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Dependence of Wheat and Rice Respiration on Tissue Nitrogen and the Corresponding Net Carbon Fixation Efficiency Under Different Rates of Nitrogen Application

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ABSTRACT

To quantitatively address the role of tissue N in crop respiration under various agricultural practices, and to consequently evaluate the impact of synthetic fertilizer N application on biomass production and respiration, and hence net carbon fixation efficiency ($E_{\rm ncf}$), pot and field experiments were carried out for an annual rotation of a rice-wheat cropping system from 2001 to 2003. The treatments of the pot experiments included fertilizer N application, sowing date and planting density. Different rates of N application were tested in the field experiments. Static opaque chambers were used for sampling the gas. The respiration as CO_2 emission was detected by a gas chromatograph. A successive biomass clipping method was employed to determine the crop autotrophic respiration coefficient ($R_{\rm a}$). Results from the pot experiments revealed a linear relationship between $R_{\rm a}$ and tissue N content as $R_{\rm a} = 4.74{\rm N} - 1.45$ ($R^2 = 0.85$, $P < 0.001$). Measurements and calculations from the field experiments indicated that fertilizer N application promoted not only biomass production but also increased the respiration of crops. A further investigation showed that the increase of carbon loss in terms of respiration owing to fertilizer N application exceeded that of net carbon gain in terms of aboveground biomass when fertilizer N was applied over a certain rate. Consequently, the $E_{\rm ncf}$ declined as the N application rate increased.

Key words: crop, nitrogen application, net carbon fixation efficiency, tissue N, respiration

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1. Introduction

Net primary production is in general determined by the difference between gross primary production and plant autotrophic respiration. Plant respiration accounts for a large fraction of the carbon cycle in terrestrial ecosystems and may be of comparable importance to photosynthesis as a determinant of net primary production (Amthor, 1989; Ryan et al., 1997). As a significant contributor to the regional carbon budgets, the agro-ecosystem plays an important role in the terrestrial ecosystem carbon cycle (Henrik et al., 2003). In comparison with the natural ecosystems of forest and grassland, the agro-ecosystem is much more complex due to human activities, particularly the application of synthetic N fertilizer, which is considered as an effective practice to promote crop production, and it also augments C input to the soil, and hence, it often increases the soil organic C (Izaurralde et al., 2000).

It has been well recognized that the addition of N fertilizer promotes crop tissue N, and the tissue N changes as the crop grows (Lawlor, 2002). Numerous studies have demonstrated that plant photosynthetic capacity correlates strongly with leaf N concentration (e.g., Field and Mooney, 1986; Reich et al., 1998b; Peterson et al., 1999) and a linear relationship exists between plant respiration and tissue N for forest

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(e.g., Ryan, 1991, 1995; Amthor, 2000). However, the regulation of crop respiration by tissue N is still far from being understood. Though previous studies have indicated that the augmentative effect of fertilization on crop productivity will decrease as the fertilizer application exceeds a certain rate (Raun and Johnson, 1999; Kumar and Yadav, 2001), all these results have come from the evaluation of fertilizer application on photosynthesis from a physiological point of view (van Keulen and Seligman, 1987) or on production benefits from an economic point of view (van Noordwijk and Scholten, 1994). Moreover, the influence of N application on crop respiration and a synthetic assessment on crop carbon sequestration with different rates of fertilizer N application is not very clear.

The objective of this paper is to quantitatively address the role of tissue N in crop respiration. We pay special attention to the effect of various agricultural practices on crop tissue N concentration and consequently on the respiration. A secondary objective is to synthetically evaluate the impact of fertilizer N application on biomass production and respiration and thus net carbon fixation efficiency under different rates of N application.

2. Materials and methods

2.1 *Description of the experiments*

Outdoor pot experiments and field experiments were conducted from 2001 to 2003 at Nanjing Agricultural University and the Jiangsu Academy of Agricultural Sciences, China, respectively. Annual rotation of rice-wheat is a local prevailing cropping system. Soil of the experiment was classified as hydromorphic, consisting of 4% sand, 45% silt and 51% clay with an initial pH of 6.7. Total organic C and N were 13.1 and 1.1 g kg^{-1}, respectively. Rice variety No. 9516 and winter wheat variety Yangmai No. 158 were planted in this study.

To address the role of tissue N in crop respiration, the treatments of different rates of N application, different planting dates and densities were performed in the pot experiments (Table 1). Three replicates were set up for each treatment. The traditional cultivation in Table 1 was in agreement with the local agricultural practice, and nitrogen fertilization in the form of urea was applied. No additional organic matter was incorporated into the soil during these experiments. Pots made of pottery clay which were 22 cm high and with an inside diameter of 20 cm were used at Nanjing Agricultural University. The top edge of the pots has a groove to hold water to seal the rim of the gas-collecting chamber. The bottom of the pot has a hole with a 2 cm diameter to percolate the rainfall in the wheat-growing season, and the hole was sealed to keep water in the rice-growing season. Four kilograms of air-dried soil was placed in each pot before crop sowing, yielding an approximate 15 cm depth of soil. To reduce the potential unevenness of temperature distribution among pots, about 4/5 of the height of each pot was buried in the soil. During the 2002–03 wheat-growing season, open-bottom pots with an inside diameter of 11 cm were buried in the field of the Jiangsu Academy of Agricultural Sciences for different planting density experiments.

To synthetically evaluate the impact of fertilizer N application on biomass production and respiration, different rates of fertilizer N were applied in the field experiment during the rice-growing season in 2002 and the wheat-growing season in 2002–03 at the Jiangsu Academy of Agricultural Sciences. Urea was used as the synthetic N fertilizer at the rates of 150 and 300 kg N hm^{-2} for the rice-growing season (N150 and N300) and 100, 200 and 300 kg N hm^{-2} for the wheat-growing season (N100, N200 and N300). The plots without synthetic fertilizer N application were designed as the control (N0). In agreement with the local practice, urea was broadcasted on the field; phosphorus fertilizer was identically applied as the basal fertilizer at the rate of 375 kg hm^{-2} during the rice and wheat seasons. Potassium chloride used as potassium fertilizer was applied at the rate of 150 kg hm^{-2} for the rice- and 225 kg hm^{-2} for the wheat-growing seasons. Rice was planted in a seedling bed on 20 May, transplanted on 20 June and harvested on 15 October 2002. Winter wheat was planted on 10 November 2002 and harvested on 5 June 2003.

2.2 *Gas sampling and analysis*

Carbon dioxide released from the soil-plant system was measured at the main developmental stage of crops between 0800 and 1130 LST, by taking samples of the headspace gas in an open-bottom cylindrical chamber. The chamber was 100 cm high and wrapped with a layer of sponge and aluminum foil to minimize temperature changes during the period of sampling. The chamber was equipped with a circulating fan to ensure complete gas mixing. While taking gas samples, the chamber was placed over the plant with the rim of the chamber fitted into the groove of the pot. A plastic syringe was used to take gas samples, and around 50 ml of gas were collected each time. Carbon dioxide mixing ratios were obtained by a gas chromatograph (Agilent 4890D) with a flame ionization detector (Wang and Wang, 2003). The CO_2 emission was determined from the slope of the mixing ratio change in the three samples taken over a 20-min sampling period. Air temperature inside the chamber was recorded with

Table 1. This is table caption.

Crop	Year	Site	Treatment	Developmental stage (mm/dd/yy)	Sampling date (mm/dd/yy)	Number of pots	Range of air temperature (°C)
Wheat	2001–02	Nanjing Agricultural University	Traditional cultivation	Sowing: 11/05/01; emergence: 11/17/01; turning green: 02/20/02; heading: 04/25; and maturity: 05/28	02/28; 03/14; 03/28; 04/11; 04/05 and 05/09/02	16	10.3–16.3
	2002–03	Nanjing Agricultural University	Different rates of N application: 0; 0.64; 1.28 and 1.93 g N pot^{-1}	Sowing: 11/10/02; emergence: 11/25/02; turning green: 02/15/03; heading: 04/17; and maturity: 06/05	02/28; 03/08 and 03/22/03	30	7.8–13.0
	2002–03	Jiangsu Academy of Agricultural Sciences	Different planting densities: 1; 3 and 5 pot^{-1}	Sowing: 11/10/02; emergence: 11/25/02; turning green: 02/15/03; heading: 04/17; and maturity: 06/05	03/16; 04/03 and 04/27/03	18	12.0–15.6
Rice	2002	Jiangsu Academy of Agricultural Sciences	Traditional cultivation	Sowing: 05/20; transplanting: 06/20; heading: 09/03; and maturity 10/21	08/09; 09/06 and 10/06/02	6	21.1–33.5
	2002	Nanjing Agricultural University	Different sowing dates	Sowing: 05/10; 06/01 and 06/20 Transplanting: 06/05; 06/21 and 07/11; respectively	07/25; 08/29; 09/24 and 10/13/02	34	22.8–30.2
	2003	Nanjing Agricultural University	Traditional cultivation	Sowing: 05/20; transplanting: 06/20; heading: 09/03; and maturity 10/21	07/09; 07/15; 07/17; 07/22; 07/27 and 08/03/03	18	25.5–34.8

each set of CO_2 emission measurements.

2.3 *Determination of crop respiration*

Ecosystem respiration (R_E) of the cropland was combined with the crop autotrophic respiration (R_A) and soil respiration (R_S). The R_A of the aboveground crop was determined by employing a successive biomass clipping method in situ. We first determined the R_E by measuring CO_2 emission from the soil-plant system. After this measurement, about one third of the total number of plants was clipped close to the soil surface and the respiration of the soil-plant system was again measured. The measurements were performed in turn for each one-third grouping of plants. The soil respiration, including crop root respiration, was determined in the last turn when all plants were clipped. Thus, four datasets of respiration ($R_{E3/3}$, $R_{E2/3}$, $R_{E1/3}$, R_{E0}) with the corresponding aboveground biomasses ($W_{3/3}$, $W_{2/3}$, $W_{1/3}$, W_0) were obtained for each pot. The subscript represents the remaining fraction of the total number of plants. The R_A of the aboveground plants was then determined by subtracting the soil respiration from the soil-plant respiration as $R_{A3/3} = R_{E3/3} - R_{E0}$, $R_{A2/3} = R_{E2/3} - R_{E0}$ and $R_{A1/3} = R_{E1/3} - R_{E0}$, respectively. During the 2002–2003 wheat-growing season, the measurements were performed in turn for each half-group of plants for the fertilizer N treatment, yielding three datasets of respiration ($R_{E2/2}$, $R_{E1/2}$, R_{E0}) with the corresponding aboveground biomasses ($W_{2/2}$, $W_{1/2}$, W_0). For the treatment of planting density, we clipped all plants after the measurement of soil-plant respiration and obtained two datasets of respiration ($R_{E1/1}$, R_{E0}) with the corresponding aboveground biomasses ($W_{1/1}$, W_0). A total of 122 pots were planted over the 3-year experiment (Table 1). Measurements were made at the different stages of crop growth.

In order to identify a potential enhancement of CO_2 emission induced by plant roots due to the clipping, the soil respiration was measured again in 6 and 24 hours after the aboveground plants were clipped. An ANOVA test indicated that there was no significant difference among these three measurements (data

not shown).

2.4 *Determinations of plant biomass and tissue N concentration*

Aboveground biomass as dry matter was measured every ten days for rice and every fifteen days for wheat in the field experiments. For determination of the aboveground biomass, individual plant size was assumed to be homogeneous in the same experimental plot. Five bunches of plants, about 20 stems (main culms plus tillers) for each bunch, were randomly sampled as replicated from each experimental plot. The aboveground plants harvested from both pot and field experiments were cleaned with water, then oven dried to constant weight at 70°C. The total N content of the plants was determined by the semimicro-Kjeldahl method.

3. Results

3.1 *Respiration coefficient*

According to Amthor (2000) and Gifford (2001), the respiration $R_{\rm A}$ can be generally described by plant biomass and environmental temperature as follows:

$$R_{\rm A} = R_{\rm a} \times Q_{10}^{(T-25)/10} \times W \ , \qquad (1)$$

where W is plant aboveground biomass (kg m^{-2}) and T is environmental temperature (°C). Q_{10} is the temperature coefficient of respiration with a value of 2 (Amthor, 1984). The $R_{\rm a}$ represents the autotrophic respiration coefficient, defined as the amount of CO_2 emitted per unit biomass per unit time (μmol kg^{-1} s^{-1}). Rearranging Eq. (1), the respiration at a reference temperature of 25°C ($R_{\rm A25}$) is defined as:

$$R_{\rm A25} = \frac{R_{\rm A}}{Q_{10}^{(T-25)/10}} = R_{\rm a} \times W \ . \qquad (2)$$

The dependence of $R_{\rm A25}$ on crop biomass was observed for all treatments. Figure 1 shows the linear relationship between $R_{\rm A25}$ and crop biomass W for the traditional cultivation in the 2001–02 wheat-growing season (Fig. 1a) and for different sowing dates in the 2002 rice-growing season (Fig. 1b). As shown, the slope of the linear relationship represents the respiration coefficient $R_{\rm a}$ in Eq. (2).

The $R_{\rm a}$ was found to be higher in the early growing stage than in the later stage over the 2001–02 wheat-growing season (Fig. 1a). Very similar to the results from the 2001–02 wheat-growing season, different sowing dates of the rice crop resulted in different values of $R_{\rm a}$ when the measurement was made on the same day (Fig. 1b). Higher values of $R_{\rm a}$ occurred in the early developmental stages when the tissue nitrogen concentration was also higher.

By employing the same method as in Fig. 1, we determined the $R_{\rm a}$ for each measurement and obtained a total of 122 $R_{\rm a}$ values. The lowest and the highest values are 3.58 and 31.49 μmol kg^{-1} s^{-1} for the wheat crop, and 1.04 and 29.56 μmol kg^{-1} s^{-1} for the rice crop, respectively. Clearly, the $R_{\rm a}$ is not a constant.

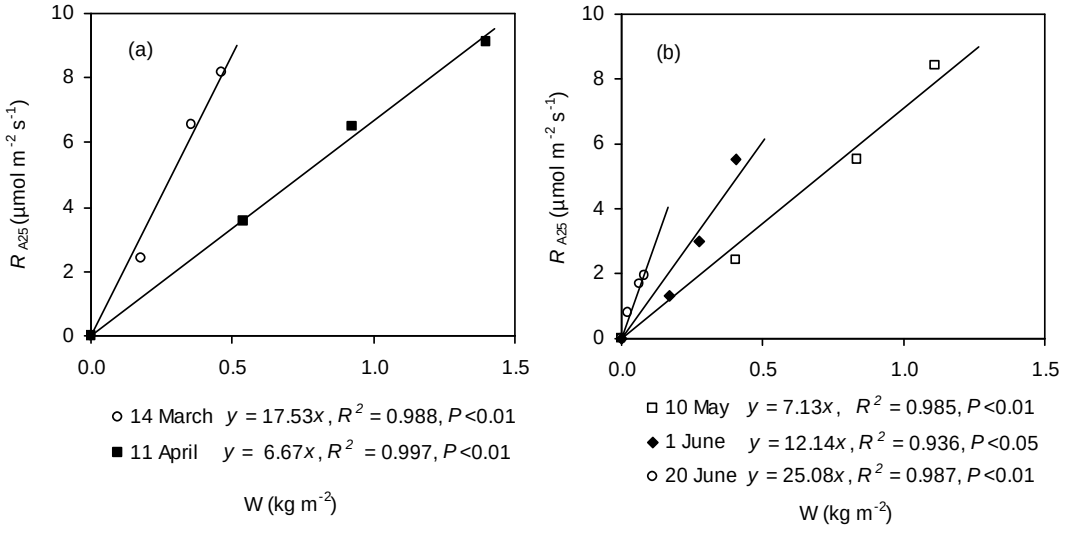

Fig. 1. Dependence of respiration on crop biomass. (a) Wheat crop with traditional cultivation; measurements were made in 2002. (b) Rice crop with different sowing dates; measurements were made on 25 July 2002.

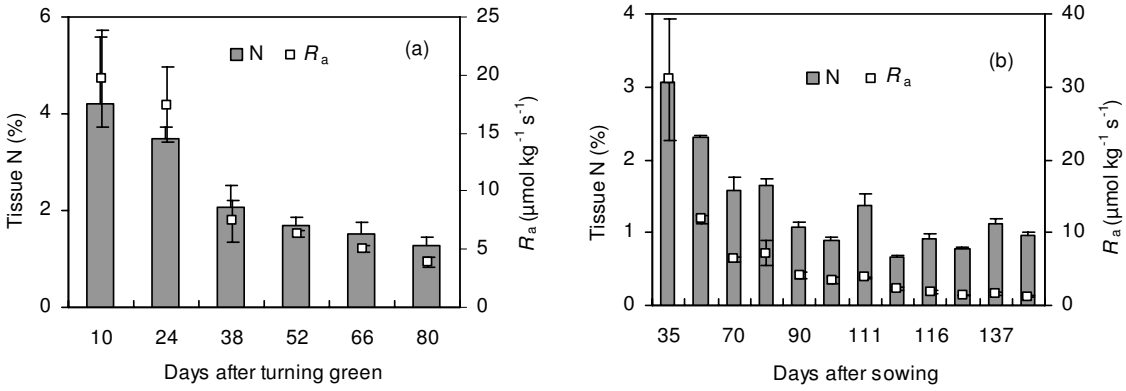

Fig. 2. Seasonal course of tissue N and respiration coefficient (R_a) respectively of (a) wheat crop with traditional cultivation and (b) rice crop with different sowing dates.

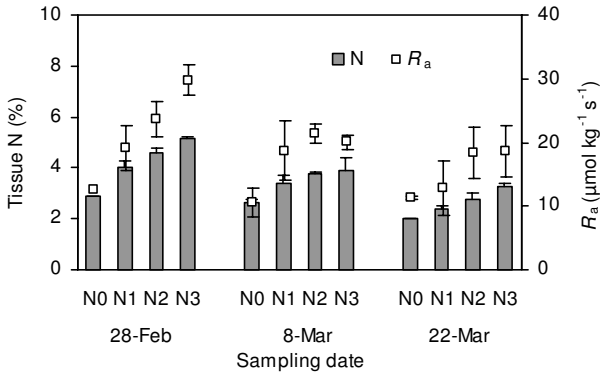

Fig. 3. Tissue N and respiration coefficient (R_a) of wheat crop with different rates of N application. N0, N1, N2 and N3 received N as urea of 0, 0.64, 1.28 and 1.93 g pot^{-1}, respectively.

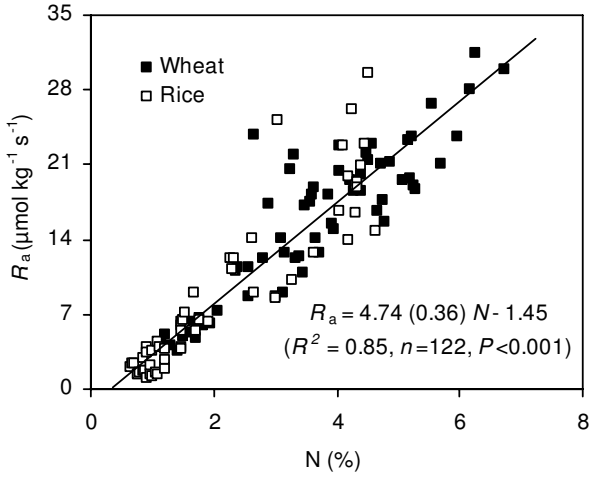

Fig. 4. Correlation of respiration coefficient (R_a) with crop tissue N content.

3.2 *Dependence of R_a on tissue N content*

The winter wheat crop generally stops growing during the period between December and mid February of the next year in this region. Thereafter, the wheat crop turns green and growth proceeds. The crop N concentration was found to be higher in the early growing stage and declined as the crop growth proceeded. Like the course of the tissue N, the R_a decreased with crop growth (Fig. 2a). Very similar to the wheat crop, synchronization in changes of tissue N and R_a occurred over the rice-growing period (Fig. 2b).

Different rates of fertilizer N application make it feasible getting the changeable values of crop tissue N and R_a. A higher rate of N application resulted in a higher content of tissue N for the wheat crop, which enhanced the crop respiration and, hence the R_a (Fig. 3).

Apparently, the R_a is associated with crop tissue N content (Fig. 2, Fig. 3). In plotting the R_a against the crop tissue N with a total of 122 datasets (64 for wheat and 58 for rice), the relationship between these two parameters becomes obvious (Fig. 4). Note that the datasets are well mixed for the crops of wheat and rice, suggesting that these two crops have similar features as far as the dependence of R_a on tissue N is quantified.

3.3 *Net carbon fixation efficiency under different rates of N application*

3.3.1 *Net carbon gain and carbon loss*

Crop biomass production is generally considered as a net carbon fixation of atmospheric CO_2. Fertilizer N application is recognized as an effective practice to promote crop biomass production, hence atmospheric CO_2 sequestration. Variations in aboveground biomass at different rates of N application are shown in Fig. 5a for rice and Fig. 5b for wheat crops. Curves

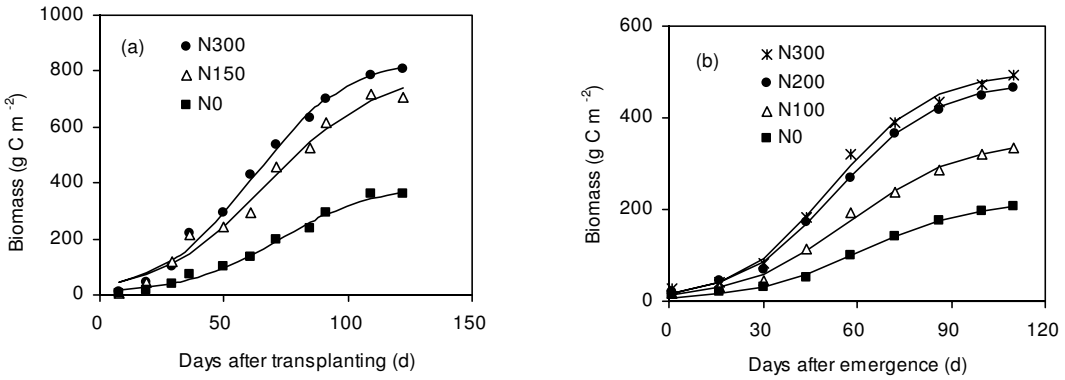

Fig. 5. Aboveground biomass accumulation for (a) rice and (b) wheat under different rates of N application. Points are datasets from the field measurements. Curves were simulated by employing a logistic growth equation.

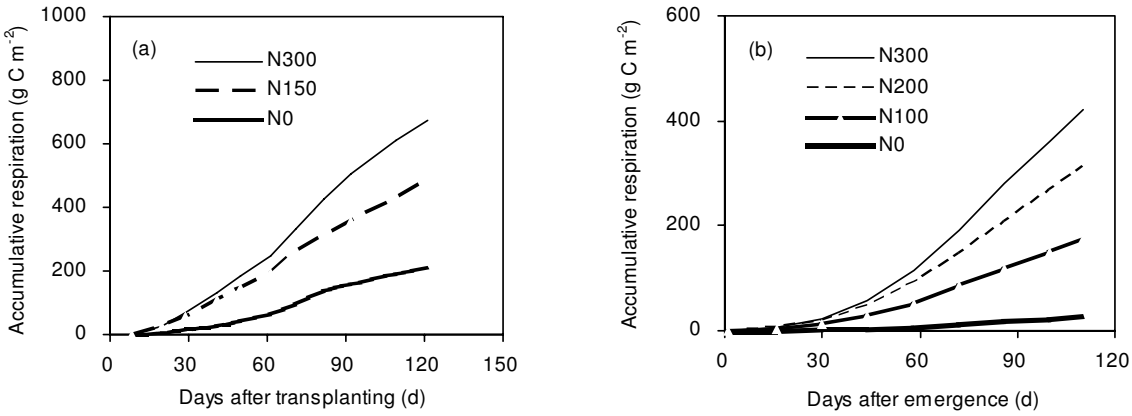

Fig. 6. Seasonal accumulation of crop respiration for (a) rice and (b) wheat at different rates of N application.

in Fig. 5 were simulated by employing a logistic growth equation as follows:

$$W = \frac{W_{\max}}{1 + B_0 \times \exp(-r \times t)} , \qquad (3)$$

where W and $W_{\max}$ represent aboveground biomass (g C m^{-2}) on a given day and at the end of a growing season, respectively. Variable t is the timescale in days after transplanting for the rice crop or after emergence for the wheat crop. Coefficients B_0 and r were statistically determined by inserting the measured aboveground biomass into the logistic Eq. (3).

Based on the result in Fig. 4 and Eq. (1), the carbon loss in terms of daily crop respiration ($R_{\mathrm{A}i}$, g C m^{-2} d^{-1}) was computed by the following equation:

$$R_{\mathrm{A}i} = 1.037 \times (4.74 N_i - 1.45) \times Q_{10}^{(T_i - 25)/10} \times W_i . \quad (4)$$

Crop tissue nitrogen concentration (N_i, %) and aboveground biomass (W_i, kg C m^{-2}) on a given day were estimated by a linear extrapolation between two adjacent observations from the field experiment and by Eq. (3), respectively. The factor 1.037 in Eq. (4) is needed to convert $R_{\mathrm{A}i}$ from μmol CO$_2$ m^{-2} s^{-1} to g C m^{-2} d^{-1}. Seasonal accumulation of crop respiration $A_{R_{\mathrm{A}i}}$ (g C m^{-2}) was obtained by the following:

$$A_{R_{\mathrm{A}i}} = \sum_i R_{\mathrm{A}i} . \qquad (5)$$

Figure 6 shows the seasonal accumulation of crop respiration for the rice and wheat crops. Apparently, the application of fertilizer N greatly enhanced not only crop biomass (Fig. 5) but also respiration (Fig. 6). Note that the magnitude of biomass increase at the end of the season is not proportional to the application rate of fertilizer N (Fig. 5). The increase of wheat aboveground biomass, for example, was 130 g C m^{-2} when the application rate of N increased from 100 kg N hm^{-2} to 200 kg N hm^{-2}, while it sharply declined to 27.7 g C m^{-2} when the N application increased from 200 kg N hm^{-2} to 300 kg N hm^{-2} (Fig. 5b). It is note-

worthy that the carbon loss via respiration (Fig. 6) is more pronounced than the net carbon gain as aboveground biomass (Fig. 5) when the rate of fertilizer N was enhanced. The increases of accumulated respiration for wheat were 136.8 g C m^{-2} and 107.4 g C m^{-2} when the application rate of N increased from 100 kg N hm^{-2} to 200 kg N hm^{-2}, and from 200 kg N hm^{-2} to 300 kg N hm^{-2}, respectively (Fig. 6b). A similar pattern was observed in the rice-growing season (Fig. 5a, Fig. 6a). The promoted respiration due to fertilizer N application and unequal increase between biomass production and respiration would initially challenge the crop net carbon fixation potential.

3.3.2 *Marginal carbon gain and loss*

Referring to the concept of marginal carbon gain or loss by previous studies (e.g., Schlesinger, 2000; Lal and Singh, 2000; Styles et al., 2002), the marginal carbon gain ($M_{\text{C-gain}}$) and marginal carbon loss ($M_{\text{C-loss}}$) are defined in Eqs. (6) and (7) to evaluate the impact of fertilizer N application on biomass production and respiration.

$$M_{C-\text{gain}} = \frac{\Delta C_{\text{BIOM}}}{\Delta N_{\text{input}}}\,, \tag{6}$$

$$M_{C-\text{loss}} = \frac{\Delta C_{\text{RESP}}}{\Delta N_{\text{input}}}\,, \tag{7}$$

where ΔN_{input} refers to the difference between two rates of fertilizer N application (kg N hm^{-2}). The ΔC_{BIOM} and ΔC_{RESP} represent the corresponding differences of aboveground biomass (kg C hm^{-2}) and of the accumulated respiration respectively at the end of the growing season. Both $M_{\text{C-gain}}$ and $M_{\text{C-loss}}$ have the same unit as kg C kg^{-1} N.

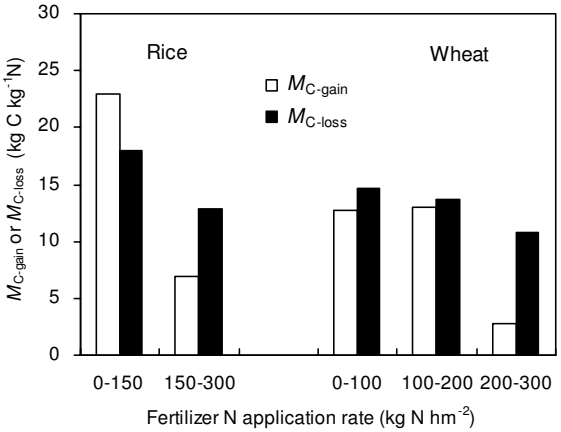

Fig. 7. Marginal carbon gain ($M_{\text{C-gain}}$) and marginal carbon loss ($M_{\text{C-loss}}$) at the same increment but different doses of N application over rice- and wheat-growing seasons.

Calculations over the rice- and the wheat-growing seasons indicated that both $M_{\text{C-gain}}$ and $M_{\text{C-loss}}$ generally decreased with increasing N application (Fig. 7). At the same application rate of 150 kg N hm^{-2} in the rice-growing season, $M_{\text{C-gain}}$ decreased by 70% with the N dose baseline of 150 kg N compared with that of 0 kg N hm^{-2}. For the wheat crop, however, the $M_{\text{C-gain}}$ did not change significantly when the N application baseline changed from 0 to 100 kg N hm^{-2} with the same interval of 100 kg N hm^{-2}, but it sharply decreased by 78% when the baseline increased from 100 to 200 kg N hm^{-2} (Fig. 7). The result of Fig. 7 suggests that a higher rate of fertilizer N application would most likely be responsible for the enhancement of crop respiration and hence reduce the nitrogen use efficiency in terms of biomass production.

Figure 7 also shows that $M_{\text{C-gain}}$ and $M_{\text{C-loss}}$ are matched in magnitude when the application of fertilizer N is at lower (0–150 kg N hm^{-2} for rice and 0–100 kg N hm^{-2} for wheat) and moderate (100–200 kg N hm^{-2} for wheat) rates, but $M_{\text{C-loss}}$ exceeds $M_{\text{C-gain}}$ significantly by 1.8 times for rice and 3.9 times for wheat when the application rate of N is increased further, i.e., from 150 to 300 kg N hm^{-2} for rice and from 200 to 300 kg N hm^{-2} for wheat. This discordance between $M_{\text{C-gain}}$ and $M_{\text{C-loss}}$ would result in the inert increase of crop biomass under higher N input. Fertilizer N application generally changes both $M_{\text{C-gain}}$ and $M_{\text{C-loss}}$ on the one hand, but $M_{\text{C-loss}}$ would exceed $M_{\text{C-gain}}$ when the N application rate is over a certain rate on the other hand. An optimal N application rate, therefore, would be expected when $M_{\text{C-loss}}$ approaches $M_{\text{C-gain}}$.

3.3.3 *Net carbon fixation efficiency*

With the assumption that crop growth functions as net carbon gain, and crop respiration is responsible for carbon loss in the gross photosynthesis, we defined the net carbon fixation efficiency (E_{ncf}) as a ratio of new biomass production to the gross photosynthesis that is presumed to be the sum of new biomass and respiration:

$$dE_{\text{ncf}} = \frac{dC_{\text{BIOM}}}{dC_{\text{BIOM}} + dC_{\text{RESP}}} \times 100\%\,, \tag{8}$$

where $d\text{C}_{\text{BIOM}}$ and $d\text{C}_{\text{RESP}}$ refer to the daily increase in aboveground biomass (g C m^{-2} d^{-1}) and daily respiration (g C m^{-2} d^{-1}), respectively. The former can be estimated from Eq. (3), and the latter is calculated by Eq. (4). The daily E_{ncf} at different rates of N application was then computed by employing Eq. (8).

The results indicate that the E_{ncf} changed seasonally for both rice (Fig. 8a) and wheat (Fig. 8b). Meanwhile, the E_{ncf} declined with increasing N application rate. The higher the N input, the lower the E_{ncf}, and

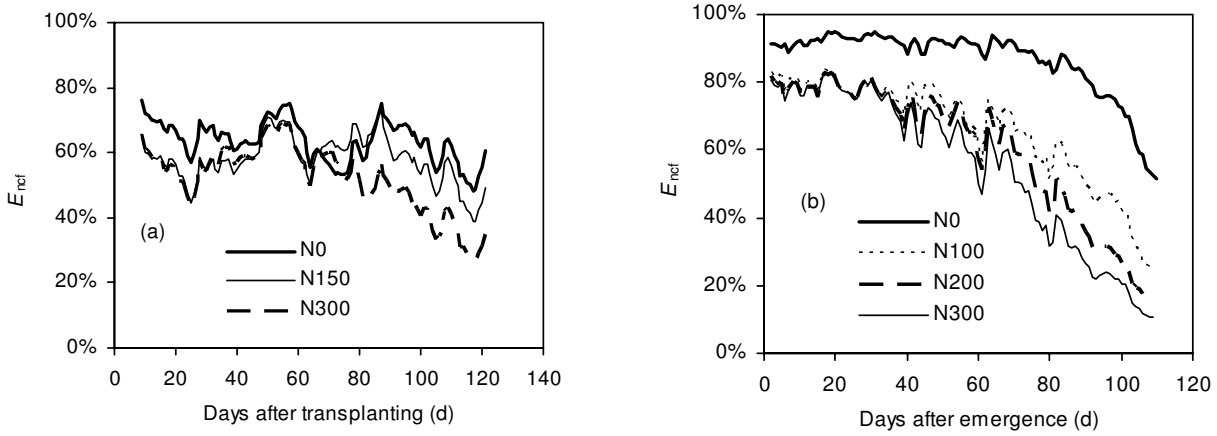

Fig. 8. Seasonal changes of net carbon fixation efficiency (E_{ncf}) of (a) rice and (b) wheat under different rates of nitrogen application.

the highest E_{ncf} appeared in the treatment of zero N application (Fig. 8). On a seasonal scale, the average E_{ncf} for rice decreased 8.9% and 18.3% for the application rates of 150 kg N hm^{-2} and 300 kg N hm^{-2}, respectively, when compared with that of zero N input. A similar trend also exists for the wheat crop. The seasonal average of E_{ncf} decreased 23.8%, 30.3% and 35.7% for the application rates of 100 kg N hm^{-2}, 200 kg N hm^{-2} and 300 kg N hm^{-2}, respectively.

4. Discussion

Penning de Vries (1975) and Ryan (1991) pointed out that typically 90% of the N in plant cells is in protein and a great part of the maintenance respiration supports protein repair and replacement. Likewise, an important fraction of dark respiration is also believed to be associated with protein turnover (Lambers et al., 1983; Ryan, 1995). Therefore, nitrogen concentration, as an easily measured surrogate for protein content, is a much better predictor of respiration than plant biomass, leaf area, or volume in some cases (Ryan, 1995; Reich et al., 1996; Amthor, 2000).

Reich et al. (1998a) studied 69 species from four functional groups (forbs, broad-leafed trees and shrubs, and needle-leafed conifers) and observed a significant relationship between leaf dark respiration and N concentration in all functional groups (pooled across sites). These species traversed the Americas in six biomes: alpine tundra/subalpine forest, cold temperate forest/grassland, cool temperate forest, desert/shrubland, subtropical forest, and tropical rain forest. Very similar results were reported for different leaf canopy positions (Mitchell et al., 1999), for trees growing in elevated CO_2 concentrations (Tjoelker et al., 1999; Tissue et al., 2002), and in conditions of irrigation and irrigation+fertilization (Ryan et al., 1996). Moreover, the respiration of tree roots was found to correlate with root N concentration (Ryan et al., 1996; Vose and Ryan, 2002).

By a literature survey of various species and tissues, Ryan (1991) reported a linear relationship between plant maintenance respiration and tissue N. These datasets were derived from leaf, bole or whole plant by using the methods of starvation, regression and mature tissue, respectively (Ryan, 1991). While not widely tested for different species and ecosystems, Ryan (1995) studied another 14 species of trees by sampling the fully expanded foliage (mature tissue method) and obtained a significant linear relationship between mass-based respiration R_{m} and N concentration as well. When correcting the R_{m} to 25°C with the same unit as the R_{a} in this study, the slope values of the relationship between respiration and N were 2.98±0.60 (R^2=0.592, n=16) and 5.22±0.67 (R^2=0.841, n=14) for Ryan's 1991 and 1995 datasets respectively. In this study, a zero-intercept linear relationship gives a slope value of 4.36±0.18 (R^2=0.842, n=122) that is comparable with the result by the mature tissue method (Ryan, 1995).

5. Conclusion

Tissue N content affects crop respiration essentially. A higher nitrogen content of crop tissue resulted in higher respiration. The application of nitrogen fertilizer promoted not only the biomass production but also the respiration of crops. The increase of carbon loss in terms of respiration owing to fertilizer N application exceeded that of net carbon gain in terms of aboveground biomass when fertilizer N was applied over a certain rate. Consequently, the net carbon fix-

ation efficiency declined with the increased N application rate.

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