Effects of different nitrogen forms on photosynthetic rate and the chlorophyll fluorescence induction kinetics of flue-cured tobacco

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Abstract

Net photosynthetic rate ($P_N$) of tobacco plants grown with NH$_4$-N as the only N source was the lowest all the times, while $P_N$ grown only with NO$_3$-N was the greatest until 22$^{nd}$ day, and $P_N$ grown with both NO$_3$-N and NH$_4$-N (1 : 1) was the greatest. Maximal photochemical efficiency of photosystem 2 (PS2), $F_v/F_m$, and actual quantum yield of PS2 under actinic irradiation ($\tilde{\gamma}_{PS2}$) in plants grown with only NH$_4$-N were greatest at early stage and then decreased and were smaller than those of other treatments. Photochemical quenching coefficient ($q_P$) and non-photochemical quenching coefficient ($q_NP$) in the NH$_4$-N plants were the greatest at all times. Hence excessive NH$_4$-N can decrease not only photochemical efficiency but also the efficiency of utilization of photon energy absorbed by pigments for photosynthesis. Therefore, excessive NH$_4$-N is a hindrance to photosynthesis of flue-cured tobacco. On the other hand, tobacco cultured with an appropriate mixture of NO$_3$-N with NH$_4$-N can sufficiently utilize photon energy and increase the efficiency of energy transformation.

Additional key words: actual quantum yield of PS2; *Nicotiana*; photochemical and non-photochemical quenching; photosystem 2.

Photosynthesis is a basic physiological process in crop production. In order to increase output, diversified cultivation measures are adopted to improve photosynthetic capability of crops (Dong et al. 1991). Nitrogen is the main constituent of proteins, chlorophyll (Chl), and enzymes involved in photosynthesis. Therefore, nitrogen affects photosynthesis of crops. The nitrogen absorbed by plants mostly includes NO$_3$-N and NH$_4^+$-N, and their uptake, deposition, and assimilation in crops are different. There have been many studies on the effects of N forms on photosynthesis, growth, yield, and quality of tobacco, but the relationship of nitrogen forms to energy conversion and distribution in photosynthesis has rarely been researched (Han 1996, Fong and Peng 1998, Yang et al. 1999). In order to provide a theoretical basis for the cultivation techniques of good quality and high yield tobacco, we studied the effects of N forms on Chl fluorescence and photosynthesis.

Tobacco seedlings (cv. K326) having 8 leaves were cultured in the nutrient solution [g m$^{-3}$] N 40, P 20, K 80, Ca 80, Mg 10, Fe 1, Zn 0.1, Mn 0.1, B 0.05, Cu 0.01, Mo 0.01 that was aerated every 24 h and exchanged every 7 d. Three treatments were included: (T1) NO$_3$-N : NH$_4$-N = 1 : 0; (T2) NO$_3$-N : NH$_4$-N = 0 : 1; (T3) NO$_3$-N : NH$_4$-N = 1 : 1. Net photosynthetic rate ($P_N$) was measured with a portable photosynthesis system (LI-6400, Li-COR, USA) and Chl fluorescence was determined with a FMS2 fluorescence monitor (Hansatech, UK) between 09:30 and 10:30 after 16, 18, 20, 22, and 24 d. Seedlings were dark-adapted for 15 min before measurements. Four tobacco seedlings were measured in every treatment, and every tobacco seedling was measured three times. The room temperature was 18–22 °C. The measured fluorescence parameters were $F_0$ (original fluorescence), $F_v$ (variable fluorescence), $F_m$ (maximal fluorescence) = $F_v$ + $F_0$, $F_s$ (steady fluorescence), $F_0'$ (original fluorescence after light adaptation), and $F_m'$ (maximal fluorescence after light adaptation) = $F_0' + F_v'$. $\tilde{\gamma}_{PS2}$, $q_P$, and $q_NP$ were calculated as $\tilde{\gamma}_{PS2} = (F_m' – F_s)/F_m'$, $q_P = (F_m' – F_s)/(F_m' – F_0')$, $q_NP = (F_m - F_m')/F_m'$.

$F_v/F_m$ is directly related with the activity of photosynthetic electron transport (Genty et al. 1989). $F_v/F_m$ in T2

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Abbreviations: Chl – chlorophyll; $F_v/F_m$ – maximal photochemical efficiency of PS2 while all PS2 reaction centres are open; $P_N$ – net photosynthetic rate; PS – photosystem; $q_NP$ – non-photochemical quenching coefficient; $q_P$ – photochemical quenching coefficient; $\Phi_{PS2}$ – actual quantum yield of PS2 under actinic irradiation.

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was the greatest at 16 d (Fig. 1A). After 18 d, Fv/Fm in T2 kept on decreasing, but in other treatments it increased. Fv/Fm in T3 was the greatest and in T2 the smallest at 24 d. Thus Fv/Fm of tobacco could be increased by growing with both NO3-N and NH4-N. NH4-N can enhance Fv/Fm in a short period, but as the growth of tobacco continues, Fv/Fm is reduced by the excessive NH4-N.

ΦPS2 reflects the ratio of energy used for transporting photosynthetic electrons to photon energy absorbed by leaves. High ΦPS2 indicates a high efficiency of photon energy transformation and more energy accumulated for the dark reaction (Schreiber et al. 1986). Both Fv/Fm and ΦPS2 in T2 were the greatest at 16 d (Fig. 1A,B). Fv/Fm in T1 was the smallest, but its ΦPS2 was greater than ΦPS2 in T3. That shows that NO3-N can control sufficient use of latent photochemical ability. After 18 d, ΦPS2 in T2 decreased slowly, but in T1 and T3 it increased slowly. ΦPS2 in T3 was the greatest at 24 d, and thus tobacco grown with the appropriate mixture of NO3-N with NH4-N can sufficiently utilize photon energy absorbed by leaves, and increase the efficiency of energy transformation to provide enough reducing power for photosynthetic carbon assimilation.

qp is a measure of the oxidation condition of the original electron receiver QA in PS2, and represents the fraction of open PS2 reaction centres, so it can reflect the ratio of energy used by photochemical reactions to the energy absorbed by antenna pigments in PS2, and is related to carbon assimilation (Gilmore and Yamamoto 1991). High qp is advantageous to the separation of electric charge in the reaction centre, and the ability to transport electrons and the quantum yield of PS2 are enhanced. qp in T2 was the greatest in the three treatments (Fig. 1C). After 18 d, qp in T2 decreased slowly, and qp in T1 and T3 slowly increased. Thus NH4-N can enhance the activity of electron transport in PS2 during short term. As the growth of tobacco continues, the activity of transporting electrons in T2 descends gradually, and that in T1 and T3 ascends slowly.

The qNP is often used to estimate the ability of plants to safely dissipate excessive excitation energy (Härtel and Lokstein 1995). In other words, it can represent the

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**Fig. 1.** The influence of different nitrogen forms (T1, T2, T3 – see the text) on Fv/Fm (A), actual quantum yield of photosystem 2, ΦPS2 (B), fluorescence quenchings qP (C) and qNP (D), and net photosynthetic rate, PN (E).
energy dissipated as heat energy which can not be utilized to transport photosynthetic electrons. qNP in T2 was the greatest at all times (Fig. 1D), which indicated that NH4-N can promote the thermal dissipation, so that tobacco does not utilize efficiently the photon energy absorbed by antenna pigment in PS2 for photosynthesis. The qNP in T3 was the smallest, which indicated that the appropriate mixture of NO3-N with NH4-N can effectively reduce the thermal dissipation and utilize energy absorbed by antenna pigment in PS2 for photosynthesis.

PN was consistently the smallest when plants were grown only with NH4-N (Fig. 1E). PN in plants grown only with NO3-N was greatest from 18 to 22 d after being transplanted, and when grown with both N forms it was greatest from 22 to 24 d after being transplanted. Thus this fertilization was advantageous for photosynthesis.

The different N forms have different influence on physiological and biochemical processes, and also have some influence on the metabolism of carbon and nitrogen. The different N forms affect the content and function of PS1 (photosystem 1) and PS2, and consequently influence the conversion of photochemical energy (Dong et al. 2002). Fv/Fm and ΦPS2 in the treatment with only NH4-N were greater at the early growth stage, and then all decreased showing a rapid promotion of the activity and photochemical reaction of PS2. The assimilation of N is an important process using the reducing power of the light reaction. NH4-N absorbed by plant can be directly used, but absorbed NO3-N cannot be used until it is deoxidized to NH4-N, and the process consumes energy and reducing power (Zhang et al. 1995). Therefore, NH4-N can be utilized rapidly at the early stage, which is in favour of chloroplast synthesis and can promote photochemical efficiency. As the growth of tobacco continues, the excessive NH4-N can be accumulated in plants so as to damage the membrane configuration and uncouple photophosphorylation with non-photophosphorylation. Thereby, the fixation of CO2 is reduced and photochemical efficiency decreases (Zhang et al. 1995). An appropriate amount of NO3-N can improve photochemical efficiency of PS2.

The leaves of tobacco cultured with only NH4-N were dark green, but their PN was the smallest at all times. There are two reasons for this. The first is that the excessive NH4-N can damage photosynthesis organs and decrease photochemical efficiency, the other is that the excessive NH4-N can markedly increase the ability of chloroplasts to dissipate the excessive energy. So they can not efficiently utilize the photon energy absorbed by pigments for photosynthesis. NH4-N partly replacing NO3-N decreases the consumption of energy and reducing power, while NO3-N partly replacing NH4-N relieves metabolic disorder induced by the excessive NH4-N and makes the physiological metabolism in tobacco balanceable.

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