown et al., 1995; Mo et al., 2003, 2004; SFA, 2007). At the same time, anthropogenic N emissions and resultant N deposition have increased substantially in China, and are projected to increase further due to agricultural and industrial activities (Zheng et al., 2002; Galloway et al., 2004; Liu et al., 2010). Lü and Tian (2007) concluded that total N deposition rates are highest (65 kg N ha^{-1} yr^{-1}) in south-central China, with a mean rate of 19 kg N ha^{-1} yr^{-1}, higher than most reported for North American and Europe (MacDonald et al., 2002; Bobbink et al., 2010), where threats to forest ecosystem health have been suggested (Percy and Ferretti, 2004).

Previous work has demonstrated that both rehabilitated and disturbed forests in tropical China are N limited (Mo et al., 2006, 2007). Little is known, however, about responses of plant diversity of secondary forests to N deposition, which is currently increasing in this region. The objective of this study was to examine the effects of N additions on plant species richness, density, and cover, and to compare these effects between the forest sites of different land-use history. We hypothesize that N additions decrease plant diversity in both rehabilitated and disturbed forests mainly from competition exclusion among species. Because the understory layer makes an important contribution to plant diversity (Gilliam, 2007; Lu et al., 2010), we focus on the diversity of understory layer in this study. Furthermore, because reforested tropical ecosystems play an important role as a reservoir of biodiversity, identifying the effects of N deposition on plant diversity will improve our understanding on forest ecosystem management and biodiversity protection in the future.

2. Methods

2.1. Site description

This study was conducted in the Dinghushan Biosphere Reserve (DHSBR), an UNESCO/MAB site. The reserve lies in the middle part of Guangdong Province in southern China (112°10′ E, 23°10′ N) and occupies an area of approximately 1200 ha. The region has a monsoon climate and is located in a subtropical/tropical moist forest life zone (*sensu* Holdridge, 1967). The mean annual rainfall of 1927 mm is distributed seasonally, with 75% of it falling from March to August; ~6% falls from December to February (Huang and Fan, 1982). Annual mean relative humidity is 80%. Mean annual temperature is 21.0 C, with an average coldest (January) and warmest (July) temperature of 12.6 C and 28.0 C, respectively. In this area, high atmospheric N deposition has been on-going since 1990's. Nitrogen deposition was 36 kg N ha^{-1} yr^{-1} in 1990 and reached to 38 kg N ha^{-1} yr^{-1} in 1999 (Huang et al., 1994; Zhou and Yan, 2001). In 2004 and 2005, N deposition in rainfall measured was 34 and 32 kg N ha^{-1} yr^{-1}, respectively, 60% of which was in the form of NH_4^+-N (Fang et al., 2008).

We have identified two types of forest at DHSBR: a pine forest (PF, disturbed) and a mixed pine and broadleaf forest (MF, rehabilitated). The disturbed forest, at about 50–200 m asl occupies approximately 20% of the reserve, and the rehabilitated forest, at about 200 m asl occupies approximately 50% of the reserve (Mo et al., 2003). The two forest types are ~4 km from each other, and originated from clearcutting in the 1930s and subsequent planting of pine; they were badly eroded and degraded following these practices (Wang et al., 1982; Mo et al., 1995, 2003). The disturbed forest has been under continuous human disturbances, largely in the form of harvesting of understory vegetation and litter during 1930–1998, while the tree layer has remained dominated by *P. massoniana* (Brown et al., 1995; Mo et al., 1995, 2003). In contrast, harvesting in the rehabilitated forest has been minimal to absent since the establishment of the forest due to relatively in accessible to the rural population (Brown et al., 1995; Mo et al., 1995, 2003). Establishment of regional broadleaf species via natural dispersal has changed plant composition in the rehabilitated forest (Mo et al., 2003).

We established our research site in both forests in 2002. Pre-treatment sampling in June 2003 showed that the disturbed forest was dominated by *P. massoniana*, and the rehabilitated forest was co-dominated by *P. massoniana* and *Schima superba* Chardn. & Champ. (Table 1). Dominant understory species in disturbed forest are *Dicranopteris dichotoma* (Thunb.) Bernh, R*hodomyrtus tomentosa* (Ait.) Hassk, and *Alchornea trewioides* (Benth.) Muell.-Arg, whereas *D. dichotoma*, *R. tomentosa*, and *Gahnia tristis* Nees dominated the understory in the rehabilitated forest. The soils in both types of forest are oxisols with variable depths. In the rehabilitated forest, depth ranges from 30 to 60 cm (to the top of the C horizon). In the disturbed forest the depth is generally less than 40 cm (Brown et al., 1995; Mo et al., 2003).

2.2. Experimental treatments

Nitrogen addition experiments were initiated in July 2003 (Mo et al., 2006). Three N addition treatments (each in three replicates) were established in both rehabilitated and disturbed forests: Control (without N added), N50 (50 kg N ha^{-1} yr^{-1}), and N100 (100 kg N ha^{-1} yr^{-1}). Nine 20-m × 10-m plots were established in each of rehabilitated and disturbed forests, with each plot surrounded by a 10-m wide buffer strip. All plots and treatments were laid out randomly. In addition, two 1-m × 1-m sub-plots were permanently established in each plot, for a total of 18 sub-plots in each forest. Monthly applications of NH_4NO_3 solution were administered by hand to the forest floor of these plots as 12 equal applications over the whole year. During each application, fertilizer was weighed, mixed with 20 L of water, and applied to the plots using a backpack sprayer below the canopy. Two passes were made across each plot to ensure an even distribution of fertilizer. The Control plots received 20 L water with no N added.

2.3. Field sampling

The understory layer, defined here as all vascular plants ≤1 m in height (similar to the herbaceous layer sensu Gilliam and Roberts, 2003; Lu et al., 2010), was monitored within the two permanent 1-m^2 sub-plots in each plot. We chose this layer and definition because (1) it is widely used in the literature, (2) this stratum is sensitive to changes in nutrient availability, and (3) most of the plant biodiversity of forests is typically found there (see Gilliam, 2007 for a review). For the sake of including all plants tallied during the pre-treatment sampling, any individual plants within this stratum that eventually grew above 1 m in height were included in further sampling and analysis. We performed a field survey of each sub-plot in July every year, and recorded all the vascular plants in the understory layer. Percent cover of individual plant species was estimated visually by using a square grid method. Field tests were carried out to check the between-observer assessment levels, and to calibrate when necessary (Lu et al., 2010).

To explore possible mechanisms for changes of understory in diversity, we carried out one collection of soil samples in September 2005 for determining soil pH, inorganic N (NH_4^+-N and NO_3^--N) and extractable soil Ca and Al in both disturbed and rehabilitated forests (Lu et al., 2009). In August 2008, we had another collection of soil and measured soil pH. Soil inorganic N was extracted with 2 mol L^{-1} KCl. Exchangeable Ca was extracted with 1 mol L^{-1} NH_4OAc and exchangeable Al was extracted with 1 mol L^{-1} KCl (10:1, solution: soil). In addition, we also used a Plant Canopy Analyzer LAI-2000 (LI-COR, Inc.) to estimate tree canopy closure during the study period (Machado and Reich, 1999; Li et al., 2008).

Table 1
Indices of the tree layer in a disturbed and a rehabilitated tropical forest at Dinghushan Biosphere Reserve in southern China. The survey was conducted in 2003, and the area was 1800 m^2 for each forest. All trees were recorded when the DBH (diameter at breast height) ≥2.5 cm.

Species	Density (Stem/ha)	Mean height (m)	Mean DBH (cm)	Breast area (m^2/ha)	Relative breast Area (%)
Disturbed forest					
Pinus massoniana	354.2	7.4	17.7	10.5	95.3
Other plants	225.0	3.9	3.9	0.5	4.7
Total	579.2			11.0	100.0
Rehabilitated forest					
Schima superba	1158.3	4.6	6.4	5.4	54.3
Pinus massoniana	95.8	8.0	21.9	4.1	40.4
Other plants	150.0	3.9	4.4	0.5	5.4
Total	1404.2			10.0	100.0

2.4. Data analysis

All plants in the understory layers were classified into two functional groups on the basis of intrinsic morphological differences: (1) woody plants (height $\leq$ 1 m), and (2) herbaceous plants including ferns. Because there were no significant changes of plant density and richness under N treatments during the study period, we mainly reported the effects of N additions on understory cover.

To simultaneously test for overall N-treatment effects over time for the study period from 2003 to 2008, we subjected data to two way repeated-measures analysis of variance (ANOVA) on the following variables: richness (mean number of species m^{-2} in each replication), density (mean number of plants m^{-2} in each replication), cover (mean percent cover of plants in each replication) and canopy closure (mean percent canopy closure of tree layers in each replication). Repeated measure ANOVA was also used to test the effects of N treatments on the above variables between two forest types, by defining N treatments and years as "Within-Subject Factors", and forest types as "Between-Subject Factors". One-way ANOVA with Tukey's honestly significantly different (Tukey's HSD) test was performed to test the differences of the above variables among treatments for the same year and among years for the same treatment. We conducted the planned contrast analysis to test differences between Control plots and N-treatment plots.

In addition, we used a general linear model to analyze the relationships between canopy closure and understory cover in all plots during the study period. For soil chemical properties (soil pH, inorganic N, and extractable K, Ca, Mg and Al), one-way ANOVA with Tukey's HSD was also performed to test the differences among treatments. Standard *t*-test was performed to examine these measurements in the control plots between the rehabilitated forest and disturbed forest. All analyses were conducted using SPSS 14.0 for Windows® (SPSS, Chicago, IL, USA). Statistical significant differences were set with *P* values <0.05 unless otherwise stated.

3. Results

Sampling within our sub-plots captured a total of 25 and 24 plant species in the disturbed and rehabilitated forests, respectively (see Appendix S1). In the two forests, herbaceous plants dominated the understory layer in all plots, based on relative density and cover. Among herbaceous species, the fern, *D. dichotoma*, was dominant in both forests, especially in the rehabilitated forest, where its cover reached about 90% of total cover. Prior to treatments in 2003, the understory vegetation of the experimental site was homogeneous and there were no significant differences between the Control and N-treatment plots for any measured variables (richness, density, and cover).

3.1. Effects of N additions on plant diversity

In the disturbed forest, there were no significant differences between N-treatment levels for the same year or years for the same treatment for measured plant parameters (total richness, density, cover, and cover of herbaceous and woody plants) (Fig. 1a–f). However, repeated measure ANOVA showed that there were significantly increasing trends of total cover, cover of woody plant and herbaceous plants, and cover of *D. dichotoma* with years. For the dominant plant of *D. dichotoma*, the interaction effects of N treatment and time were also significant ($F = 3.00$, $P = 0.018$).

In the rehabilitated forest, N additions had no significant effects on total richness and density (Fig. 1g, h), or on density and richness of woody plant and herbaceous plants (Figure not shown). However, plant cover decreased significantly in response to N treatments (Fig. 1i–l). Total cover and cover of herbaceous plants showed minor variations between years in the Control plots, but decreased slightly with time in the N50 plots. This decreasing trend was more pronounced in the N100 plots, where these parameters decreased significantly with time, especially since 2005. Total cover and the cover of herbaceous plants decreased by approximately 69% from 2003 to 2008 following five years of N additions in the N100 plots.

N-meditated decreases were found for the dominant understory species, *D. dichotoma*, whose cover decreased by approximately 92.4% from 2003 to 2008 (Fig. 1l). For woody plants, the cover showed a minor increasing trend with years in the Control and N50 plots, but decreased slightly in the N100 plots since 2007. Although none of the N treatments significantly altered plant cover in 2003–2004, N100 treatment significantly decreased total cover, and the cover of herbaceous plants, relative to the Controls beginning in 2005. Repeated measure ANOVA showed significant ($P < 0.05$) effects of N treatment, time and their interactions on plant cover, but there were no significant ($P > 0.05$) effects on plant richness and density in the rehabilitated forest.

While comparing the effects of N treatments between two forest types, repeated measure ANOVA showed that there were significant differences for N-treatment effects between forest types only for total cover, and the cover of herbaceous plants and dominant plant *D. dichotoma* ($F = 10.33$, $P = 0.006$; $F = 7.25$, $P = 0.016$; $F = 3.56$, $P = 0.079$, respectively). There were also significant interactive effects of N treatments, forest types and years for the cover of herbaceous plants and dominant plant *D. dichotoma* ($F = 2.28$, $P = 0.032$; $F = 2.67$, $P = 0.013$, respectively).

3.2. Effects of N additions on canopy closure

In the disturbed forest, canopy closure increased with years in all plots. However, N additions had no significant effects on the canopy closure (Fig. 2a). In the rehabilitated forest, N additions significantly increased the canopy closure by 2007, especially under N100 treatment (Fig. 2b). Furthermore, the inter-annual N-treatment differences became significant in 2005, compared with the first year, in the N50 and N100 treatment plots, respectively. Repeated measure ANOVA showed that there were no significant differences for N-treatment effects between forest types ($F = 2.77$, $P = 0.12$).

When compared across all plots and treatments, there was no significant relationship between canopy closure and understory cover in the disturbed forest ($R^2 = 0.019$, $P = 0.76$) (Fig. 3a). However, canopy closure was significantly and negatively correlated with understory cover in the rehabilitated forest ($R^2 = 0.17$, $P = 0.002$) (Fig. 3b).

3.3. Effects of N additions on soil chemistry parameters

In the control plots, there were no significant differences for soil chemistry parameters between the disturbed and rehabilitated forests, except for soil exchangeable Ca (Table 2). Total inorganic N (the sum of NH_4^+-N and NO_3^--N) increased significantly ($P < 0.05$) in response to N additions, and NO_3^--N accounted for 55% and 37% of total inorganic N for all treatments in the disturbed and rehabilitated forests, respectively, after two years of N additions (Table 2). However, there were no significant negative effects of N additions on base cations (K, Ca, Mg) in both forests, and exchangeable Mg and Ca increased significantly in N100 treatments in the disturbed forest and rehabilitated forest, respectively (Table 2). Furthermore, N additions did not significantly affect extractable Al in both forests. For soil pH, there were no significant differences among N treatments in mean soil pH in both disturbed and rehabilitated forests over the course of the study (data not shown).

4. Discussion

Contrary to our expectations, experimental additions of N, regardless of amount, did not decrease species richness of the understory of either disturbed or rehabilitated forests. This is in sharp contrast to previous results for an adjacent undisturbed forest, wherein we found that understory richness of a >400 yr old forest was at least 4-fold higher in control plots than in high N plots following the same number of years of treatment as the present study (Lu et al., 2010). This contrast may have arisen in part from the initially lower understory richness in the second-growth

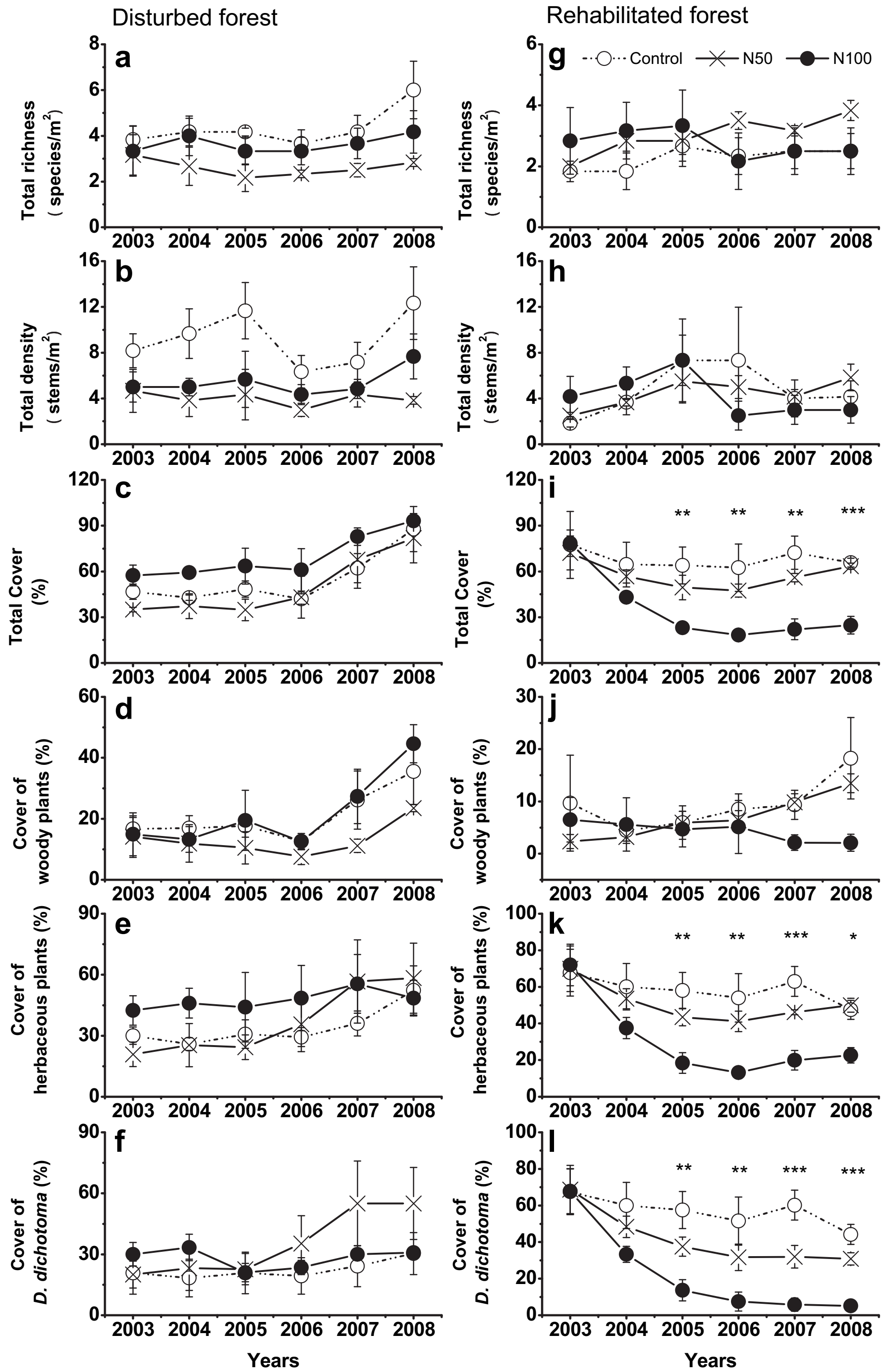

Fig. 1. Temporal patterns of responses of plant diversity (±S.E) to N-treatment levels in understory layers for years 2003–2008 in the disturbed forest (a–f) and rehabilitated forest (g–l). (a, g), total richness; (b, h) total density (measured as number of plants); (c, i), total cover; (d, j), cover of woody plants; (e, k), cover of herbaceous plants; (f, l) cover of *Dicranopteris dichotoma*. Asterisks *, ** and *** indicate significant difference between Control plots and N-treatment plots at $P < 0.1$, $P < 0.05$ and $P < 0.01$ levels by using planned contrast analysis, respectively. Notes: open circles, Control; furcations, N50 treatment; solid circles, N100 treatment.

forests. Indeed, species richness for the understory of the old-growth forest was twice higher than that of the secondary forests prior to N treatments in 2003 (Lu et al., 2010). Furthermore, comparisons between understory communities of old-growth versus secondary forests harvested circa 1930's suggest that the understory of these forests may take >80 yr to recover, consistent with findings in temperate hardwood forests of North America (Wyatt and Silman, 2010). Indeed, because these forests have undergone nearly a century of secondary succession following initial harvesting, understory communities may be more responsive to variation in canopy-mediated changes in the light environment. This was hypothesized by Gilliam and Turrill (1993) and has been supported by additional studies in the literature (e.g., Moola and Vasseur, 2008; Bartels and Chen, 2010).

We further suggest that the different responses of understory diversity to N additions between the rehabilitated and disturbed

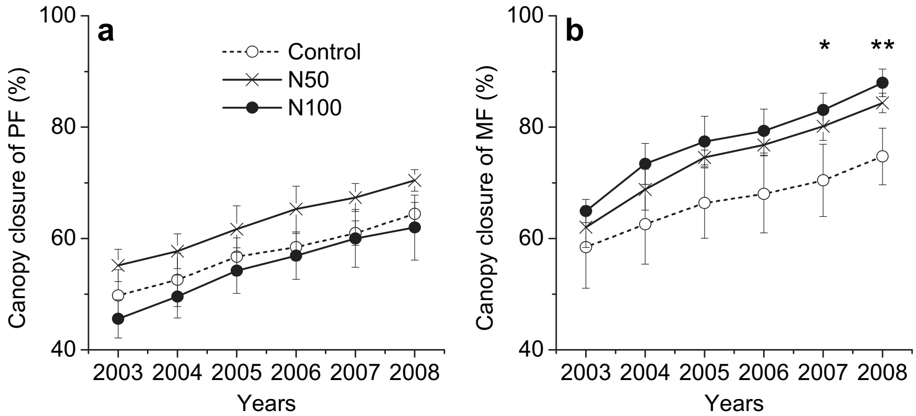

Fig. 2. Effects of N additions on canopy closure in the disturbed forest (PF, a) and rehabilitated forest (MF, b) for years 2003–2008. Error bars indicate ±1 S.E. Notes: open circles, Control; furcations, N50 treatment; solid circles, N100 treatment. Asterisks * and ** indicate significant difference between Control plots and N-treatment plots at $P < 0.1$ and $P < 0.05$ levels by using planned contrast analysis, respectively.

forests may be related to different land-use history, particularly as such differences are related to canopy-mediated changes in light availability to the understory community. The rehabilitated forest originated as a pine plantation in 1930's that was naturally invaded and colonized by regional broadleaf species from animal and wind dispersal. However, it has yet to recover fully to its pre-disturbance condition over the past several decades (Mo et al., 2003, 2004, 2006), creating and maintaining N-limiting conditions (Mo et al., 2006), i.e., N demand by recovering woody vegetation continues to exceed supply of available N. Under N limitation, increasing N commonly decreases biodiversity by enhancing competitive abilities of fast-growing nitrophilous plants with high maximum growth rates, at the expense of slower growing neighbors of smaller stature (Aerts and Chapin, 2000; Gilliam, 2006; Hautier et al., 2009; Bobbink et al., 2010). Because there were no significant increases in understory plant growth in the rehabilitated forest, it is unlikely that competitive exclusion among understory plants contributed to the observed decline of understory cover. On the other hand, intense shading by overstory trees may have caused such declines, as there was a significant increase in canopy closure in N-treatment plots (Fig. 2b) and a significant negative relationship between canopy closure and understory cover at this site (Fig. 3b). In addition, it has been reported that *D. dichotoma*, which dominated understory layer in this study, is a highly shade-intolerant species and commonly declines in growth with decreases in light intensity (Takeuchi, 1988).

Unlike the rehabilitated forest, the disturbed forest has been constantly subjected to anthropogenic pressure (primarily harvesting of understory vegetation and litter) since time of planting in 1930's and continuing until the late 1990's (Brown et al., 1995; Mo et al., 1995, 2003, 2006). This type of land use may mitigate effects of N additions, resulting in no significant changes in understory community, and do so for two reasons. First, understory/litter harvesting greatly erodes and degrades the disturbed forest (Wang et al., 1982; Mo et al., 1995, 2003), leading to a decrease in soil N stock and maintaining N limitation (Mo et al., 2006), hindering successful development of the understory community (Mo et al., 1995, 2003). Second, it may simultaneously minimize competitive interaction among understory plants and maintain overstory dominance by *P. massoniana* by eliminating seedlings of potential dominant/co-dominant species. The slow growth and low nutrient turnover rates of *P. massoniana* even at high N inputs (Mo et al., 1995) may result in no significant changes of canopy closure under N treatments during the study period (Fig. 2a). Thus, light

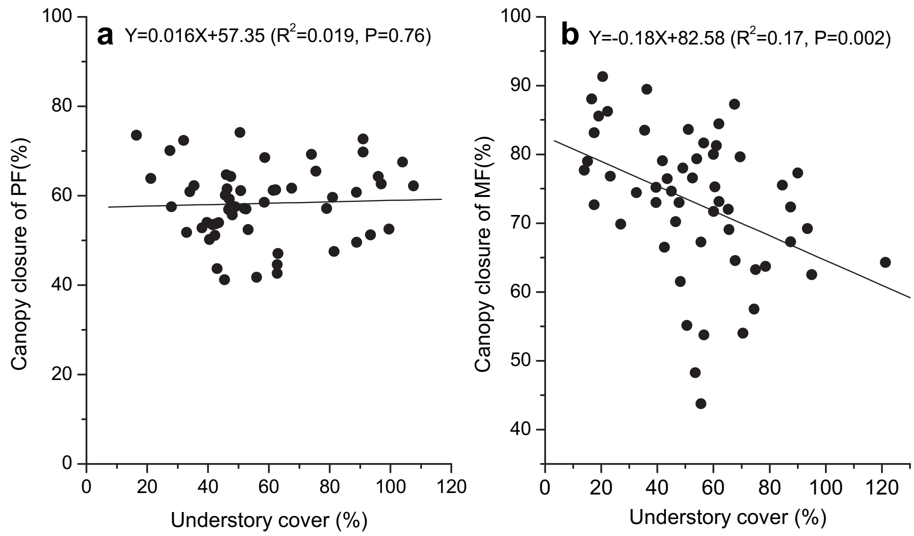

Fig. 3. Relationships between canopy closure and understory cover in all plots and treatments for years 2003–2008 in the disturbed forest (PF, a) and the rehabilitated forest (MF, B). Each point represents a replication for one treatment level ($n = 54$).

Table 2
Effects of different N-treatment levels on soil total inorganic N (the sum of NH_4^+-N and NO_3^--N), and soil exchangeable K, Ca, Mg and Al in the disturbed forest and rehabilitated forest. The different lowercase letters indicate significant differences at $P < 0.05$ level among N-treatment levels (Tukey's HSD test). Values are means with S.E. in parentheses. Asterisk * means significant differences at $P < 0.05$ level between control plots of two forests by using standard *t*-test.

Forest types	Treatment	Total inorganic N	K	Ca*	Mg	Al
Disturbed forest	Control	5.26(0.18)a	61.22(3.95)a	384.67(21.29)a	18.83(0.33)a	321.17(14.58)a
	N50	7.16(0.70)ab	61.72(4.65)a	449.44(7.83)b	21.49(0.80)ab	335.72(17.41)a
	N100	8.19(0.55)b	57.56(2.12)a	438.55(9.14)ab	23.05(1.14)b	303.11(28.38)a
Rehabilitated forest	Control	5.02(0.21)a	50.83(5.36)a	251.22(9.07)a	18.00(1.60)a	337.83(12.68)a
	N50	7.63(0.50)b	58.83(1.96)a	284.22(27.47)ab	19.94(1.71)a	370.67(7.91)a
	N100	6.91(0.74)ab	53.89(9.05)a	384.06(32.86)b	19.55(1.28)a	368.83(11.11)a

limitation induced by N additions may not happen to the understory layer in the disturbed forest. Habitat management practices (e.g., from harvesting/mowing) decreasing ecosystem N stocks and mitigating the effects of N additions have also been found in grassland or heathland ecosystems (Willems, 2001; Power et al., 2001; Barker et al., 2004). Barker et al. (2004) suggested that intensive mowing treatments in heathlands could result in a shift in balance between competing species by decreasing the response of the originally dominated species to N deposition.

Lack of response of the understory community to N additions may also arise from P limitation, which is typical of many tropical forest ecosystems (Vitousek, 1984). Using the extensive chronosequence of the Hawai'i archipelago (from 4.1 million-year substrates on Kaua'i to 300-year substrates on Hawai'i), Vitousek (2004) has clearly demonstrated the loss of available P through pedogenesis of tropical soils. Excess N deposition has also been shown to initiate the onset of P limitation (Gress et al., 2007). Rocks underlying our study sites are sandstones and shales belonging to the Devonian period (Wu et al., 1982). Soils are old and classified as lateritic red earth (oxisol) (He et al., 1982). In addition, our study sites have been experienced high atmospheric N deposition of >30 kg N ha^{-1} yr^{-1} since 1990 (Huang et al., 1994; Zhou and Yan, 2001; Fang et al., 2008), which greatly exceeds most areas considered at risk for N saturation (Gilliam, 2006; Bobbink et al., 2010). Therefore, P limitation is likely for our forests, and indeed has been suggested by the further study (Lu et al., unpublished data).

In our previous study in the adjacent undisturbed mature forest, we concluded that N additions significantly decreased understory plant diversity, and that the mechanism for change appeared to be excess N-mediated soil acidification (e.g., significant decreases in pH and extractable Ca, and increases in extractable Al), rather than competition-based mechanisms (e.g., for light) (Lu et al., 2010). Although soil acidification process can contribute to decline of diversity (Gilliam, 2006; Bobbink et al., 2010; Lu et al., 2010), there was no evidence that it was important in the present study. In both disturbed and rehabilitated forests, we found no negative effects of N additions on leaching of base cations (K, Ca, and Mg) and release of soil Al (Table 2). At the same time, soil pH also showed no significant changes under N additions over the course of the study (data not shown).

Although forest management practices can create legacy effects on soil N dynamics (Fraterrigo et al., 2005), such a response is not always found (Gilliam et al., 2004). Similarly, the lack of response of the understory community to N additions was also found in an Appalachian hardwood forest after six years of N additions (Gilliam et al., 2006). However, Gilliam et al. (2006) suggested that the lack of observed response was the consequence of high ambient levels of N deposition and N saturation status, and thus N treatment represented a comparatively small addition of an essential nutrient that is no longer growth-limiting. This mechanism is in contrast to that of our study. Although our study area has been receiving long-term high N deposition since 1990's (Huang et al., 1994; Zhou and Yan, 2001; Fang et al., 2008), N saturation has not developed because of previous land-use history (Mo et al., 2006).

In conclusion, our results in the rehabilitated forest are consistent with canopy-mediated decreases in availability of light as a major mechanism of understory change in response to N addition in N-limited ecosystems. Understory cover in the rehabilitated forest was very susceptible to N additions, which may indirectly affect understory dynamics by increasing canopy closure of tree layers. Surprisingly, we found no diversity losses in the disturbed forest under the same amount of N additions. This implies that diversity losses induced by N deposition may be affected by the degree of human disturbance, and that land-use practices may mitigate the effects of N additions on understory plant communities.

Acknowledgements

This study was founded by National Natural Science Foundation of China (Nos. 30970521, 30900202), and National Key Basic Research 973 Program (2010CB833502), and Natural Science Foundation of Guangdong Province, China (Grant 83510650050 00001), and Doctoral Fund of South China Botanical Garden, Chinese Academy of Sciences (200806). We wish to thank Dejun Li, Xiaoming Fang, Youchang Zhang, Dingsheng Mo, Yujia Huang, Lei Liu, Hui Wang and Jurong Long for their skilful assistance in field work, Qingfa Yu for his assistance in laboratory work, and Dr. Sandra Brown, Dr. Per Gundersen, Yongfei Bai, Weixing Zhu, Deqiang Zhang, Zhi'an Li and two anonymous reviewers for invaluable suggestions in this paper.

Appendix S1. A complete species list of the understory layer during the whole studied period from year 2003 to 2008, including Latin name, family, and functional group to which plants belong in the disturbed forest and rehabilitated forest, respectively.

Latin name	Family name	Founctional group
Disturbed forest		
Dicranopteris dichotoma (Thunb.) Bernh	Gleicheniaceae	Herbaceous plant
Schizoloma heteropyllum (Dry.) J. Sm.	Lindsaeaceae	Herbaceous plant
Blechnum orientale Linn.	Blechnaceae	Herbaceous plant
Lygodium japonicum (Thunb.) Sw	Lygodiaceae	Herbaceous plant
Lophatherum gracile Brongn.	Gramineae	Herbaceous plant
Miscanthus sinensis Anderss.	Gramineae	Herbaceous plant
Arthraxon hispidus (Trin.) Makino	Gramineae	Herbaceous plant
Dianella ensifolia (L.) DC.	Liliaceae	Herbaceous plant
Adenosma glutinosum (Linn.) Druce	Scrophulariaceae	Herbaceous plant
Rhodomyrtus tomentosa (Ait.) Hassk	Myrtaceae	Woody plant
Melastoma candidum D. Don	Melastomataceae	Woody plant
Alchornea trewioides (Benth.) Muell.-Arg	Euphorbiaceae	Woody plant
Mallotus paniculatus (Lam.) Muell. Arg.	Euphorbiaceae	Woody plant
Glochidion eriocarpum Champ. ex Benth.	Euphorbiaceae	Woody plant

(*continued on next page*)

Appendix S1 (*continued*)

Latin name	Family name	Founctional group
Ficus variolosa Lindl. ex Benth.	Moraceae	Woody plant
Litsea rotundifolia var. oblongifolia	Lauraceae	Woody plant
Litsea cubeba (Lour.) Pers.	Lauraceae	Woody plant
Clerodendron fortunatum L.	Verbenaceae	Woody plant
Ixora chinensis Lam.	Rubiaceae	Woody plant
Psychotria serpens L.	Rubiaceae	Woody plant
Mussaenda pubescens Ait.f.	Rubiaceae	Woody plant
Gardenia jasminoides Ellis	Rubiaceae	Woody plant
Rhus succedanea L.	Anacardiaceae	Woody plant
Evodia lepta (Spreng.) Merr.	Rutaceae	Woody plant
Embelia laeta (Linn.) Mez	Myrsinaceae	Woody plant
Rehabilitated forest		
Dicranopteris dichotoma (Thunb.) Bernh	Gleicheniaceae	Herbaceous plant
Gahnia tristis Nees	Cyperaceae	Herbaceous plant
Dianella ensifolia (L.) DC.	Liliceae	Herbaceous plant
Schizoloma heteropyllum (Dry.) J. Sm.	Lindsaeaceae	Herbaceous plant
Miscanthus sinensis Anderss.	Gramineae	Herbaceous plant
Lophatherum gracile Brongn.	Gramineae	Herbaceous plant
Rhodomyrtus tomentosa (Ait.) Hassk	Myrtaceae	Woody plant
Syzygium rehderianum Merr. & Perry	Myrtaceae	Woody plant
Acmena acuminatissima (Blume) Merr. et Perry	Myrtaceae	Woody plant
Smilax china L.	Smilacaceae	Woody plant
Fissistigma glaucescens (Hance)Merr	Annonaceae	Woody plant
Ficus variolosa Lindl. ex Benth.	Moraceae	Woody plant
Clerodendron fortunatum L.	Verbenaceae	Woody plant
Schima superba Chardn. & Champ	Theaceae	Woody plant
Alchornea trewioides (Benth.) Muell.-Arg	Euphorbiaceae	Woody plant
Crypwcorya concinna Hance	Lauraceae	Woody plant
Litsea cubeba (Lour.) Pers.	Lauraceae	Woody plant
Artabotrys chinensis Lour.	Annonaceae	Woody plant
Psychotria rubra (Lour.) Poir.	Rubiaceae	Woody plant
Ixora chinensis Lam.	Rubiaceae	Woody plant
Psychotria serpens L.	Rubiaceae	Woody plant
Mussaenda pubescens Ait.f.	Rubiaceae	Woody plant
Ilex pubescens Hook. et Arn.	Aquifoliaceae	Woody plant
Evodia lepta (Spreng.) Merr.	Rutaceae	Woody plant

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