

空气 NH_3 增高和不同氮源供应下大叶相思叶片光合参数的变化

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摘要: 生长在空气 NH_3 增高下 45d 的 NO_3^- -N 大叶相思植株, 其光饱和光合速率较对照的植株高; 而生长在空气 NH_3 增高下的 NH_4^+ -N 和 NH_4NO_3 -N 的大叶相思, 当光强在 $700\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ 左右时 P_n 达到最大值, 较对照植株的要高。而当光强 $>700\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ 时, P_n 降低, 且较生长在对照条件下的低。表明在空气 NH_3 增高下生长的 NH_4^+ -N 和 NH_4NO_3 -N 植株, 其净光合速率 P_n 会受到强光抑制。空气 NH_3 增高并不明显改变光呼吸 (R_d) 和无光呼吸下的 CO_2 补充点 (Γ^*)。无论生长在何种氮源下的大叶相思, 其最大 RuBP 饱和羧化速率 (V_{cmax}) 和最大电子传递速率 (J_{max}) 均较生长在对照植株的高 ($P < 0.05$), 其叶氮含量亦较高 ($P < 0.05$), 其碳氮比较对照的低。在空气 NH_3 增高下, 无论何种氮源生长的大叶相思, 其 P_R 和 P_B 明显高于对照的植株, 表明大叶相思能从空气 NH_3 中摄取和同化氮, 增加氮积累和有利于 Rubisco 和电子传递组分的合成, 增高光合速率。空气 NH_3 增高可能有利于 Rubisco 和电子传递组分的合成, 在较低光强下能增高光合速率。空气 NH_3 增高可能有利于退化生态系统的生态恢复过程中的氮积累和先锋植物的早期生长。

关键词: 大叶相思; 光合变量; 空气 NH_3 增高

Variations of photosynthetic parameters in leaves of *Acacia auriculaeformis* grown in different nitrogen sources under increased atmospheric NH_3

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Abstract: Higher light-saturated photosynthetic rate was observed for the NO_3^- -N plants of *Acacia auriculaeformis* under elevated atmospheric NH_3 in comparison with that grown in control. As the irradiance intensity reached about $700\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, the maximum rate of photosynthesis occurred in leaves of NH_4^+ -N and NH_4NO_3 -N plants of *A. auriculaeformis* in the elevated NH_3 , and higher than that of the plants grown in control. When irradiance intensity was higher than $700\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, their net photosynthetic rate (P_n) decreased and even lower than that in control. It may suggest that higher light

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intensity restrict P_n of NH_4^+-N and $\text{NH}_4\text{NO}_3-\text{N}$ plants grown in the elevated NH_3 . There were no significant effects of increased NH_3 on the mitochondrial respiration rate in the light (R_d) and the CO_2 compensation point in the absence of R_d (Γ^*). The maximum RuBP-saturated rate of carboxylation (V_{cmax}) and the maximum rate of electron transfer (J_{max}) in plant of *A. auriculaeformis* supplied with different nitrogen sources and grown in increased atmospheric NH_3 were higher than those in control ($p < 0.05$), and so was the leaf N content ($p < 0.05$). Lower C/N ratio was found in plants grown in the elevated NH_3 . However, the leaf N investment in carboxylation capacity (P_R) and N investment for the capacity of electron transport (P_B) in the plants grown in the elevated NH_3 with different N sources were higher than those of the control. It shows that more nitrogen was acquired by plants from the atmosphere with elevated NH_3 and it favors the syntheses of Rubisco and composition of electron transport chain. Increased atmospheric N deposition would facilitate nitrogen accumulation and early growth of plants in the process of vegetation restoration.

Key words: *Acacia auriculaeformis*; photosynthetic parameter; increased atmospheric NH_3

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1 Introduction

With the development of agriculture and livestock farming, usage of large amount of nitrogen fertilizers and manure of domestic animal in crop fields has given rise to release of excessive ammonia into the atmosphere and increased concentration of atmospheric NH_3 . The total N deposition in Europe continent had continuously increased in the 20th century, of which 50%~80% were NH_3 deposition. In Holland and United Kingdom, the NH_3 deposition reached 40~50 and 15~20 $\text{kg} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$ respectively in the 20th century^[1]. As early as in 1972, Hutchinson *et al.*^[2] estimated that it would cause serious impact on ecosystem when the NH_3 deposition on plant canopy reached 20 $\text{kg} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$. Absorption of atmospheric NH_3 by plant leaves would disturb normal physiological metabolism and nutrient equilibrium, reduce plant competition ability against other co-growing individuals, and cause decrease in biodiversity^[3] and decline of forest^[4]. It was reported that leaves of *Pseudotsuga menziesii* had higher photosynthetic rate when the NH_3 concentration in the air was 66 $\mu\text{g m}^{-3}$ compared to those in the normal air. *Populus euramericana* also had higher leaf photosynthesis when treated with 100 $\mu\text{g m}^{-3}$ NH_3 in the air^[5]. van Hove *et al* attributed this to a possible increase in the number of photosynthesizing units, since increased atmospheric NH_3 enhanced N content in leaves. The underlying mechanism, however, had not been clear^[6]. Since plant releases H^+ when taking in $\text{NH}_3/\text{NH}_4^+$ from the air into its cells, excessive assimilation of NH_3 could not maintain a stable pH microenvironment within cell and would affect the regulation of pH. Our question is: would supply with different forms of nitrogen alter proton flux produced by N-assimilation, which in turn affect leaf photosynthetic rate? Addressing such question will help to clarify the physiological effect of increased atmospheric NH_3 on plant photosynthesis.

Acacia auriculaeformis is an evergreen tree species distributed in tropics and lower subtropics. It grows fast and has been major tree species widely used for vegetation restoration on degraded ecosystems in South China. Results of in situ experiments showed that young *A. auriculaeformis* could not grow well without addition of nitrogen fertilizer^[7]. The practice of applying manure of domestic animal and the N-deposition due to current global change are and will be two important factors affecting N-assimilation of plants from the air. It can be of importance to study the photosynthetic response of *A. auriculaeformis* to the increased atmospheric NH_3 . Research results will be expected to provide experimental evidence for how to facilitate growth of *A. auriculaeformis* at an early stage by making use of increased atmospheric NH_3 so

that we can reduce the cost for accelerating vegetation restoration in tropical and lower subtropical areas.

2 Materials and Methods

2.1 Plant materials

Young *A. auriculaeformis* plants with height of 20~25 cm were grown in plastic plots of 15 cm in diameter, one plant per plot. All plots were watered every day to keep the soil water content at the field water capacity. Nutrient solution containing 2 mmol · L⁻¹N of KNO₃, or of (NH₄)₂SO₄, or of NH₄NO₃ as different N sources was added once a week (Here the plants that were applied with the different N sources are stated as NO₃⁻-N plant, NH₄⁺-N plant and NH₄NO₃-N plant respectively). The nutrient solution also contained 0.1 mmol · L⁻¹KH₂PO₄, 1 mmol · L⁻¹CaCl₂, 1 mmol · L⁻¹K₂SO₄, 0.5 mmol · L⁻¹MgSO₄, 50 mmol · L⁻¹KCl, and micro-elements. The pH value was regulated at about 5.5. Each plot was placed into a transparent plastic cover with an inner volume of 1.7 cm³. Experimental plants received two kinds of treatments separately: ambient air and increased NH₃ in the air. Each treatment had 3 replicates. The method used to produce increased NH₃ (250 μg · m⁻³) was performed by Wellenweher & Raven^[8]. Examined plants grew for 45 days under natural light condition. The relative humidity and temperature under the cover were kept at 60%~80% and 25±3 °C respectively.

2.2 Measurement of leaf photosynthetic rate

Three to five recently matured leaves from each plot were chosen for measurement of photosynthetic rate by using Li-Cor 6200 Portable Photosynthesis System at room temperature. Electrical bulb generating cold light was applied to obtain different levels of light intensity by adjusting the electrical voltage. By switching-on and -off the CO₂ scrubber (soda lime) of the Li-Cor 6200 system, the CO₂ partial pressure in leaf chamber was regulated at the intended values^[9]. The net photosynthetic rate (P_n)-CO₂ partial pressure (P_i) responses were measured at two light levels: higher photosynthetically active radiation (PAR , 800 μmol · m⁻² · s⁻¹) and lower PAR (150 μmol · m⁻² · s⁻¹), from which the lines of initial part of the P_n - P_i curves in the lower P_i ranges (<19.8 Pa) were established. The intersection coordinates of the two lines on Y and X axes represent the mitochondrial respiration rate in the light (R_d) and the CO₂ compensation point in the absence of R_d (Γ^*)^[10,11]. At the same time, the P_n - P_i curve under higher PAR (1000 μmol · m⁻² · s⁻¹) and the P_n - PAR curve under higher CO₂ partial pressure (50 Pa) were also measured.

2.3 Other measurements

The leaves after measurement of photosynthetic rate were taken off for area determination. Some of them were dried to constant weight in an oven for the calculation of specific leaf weight (SLW). And the other detached fresh leaves were ground and extracted with 80% acetone solution. Leaf chlorophyll content (C_c) was then determined by using Cambds 25 Ultra-violet Visible Light Spectrometer with the extraction that had been centrifuged at 1000 rotation s⁻¹. The leaf C, H, and N contents were measured by using Perkin Elmer 24CHNS/O Element Analyzer.

2.4 Calculation of photosynthetic parameters

Carboxylation under higher light condition is restricted by Rubisco activity and by the CO₂ and O₂ partial pressures on carboxylating sites. The maximum photosynthetic rate (P_{nc}) when limited by Rubisco activity is defined as^[12]:

$$P_{nc} = V_c \max \frac{P_i - \Gamma^*}{P_i + K_c(1 + P_o/K_o)} - R_d \quad (1)$$

where $V_{c\max}$ 万方数据 maximum RuBP-saturated rate of carboxylation, P_i is the intercellular CO₂ partial pressure, and P_o is the O₂ partial pressure on the carbonxylating site (20.5 × 10³ Pa at 25 °C). K_c and K_o

are Michaelis constants of carboxylation/oxidation reaction (40Pa and $24.8 \times 10^3\text{Pa}$ respectively at 25°C), which should be calibrated according to Friend^[13] when the temperature changes.

In the conditions of higher CO_2 partial pressure and lower PAR , the regeneration of RuBP is limited by the rate of photosynthetic electron transfer. Photosynthetic rate increases with the PAR increment. The maximum RuBP-regeneration-limited rate of photosynthesis (P_{nj}) is defined as:

$$P_{nj} = \frac{J(P_i - \Gamma^*)}{4(P_i + 2\Gamma^*)} - R_d \quad (2)$$

where J is the potential electron transfer rate that depends on PAR . J_{\max} is the maximum rate of electron transfer.

$$\theta J^2 - (PAR_a + J_{\max})J + PAR_a \cdot J_{\max} = 0 \quad (3)$$

$$PAR_a = PAR(1 - f)/2 \quad (4)$$

where θ is curvature of the light response of J that is 0.7 according to de Pury and Farquhar^[12]. PAR_a is virtual radiation absorption of Photo System II, f is the spectral calibration factor that is 0.15 ^[10].

The leaf N partitioning coefficient among components of carboxylation, bioenergetics and light-harvesting components on thylakoid membranes were estimated based on a model proposed by Niinenmets & Tenhunen^[14]. It is supposed that P_R be the leaf N investment in carboxylation capacity (i.e. influencing $V_{c\max}$), P_B be the N investment for the capacity of electron transport (i.e. influencing J_{\max}), and P_L be the N investment in light harvesting. Their relationships are described as follows:

$$P_R = V_{c\max}/(6.25 \times V_{cr} \cdot SLW \cdot N_m) \quad (5)$$

$$P_B = J_{\max}/(8.06 \times J_{mc} \cdot SLW \cdot N_m) \quad (6)$$

where V_{cr} is the specific activity of Rubisco, namely the maximum rate of RuBP carboxylation per unit Rubisco protein, J_{mc} is the potential rate of photosynthetic electron transport per unit $cyt f$, 6.25 is the coefficient for conversion of N to protein, and 8.06 is a molar ratio constant of $1:1:1.2$ for $cyt f$: ferredoxine NADP reductase: coupling factor^[14,15]. V_{cr} is $32.5\mu\text{mol CO}_2(\text{g Rubisco})^{-1}\text{s}^{-1}$ ^[16] and J_{mc} is $156\text{mol electrons}(\text{mol } cyt f)^{-1}\text{s}^{-1}$ ^[14] at a leaf temperature of 25°C . SLW is specific leaf weight. N_m is leaf N content per unit dry mass.

The partitioning coefficient of leaf N in the chlorophyll protein compound of thylakoid is given as:

$$P_L = C_c/N_m C_B \quad (7)$$

where C_c is chlorophyll content in leaf, C_B is chlorophyll combined to protein compound of thylakoid, which is $5.79\text{mmol chl}(\text{g N})^{-1}$ ^[17,18].

3 Results

3.1 Light-response of photosynthetic rate

Figure 1 shows the light-responses of photosynthetic rate of plants with different treatments. The average of light-saturated photosynthetic rate of the plants supplied with $\text{NO}_3\text{-N}$ and grown in control condition (in ambient air) was $12.2 \pm 1.0\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ ($n=5$, $p<0.05$), lower than those supplied with $\text{NH}_4^+\text{-N}$ ($14.0 \pm 1.0\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, $n=4$, $p<0.05$) or with $\text{NH}_4\text{NO}_3\text{-N}$ ($14.3 \pm 1.5\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, $n=6$, $p<0.05$). When grown in increased atmospheric NH_3 , the $\text{NO}_3\text{-N}$ plants had higher P_n than those in control by 17% . The $\text{NH}_4^+\text{-N}$ plants under the condition of increased atmospheric NH_3 reached their highest P_n at light levels of above $700\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, and their P_n were slightly higher than those grown in control below this light level ($p<0.05$). As PAR reached as high as $900\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, their P_n decreased and was lower than those grown in control, indicating that higher light intensity restricted the P_n of NH_4^+ 万方数据 grown under higher atmospheric NH_3 . $\text{NH}_4\text{NO}_3\text{-N}$ Plants grown under higher atmospheric NH_3 showed that the P_n response was similar to the $\text{NH}_4^+\text{-N}$ plants. Their P_n was higher than

that of those in control before reaching the highest value at $700\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Continuous increment of light intensity caused decrease of P_n , lower than control plants. The results demonstrated that increased atmospheric NH_3 would raise P_n of *A. auriculaeformis* under lower light intensity ($<700\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) no matter what N source was supplied. Nevertheless, higher light intensity would decrease P_n of NH_4^+-N and $\text{NH}_4\text{NO}_3-\text{N}$ plants grown under higher atmospheric NH_3 .

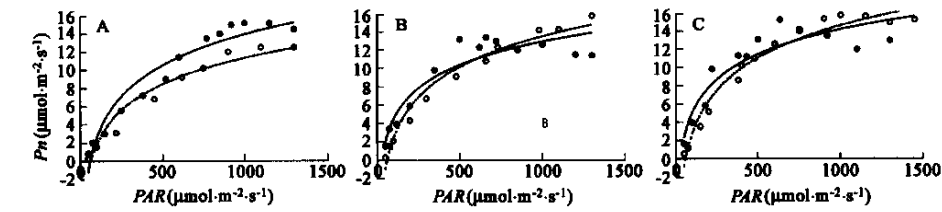


Fig. 1 Light-response curves of photosynthetic rate for leaves of *A. auriculaeformis* grown in the elevated NH_3 and in control supplied with different nitrogen sources

●—● Increased atmospheric NH_3 , ○····○ In control; A: NO_3^--N ; B: NH_4^+-N ; C: $\text{NH}_4\text{NO}_3-\text{N}$

3.2 Leaf photosynthetic parameters

Experimental results showed that increased atmospheric NH_3 did not obviously change leaf Γ^* and R_d (Table 1). The Γ^* and R_d of *A. auriculaeformis* grown both in control and in increased atmospheric NH_3 were close no matter what N source was supplied ($p>0.05$). In the normal air condition, the NO_3-N and $\text{NH}_4\text{NO}_3-\text{N}$ plants had similar maximum RuBP-saturated carboxylation (V_{cmax}), whereas the V_{cmax} of NH_4^+-N plants was higher than that of the NO_3-N and $\text{NH}_4\text{NO}_3-\text{N}$ plants. However, all *A. auriculaeformis* with different supply of N sources showed higher V_{cmax} when the atmospheric NH_3 was increased ($p<0.05$). Similarly, J_{max} of all plants supplied with different N sources grown in increased atmospheric NH_3 were higher than in control ($p<0.05$). Therefore increased atmospheric NH_3 would elevate V_{cmax} and J_{max} regardless of the form of N sources supplied.

Table 1 Changes of photosynthetic parameters in leaves of *A. auriculaeformis* grown in the elevated atmospheric NH_3 and in control supplied with different nitrogen sources

Treatment	N sources	Γ^* (Pa)	R_d ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	V_{cmax} ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	J_{max} ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)
In control	NO_3^--N	4.79 ± 0.53	2.75 ± 0.95	51.2 ± 4.6	65.1 ± 6.3
	NH_4^+-N	4.54 ± 0.12	2.03 ± 1.02	55.4 ± 3.2	65.7 ± 5.6
	$\text{NH}_4\text{NO}_3-\text{N}$	4.18 ± 0.09	2.91 ± 0.53	51.9 ± 5.1	66.6 ± 5.2
Elevated NH_3	NO_3^--N	4.75 ± 0.25	2.80 ± 0.13	$76.9 \pm 3.8^*$	$120.9 \pm 7.6^*$
	NH_4^+-N	4.56 ± 0.04	2.81 ± 0.58	$75.4 \pm 1.8^*$	$105.5 \pm 5.2^*$
	$\text{NH}_4\text{NO}_3-\text{N}$	4.44 ± 0.61	2.61 ± 0.34	$82.5 \pm 2.5^*$	$98.1 \pm 4.3^*$

Γ^* : The CO_2 compensation point in the absence of R_d ; R_d : The mitochondrial respiration rate in the light; V_{cmax} : The maximum RuBP-saturated rate of carboxylation; J_{max} : The maximum rate of electron transport; *: The statistically different level at 5% ($P<0.05$)

3.3 Leaf characters and composition

Under normal air condition, specific leaf weight (SLW) of $\text{NH}_4\text{NO}_3-\text{N}$ plant was higher than those of NO_3-N and NH_4^+-N plants. No obvious difference was found among the three N-source treatments when NH_3 in the atmosphere was higher ($p>0.05$), indicating that increased atmospheric NH_3 did not cause significant change in SLW. When grown in the air of increased NH_3 concentration, leaf N content per unit dry mass (N_m) tended to increase ($p<0.05$), and the $\text{NH}_4\text{NO}_3-\text{N}$ plants had the highest value. The leaf

chlorophyll content (C_c) did not show significant difference statistically except for NH_4NO_3 plants ($p > 0.05$), namely increased atmospheric NH_3 caused no obvious change in C_c (table 2).

Table 2 The leaf dry mass per unit area, nitrogen content and chlorophyll content in leaves of *A. auriculaeformis* grown in the elevated atmospheric NH_3 and in control supplied with different nitrogen sources

Treatment	N sources	SLW ($\text{g} \cdot \text{m}^{-2}$)	N_m ($\text{mg} \cdot \text{g}^{-1}$)	C_c ($\mu\text{mol chl} \cdot \text{g}^{-1}$)
In control	NO_3^- -N	61.5 ± 1.32	28.0 ± 5.0	15.9 ± 1.8
	NH_4^+ -N	61.21 ± 0.89	33.0 ± 1.6	16.9 ± 4.2
	NH_4NO_3 -N	64.58 ± 1.02	23.0 ± 2.0	12.7 ± 5.3
Elevated NH_3	NO_3^- -N	64.48 ± 1.53^a	$38.0 \pm 7.0^*$	16.6 ± 5.2^a
	NH_4^+ -N	63.25 ± 0.78^a	$41.0 \pm 12.0^*$	18.7 ± 1.8^a
	NH_4NO_3 -N	65.83 ± 0.83^a	$34.0 \pm 5.0^*$	$196.0 \pm 1.7^*$

SLW specific leaf weight; N_m Leaf nitrogen content per unit dry mass; C_c Chlorophyll content; * The statistically different level at 5% ($p < 0.05$); a No statistically different at 5% ($p > 0.05$)

It is seen from table 3 that the leaf C/H ratio of NH_4^+ -N and NH_4NO_3 -N plants in increased atmospheric NH_3 tended to increase ($p < 0.05$). Since there is difference in C/H ratio between ammonia acid and sugar, this change indicates that different N source supplies would lead to the change in plant structure composition. The higher C/H induced by increased NH_3 in the air promoted the formation of amino acid derived from C frame. For the C/N ratio, the decrease tendency was found in the plants of all three N-source treatments when grown in increased atmospheric NH_3 . It indicated that increased atmospheric NH_3 would elevate leaf N content and then alter the C/N ratio.

Table 3 Changes of carbon and hydrogen contents, C/H and C/N ratios in leaves of *A. auriculaeformis* grown in the elevated atmospheric NH_3 and in control supplied with different nitrogen sources

Treatment	N sources	Carbon (%)	Hydrogen (%)	C/H	C/N
In control	NO_3^- -N	45.81	3.15	14.54	16.24
	NH_4^+ -N	45.76	3.72	12.30	12.92
	NH_4NO_3 -N	43.09	3.71	11.64	18.72
Elevated NH_3	NO_3^- -N	45.13	3.06	14.75 ^a	11.78 [*]
	NH_4^+ -N	46.10	3.02	15.26 [*]	11.08 [*]
	NH_4NO_3 -N	44.30	3.28	13.51 [*]	12.84 [*]

* The statistically different level at 5% ($p < 0.05$); a No statistically different at 5% ($p > 0.05$)

3.4 Leaf N partitioning within the photosynthetic apparatus

It was found that the investments of leaf N both in Rubisco (P_R) and in bioenergetics components (P_B) were higher in the plants grown in increased atmospheric NH_3 than in control regardless of the form of N source supplied ($p < 0.05$) (Table 4). Slight decrease of investments of leaf N into light-harvesting components (P_L) when grown in the increased atmospheric NH_3 was observed except for NO_3^- -N plants, but the difference was not statistically significant ($p > 0.05$). The results showed that excessive N acquired and assimilated from the increased atmospheric NH_3 would favor the syntheses of Rubisco and electron transfer components, but did not obviously alter the leaf N investment into light-harvesting components.

4 Discussion

The usage of NH_3 in the air by *A. auriculaeformis*, however, has not been intensively studied before. Plants can absorb NH_3 in the air and, at the same time, release NH_3 produced through catabolism into atmosphere. The absorption of NH_3 by plant depends on NH_3 concentration in the atmosphere and the NH_3 -use compensation point of plant. If the former exceeds the latter, NH_3 enters into intercellular space through stomata, dissolves in moisture, and is finally assimilated. Our experimental results showed that increased NH_3 could raise net photosynthetic rate of leaves. However, plants supplied with

Table 4 The partitioning coefficients of leaf nitrogen in main photosynthetic functional components in leaves of *A. auriculaeformis* grown in the elevated atmospheric NH₃ and in control supplied with different nitrogen sources

Coefficient	N sources					
	NO ₃ ⁻ -N		NH ₄ ⁺ -N		NH ₄ NO ₃ -N	
	In control	Increased NH ₃	In control	Increased NH ₃	In control	Increased NH ₃
P_R	0.191±0.012	0.218±0.028 *	0.194±0.018	0.214±0.075 *	0.177±0.009	0.207±0.031 *
P_B	0.030±0.006	0.038±0.011 *	0.026±0.010	0.034±0.005 *	0.026±0.002	0.038±0.009 *
P_L	0.098±0.017	0.075±0.012 *	0.086±0.006	0.079±0.010 ^a	0.292±0.013	0.207±0.005 ^a

P_R The partitioning coefficient for nitrogen in Rubisco; P_B The partitioning coefficient for leaf nitrogen in bioenergetics; P_L The partitioning coefficient for leaf nitrogen in thylakoid light-harvesting components; * The statistically different level at 5% ($p<0.05$); a No statistically different at 5% ($p>0.05$)

different N sources differ in their photosynthetic response to increased NH₃ in the air. The fact that *A. auriculaeformis* supplied with NH₄⁺-N and NH₄NO₃-N and grown in increased atmospheric NH₃ displayed higher P_n than those grown in control under lower light intensity indicates that plant acquires and assimilates additional N by absorbing NH₃ from the air. And excessive leaf N facilitates N investment into Rubisco that promotes the synthesis of Rubisco and the leaf photosynthetic rate. von Hove *et al.* proved that P_n and biomass of *Pseudotsuga manziesii* grown under increased atmospheric NH₃ were elevated^[19]. Nevertheless, our experimental results showed that NH₄⁺-N and NH₄NO₃-N plants grown in increased atmospheric NH₃ had lower leaf photosynthetic rates when light intensity was higher. This could be due to the pH change induced by increased NH₃ that alter acid-alkali balance within cell. Under the condition of higher light intensity, the accumulation of NH₄⁺ and enhanced pH value would lead to intoxication to photosynthetic apparatus as pointed out by Yin *et al.*^[20] which causes decline of photosynthetic rate. The mechanism of this phenomenon needs further research. The reduction of NO₃⁻ absorbed by plant roots is undertaken mainly in the leaves, which is an energy-consuming process. Kaiser and Huber reported^[21] that 20% of activated electrons produced through light conversion in photosynthetic apparatus were used by NO₃⁻-reduction when C/N was 10. Therefore NO₃⁻-N plants grown in control condition displayed lower photosynthetic rate than NH₄-N and NH₄NO₃-N plants. Obvious increase of leaf photosynthetic rate in NO₃⁻-N plants was observed when grown in atmosphere with enriched NH₃ than in the control. Although this study did not provide direct evidence proving if the increased atmospheric NH₃ reduced the NO₃⁻-N absorption, and then decreased the energy consumption by NO₃⁻-reduction or not, it did increase both the photosynthetic rate and leaf N content ($p<0.05$). These results suggest that the N use from the atmospheric NH₃ by plant closely related to the supplied N sources of plant growth.

The enhancement of leaf N content and reduction of C/N ratio of *A. auriculaeformis* treated with different N sources and grown in increased atmospheric NH₃ showed that plants could take in and assimilate the atmospheric NH₃ no matter what N sources were supplied. Similar experimental results had been observed in wheat and maize^[20]. The atmospheric NH₃ use efficiencies by *A. auriculaeformis* supplied with NH₄NO₃-N and NO₃⁻-N were higher than those of the plants supplied with NH₄⁺-N, which could be explained by their significant increase of leaf N content.

The calculated V_{cmax} and J_{max} of *A. auriculaeformis* grown in increased atmospheric NH₃ were higher than in the control regardless of N source supplies. V_{cmax} and J_{max} closely relate to photosynthetic rate, since the photosynthetic rate depends on light use efficiency, on maximum RuBP-saturated carboxylation, on maximum electron transfer rate, and on the other parameters. V_{cmax} is also correlated positively with Rubisco content and its activity^[22]. Even though the measurement of Rubisco activity was not made, A.

auriculaeformis grown in increased atmospheric NH_3 showed higher V_{cmax} than that in control, indicating that the former had higher Rubisco activity in leaf. The increase of J_{max} also showed that the plant grown in increased atmospheric NH_3 had higher potential photosynthetic electron transfer rate in leaf. Since no significant changes in leaf chlorophyll content and leaf N investment in light-harvesting compounds were observed in the leaves of *A. auriculaeformis* grown in increased atmospheric NH_3 , it implies that the photosynthetic rate was elevated mainly by increasing Rubisco content and by increasing investment of leaf N into electron transfer components that could speed up the turnover of light system. Therefore, with any one of the three kinds of N sources used in this study, the increased atmospheric NH_3 increased photosynthetic rate of *A. auriculaeformis*, and the NO_3^- -N effect on P_n was especially strong.

Owing to high temperature and plentiful precipitation, nitrogen nutrient is seriously impoverished in the soil of degraded ecosystem in South China. Our study results provide useful implication that increased atmospheric NH_3 would be beneficial to some early-successional tree species of re-vegetation that have similar biological characters with *A. auriculaeformis*. It would promote photosynthetic rate of those plants that can assimilate N by in-taking atmospheric NH_3 , facilitate their growth, and then accelerate the process of vegetation restoration. Acquiring N nutrient by way of increased atmospheric NH_3 would be a low cost and fast way for N accumulation in soil and for acceleration of vegetation restoration. From these conclusions it may imply that increased atmospheric N deposition would, in some extent, be conducive to the effort for ecological restoration in the continuously increased degraded lands in South China.

References:

- [1] Bobbink R, Heil G W, Raesen M B A G. Atmospheric deposition and canopy exchange processes in the heath land ecosystems. *Environmental Pollution*, 1992, **75**: 29~37.
- [2] Hutchinson G L, Millington R J, Peters D B. Atmospheric ammonia: absorption by plant leaves. *Science*, 1972, **175**: 771~772.
- [3] Van der Eerden L J, Dueck T A, Berdowski J J M, *et al.* Influence of NH_3 and $(\text{NH}_4)_2\text{SO}_4$ on heathland vegetation. *Acta Botanica Neerlandica*, 1991, **40**: 281~296.
- [4] van Hove L W A, Van Kooten O, Van Wijk K J, *et al.* Physiological effects of long term exposure to low concentration of SO_2 and NH_3 on poplar leaves. *Physiologia Plantarum*, 1991, **82**: 32~40.
- [5] van Hove L W A, Van Kooten O, Adema E H, *et al.* Physiological effects of long-term exposure to low and moderate concentrations of atmosphere NH_3 on poplar leaves. *Plant Cell and Environment*, 1989, **12**: 899~908.
- [6] Pearson J and Stewart G R. The deposition of atmospheric ammonia and its effects on plants. *New Phytologist*, 1993, **125**: 283~305.
- [7] Li Z A, Yu Z Y, Wen H, *et al.* The relationship between the soil fertility and artificial vegetation recovery. In: Yu Z Y and Peng S L eds. *Ecological Studies on Vegetation Rehabilitation of Tropical and Subtropical Degraded Ecosystems*. Guangzhou: Guangdong Science & Technology Press, 1996. 155~170.
- [8] Wellenweber B and Raven J A. Nitrogen acquisition from atmospheric NH_3 by *Lolium perenne*: Utilization of NH_3 and implications for acid-base balance. *Botanica Acta*, 1993, **106**: 42~51.
- [9] Zhao P, Sun G C, Zeng X P, *et al.* A comparative study on chlorophyll fluorescence and diurnal course of leaf gas exchange of two ecotypes of banyan. *Chinese Journal of Applied Ecology*, 2000, **11**(3): 327~32.
- [10] Brook S A and Farquhar G D. Effect of temperature on the CO_2/O_2 specificity of Ribulose 1,5 bisphosphate carboxylase/oxygenase and the rate of respiration in light. Estimates from gas exchange measurement on spinach. *Planta*, 1985, **165**: 397~406.
- [11] Sun G C, Zhao P, Peng S L, *et al.* Response of photosynthesis to water stress in four saplings from subtropical forests under increased atmospheric CO_2 concentration. *Acta Ecologica Sinica*, 2001, **21**(5): 739~746.
- [12] de Pury D G G and Farquhar B D. Simple scaling of photosynthesis from leaves to canopies without the error of

- big-leaf modal. *Plant Cell and Environment*, 1997, **20**: 537~557.
- [13] Friend A D. An integrated model of leaf photosynthesis transpiration and conductance. *Ecologia Modeling*, 1995, **77**: 233~255.
- [14] Niinemets V, Tenhunen J D. A model separating leaf structure and physiological effects on carbon gain along light gradients for the shade-tolerant species *Acer saccharum*. *Plant Cell and Environment*, 1997, **20**: 845~866.
- [15] Frak E, Le Roux S L, Millard P, *et al.* Changes in total leaf nitrogen and partitioning of leaf nitrogen drive photosynthetic acclimation to light in fully developed walnut leaves. *Plant, Cell and Environment*, 2001, **24**: 1279~1288.
- [16] Jordan D B and Orgen W L. The CO_2/O_2 specificity of rubulose 1, 5-biphosphate carboxylase/oxygenase, dependence on ribulose bisphosphate concentration, pH and temperature. *Planta*, 1984, **161**: 308~308.
- [17] Kellomaki S and Wang K Y. Effects of elevated O_2 and CO_2 concentration on photosynthesis and stomatal conductance in Scots pine. *Plant Cell and Environment*, 1997, **20**: 995~1006.
- [18] Sun G C, Zhao P, Zeng X P, *et al.* Influence of UV-B radiation on photosynthesis and nitrogen utilization of *Musa paradisiaca* grown in different nitrogen sources. *Acta Phytoecologica Sinica*, 2001, **25**(3): 317~324.
- [19] van Hove L W A, Bossen M E, Mensink M G J, *et al.* Physiological effects of a long term exposure to low concentration of NH_3 , NO_2 and SO_2 on Douglas fir (*Pseudotsuga menziesii*). *Physiologia Plantarum*, 1992, **86**: 559~563.
- [20] Yin Z H and Raven J A. A comparison of the impacts of various nitrogen sources on acid-base balance in C_3 *Triticum aestivum* L. and C_4 *Zea may* L. plants. *Journal of Experimental Botany*, 1997, **48**: 315~324.
- [21] Kaiser W and Huber S C. Posttranslation regulation of nitrate reduction in higher plants. *Plant Physiology*, 1994, **106**: 817~821.
- [22] Farquhar G D and von Caemmerer S. Modeling of photosynthetic response to environmental conditio. In: Lang O L eds. *Encyclopedia of Plant Physiology*, Vol. 12B. Heidelberg: Springer-verlag, 1982. 549~587.

参考文献:

- [7] 李志安, 余作岳, 翁轰, 等. 热带亚热带人工植被恢复与土壤肥力发育之关系. 见: 余作岳, 彭少麟 主编. 热带亚热带退化生态系统植被恢复生态学研究. 广州: 广东科技出版社, 1996. 155~171.
- [9] 赵平, 孙谷畴, 曾小平, 等. 两种生态型榕树的叶绿素含量、荧光特性和叶片气体交换日变化的比较研究. 应用生态学报, 2000, **11**(3): 327~332.
- [11] 孙谷畴, 赵平, 彭少麟, 等. 在高 CO_2 浓度下四种亚热带幼树光合作用对水分胁迫的响应. 生态学报, 2001, **21**(5): 739~746.
- [18] 孙谷畴, 赵平, 曾小平, 等. UV-B 辐射对香蕉光合作用和不同氮源利用的影响. 植物生态学报, 2001, **25**(3): 317~324.