

Static opaque chamber-based technique for determination of net exchange of CO₂ between terrestrial ecosystem and atmosphere

ZOU Jianwen¹, HUANG Yao^{1,2}, ZHENG Xunhua²,
WANG Yuesi² & CHEN Yuqian³

1. College of Resources and Environmental Sciences, Nanjing Agricultural University, Nanjing 210095, China;
 2. Institute of Atmospheric Physics, Beijing 100029, China;
 3. Agricultural Resource and Environment Research Center, Jiangsu Academy of Agricultural Sciences, Nanjing 210014, China
- Correspondence should be addressed to Huang Yao (e-mail: huangy@mail.iap.ac.cn)

Abstract Terrestrial carbon cycling is one of the hotspots in global change issues. In this paper, we presented the rationale for determination of net exchange of CO₂ between terrestrial and the atmosphere (NEE) and the methods for measuring several relevant components. Three key processes for determination of NEE were addressed, including the separation of shoot autotrophic respiration from total CO₂ emissions of the ecosystem, the partition of root respiration from soil CO₂ efflux, and the quantification of rhizodeposition C from NPP. With an understanding of the processes involved in the CO₂ exchange between terrestrial and the atmosphere, we estimated NEE of rice ecosystem in Nanjing based on field measurements of CO₂ emissions and several relevant biotic components as well as abiotic factors. The field measurements of CO₂ emissions were made over the rice-growing seasons in 2001 and 2002 with the static opaque chamber method. Calculations indicated that the seasonal pattern of NEE is comparable for two seasons. Either net carbon emission or fractional carbon fixation occurred during 3 weeks after rice transplanting and thereafter net carbon fixation appeared with an increasing trend as rice growing. Higher net carbon fixation occurred in the rice developmental period from elongating to heading. A decline trend in the fixation was documented after rice heading. The mean daily NEE was $-6.06 \text{ gC} \cdot \text{m}^{-2}$ in 2001 season and $-7.95 \text{ gC} \cdot \text{m}^{-2}$ in 2002 season, respectively. These values were comparable to the results obtained by Campbell et al. who made field measurements with the Bowen ratio-energy balance technique in irrigated rice, Texas USA. Moreover, the mean daily NEE in this study was also comparable to the values obtained from a Japanese rice paddy with the eddy covariance method under the similar water regime, either drainage course or waterlogged. It is concluded that NEE determined by the static opaque chamber method is compa-

table and in agreement with those measured by Bowen ratio-energy balance and eddy covariance methods.

Keywords: static opaque chamber method, terrestrial ecosystem, CO₂, NEE, comparison.

DOI: 10.1360/03wd0270

Carbon dioxide (CO₂), a key greenhouse gas, contributes greatly to global warming. The atmospheric CO₂ concentration has increased by 31% since 1750^[1]. The increase rate was $3.2 \pm 0.1 \text{ Pg a}^{-1}$ ($1 \text{ Pg} = 10^{15} \text{ g}$) in the 1990s and the current increase rate is unprecedented over the past 20000 years^[1]. The atmospheric CO₂ content is mostly dependent on the net exchange of CO₂ within carbon pools involved in the carbon cycle processes. Investigation of the processes and mechanisms of CO₂ exchange between terrestrial ecosystem and the atmosphere has been becoming one of the hotspots with respect to global change and regional sustainable development. This kind of investigation has been gaining international interest for several important programs, such as Integrated Global Carbon Observations (IGCO) initiated by IGBP, WCRP and IHDP, Global Carbon Project (GCP) in ESSP^[2], and Study on Carbon Budget in Terrestrial and Marginal Sea Ecosystems of China supported by the Knowledge Innovation Program of the Chinese Academy of Sciences^[3].

Fluxes of CO₂ from terrestrial ecosystems are often determined by eddy covariance or static chamber methods that are now adopted in Chinese Terrestrial Ecosystem Flux Observational Research Network (ChinaFLUX). Based on the micrometeorological theory, the eddy covariance technique is able to directly detect mass and energy exchange between terrestrial and the atmosphere from the change in wind speed and air density on a certain height above the canopy. This technique is characterized as quick and continuous measurement without disturbance for plant community. However, reliable measurements are usually obtained from fields with adequate flat area under appropriate vertical airflow. Moreover, equipments and facilities for this method are expensive that makes it difficult to be used in multiple sites. In contrast, the static chamber method has the advantages of higher adaptability and sensitivity, straightforward operation, and lower cost, which is therefore widely used to simultaneously measure CO₂, CH₄ and N₂O fluxes from terrestrial ecosystem in China^[4–6]. The static chamber with open bottom is covered a known area of ground that allows objective gas inside the chamber to be accumulated within a certain time interval. The emission rate is determined from changes in a mixing ratio of objective gas in samples in

Abbreviations: ESSP, Earth System Science Partnership; GCP, Global Carbon Project; IGBP, International Geosphere-Biosphere Programme; IGCO, Integrated Global Carbon Observations; IHDP-International Human Dimensions Program on Global Environmental Change; IPCC, Intergovernmental Panel on Climate Change; WCRP, World Climate Research Programme.

ARTICLES

side the chamber. It is well recognized that temperature affects not only plant photosynthesis and respiration but also evaporation, which influences directly CO₂ emission. The chamber is therefore usually made of opaque rather than transparent to control air temperature inside the chamber. On the other hand, since CO₂ emission from the static opaque chamber includes soil respiration and plant autotrophic respiration but excludes plant photosynthesis, net exchange of CO₂ between terrestrial and the atmosphere (NEE-Net Ecosystem Exchange) is difficult to be directly determined. Nevertheless, quantification of NEE with the static opaque chamber is worthwhile.

With an understanding of the process of CO₂ exchange between terrestrial and the atmosphere, we carried out a two-year field experiment to determine NEE with the static opaque chamber. NEE in this study was compared with that by Bowen ratio-energy balance technique and eddy covariance method from similar rice paddy. The objective of this paper is to address the feasibility of determination of NEE with static opaque chamber technique.

1 Rationale for NEE determination

In the absence of disturbances that remove carbon from the ecosystem (such as harvest or fire), terrestrial carbon processes can be generalized as follows. Plants acquire CO₂ by diffusion through stomata into leaves and thus photosynthesis performs to shape plant biomass. Thereafter, dead root and litter retained into the soil as organic matter, which is further converted back to atmospheric CO₂ by heterotrophic decomposition. The physical and structural interactions of carbon processes in the expanded temporal and spatial scales constitute interrelationships in terrestrial ecosystem^[7]. The amount that is “fixed” from the atmosphere, i.e. converted from CO₂ to carbohydrate during photosynthesis, is known as gross primary production (GPP). The difference between photosynthesis and plant autotrophic respiration (R_A) is referred to net primary production (NPP). Eventually, carbon fixed as NPP is returned to the atmospheric CO₂ pool through heterotrophic respiration (R_H) by decomposers (bacteria and fungi feeding on dead tissue and exudates) and herbivores. Net ecosystem exchange (NEE) is referred to how much carbon lost or gained for an ecosystem, equal to the difference between R_H and NPP. When other losses of carbon are accounted for, such as fires, harvesting/removals (eventually combusted or decomposed), the remains are called net biome production (NBP). NBP represents the carbon accumulated by the terrestrial biosphere, which is usually used to describe what the atmosphere ultimately “sees” as the net land uptake on a global scale over period of a year or longer. NEE is in general represented as

$$NEE = R_H - (GPP - R_A)$$

$$= R_H - NPP. \quad (1)$$

Similar as the measurement of CH₄ and N₂O fluxes, static chamber sealed a certain volume of air above the vegetation for allowing CO₂ inside the chamber to be accumulated. The emission rate was determined from changes in a mixing ratio of CO₂ detected by a modified gas chromatograph (GC-Agilent 4890D). The gas sample was taken from the closed chamber within a certain interval^[6]. CO₂ emission (M) by the opaque chamber method is attributed to shoot autotrophic respiration (R_{AS}) and soil respiration (R_S). The R_S includes soil heterotrophic respiration (R_H) and root autotrophic respiration (R_{AR}). The M is thus expressed as eq. (2). Combining eq. (1) with eq. (2), NEE can be estimated by eq. (3).

$$M = R_H + R_{AS} + R_{AR}, \quad (2)$$

$$NEE = R_H - NPP \\ = M - R_{AS} - R_{AR} - NPP. \quad (3)$$

Based on the description of eq. (3), the estimation of NEE from M , R_{AS} , R_{AR} and NPP becomes possible. Temporal dynamics of these components can be also used to describe the seasonal pattern of NEE.

2 Component measurement

(i) NPP. Plant biomass is referred to as the amount of above- and below-ground living plant mass. NPP is a measure of plant community accumulation, i.e. the increase of biomass per unit area within a certain period. Conventionally, NPP is calculated as a summation of the increment of biomass (ΔW), plant litter and dead tissues/organs (D_L), and rhizodeposition (D_E) such as root secretion within a certain interval as follows:

$$NPP = \Delta W + D_L + D_E. \quad (4)$$

It is regretted that rhizodeposition C was not specified in quantification of NPP for natural and agroecosystem^[8–10]. The D_E was primarily measured in some laboratory studies or derived from rhizosphere microbe growth rate^[11]. Measurement of rhizodeposition carbon *in situ* has been becoming one of the most difficulties in terrestrial carbon cycling investigation. Currently, NPP is merely derived from biomass by harvest method^[12]. Presupposition for this method is that neither vegetation nor litter from previous season is retained and no litter was decomposed before harvest. Thus, the NPP was estimated by eq. (5).

$$NPP = W_{MAX} + D_L, \quad (5)$$

where W_{MAX} is the maximum biomass at maturity from the plots where CO₂ emissions were measured. In order to obtain plant litter without disturbing the measurements of CO₂ emission, especially the emission from litter decomposition, we collected plant litter from the plots where gas sample was not taken over an entire growing season. Shoot growth in these plots were measured within a certain interval over the season. Seasonal changes in plant growth were simulated by inserting the measured data into

a logistic curve (Fig. 1(a)). By adapting parameters of the logistic curve and the W_{\max} in the plots where CO_2 fluxes were measured, seasonal changes in above-ground NPP were simulated. Seasonal dynamics of below-ground NPP was determined from the above-ground NPP and root/shoot ratio. Precondition for the NPP simulation is that plant development in two plots was fully synchronous where CO_2 fluxes were and were not measured.

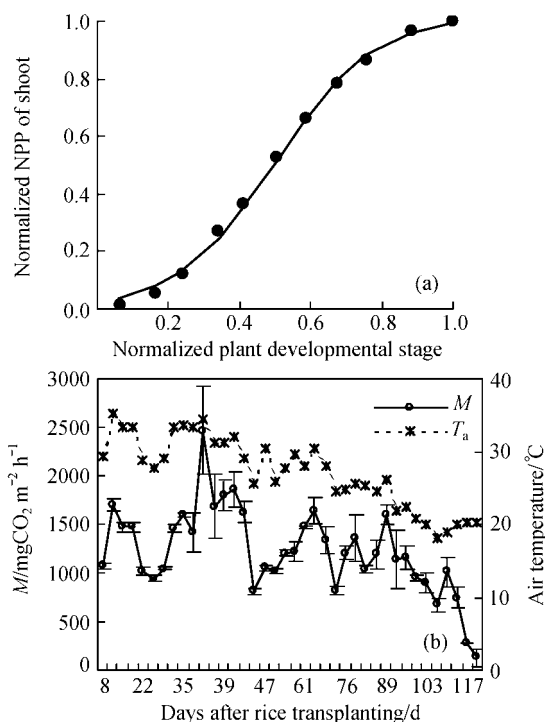


Fig. 1. Seasonal dynamics of NPP (a) derived from above ground biomass and total CO_2 fluxes (M) as well as air temperature (T_a) in rice paddy (b).

(ii) CO_2 emissions measured by opaque chamber method (M). CO_2 emissions from ecosystem (M) were measured by the static opaque chamber method. The chamber has the dimensions of $50 \text{ cm} \times 50 \text{ cm} \times 50 \text{ cm}$ and $50 \text{ cm} \times 50 \text{ cm} \times 100 \text{ cm}$ equipped with a circulating fan to ensure complete gas mixing. The measured CO_2 flux consisted of shoot dark respiration and soil respiration since plant photosynthesis inside the chamber was restricted while taking gas samples. When solar radiation is screened there is a rapid evolution of CO_2 greatly exceeding dark respiration rate for C3 plants, which is called the post-illumination burst (PIB). The PIB comes from the advanced metabolism of substrates associated with photorespiration when the light is screened. These substrates are formed during illumination. Experiment with simulating apparatus by Wang and Gao showed that the PIB from wheat leaves lasted about 1.5 min^[13]. Results from this research demonstrated that CO_2 concentration of five sets

of gas sample was linearly increased within 20 min after chamber was closed. The difference of CO_2 fluxes resulting from PIB was less than 1%, suggesting that CO_2 absorption lasted a short time and thus its influence on ecosystem respiration is negligible. In addition, the bigger chamber is more advantageous to reduce the influence of O_2 content dropping on plant respiration and thus Pasteur Effect emergency. Fig. 1(b) shows the seasonal variation of CO_2 fluxes from rice ecosystem measured in 2001 by the static opaque chamber method.

Parameter Q_{10} is usually used to describe the dependence of plant and soil respiration on temperature (Fig. 1(b)) by biologists. Respiratory Q_{10} for majority of plants is 2.0–2.4 within 5–25°C. As temperature shifts to 30–35°C, the value of Q_{10} often descends since plant respiration increases at a lower rate. Recent study in this group showed that plant respiratory Q_{10} is about 2.0^[14]. For soil respiration, Q_{10} is usually recognized as constant since soil temperature changes slowly within a relative narrow range. We took gas samples manually within a short period of time (e.g. 08:00–10:00 AM) at certain intervals (e.g. once or twice every week), while respiration of the ecosystem is significantly dependent on air temperature with a diurnal variation. In order to obtain daily CO_2 emission, CO_2 flux must be corrected by Q_{10} and daily mean temperature^[15]. Plant respiratory Q_{10} was obtained from diurnal variation of CO_2 flux in main developmental stages. The Q_{10} was then used to correct daily CO_2 emission.

(iii) Shoot autotrophic respiration. Plant dark respiration is simply entitled plant respiration since the respiration without light needs. In plant physiology, plant respiration is expressed either by respiratory coefficient (respiratory quotient) or by respiration rate. The respiratory coefficient is expressed as a mole ratio of CO_2 to O_2 exchange per day. The respiration rate is defined as the amount of CO_2 emitted from per unit dry matter of plant per day ($\text{gCO}_2\text{-Cg}^{-1}\text{Cd}^{-1}$)^[16]. Note that the respiration rate usually refers to CO_2 flux ($\text{mgCO}_2\text{-C m}^{-2} \text{ h}^{-1}$) in carbon exchange studies, while it is represented as the respiratory coefficient (R_f) in plant physiology. Similarly, we defined the respiratory coefficient as the amount of CO_2 emitted from per unit dry matter of plant per day. Taking the effect of temperature on respiration into account, we took 25°C as reference temperature.

To quantify NEE, deduction of shoot autotrophic respiration (R_{AS}) from the total fluxes of CO_2 (M) is essential according to eq. (3). Ordinarily, shoot autotrophic respiration rate can be identified through two ways, namely, harvest method and plant or living organism isolated culture. By the harvest method, R_{AS} is quantitatively identified as the difference of CO_2 fluxes of ecosystem before and after cutting plant shoot at the basal internodes. The respiratory coefficient determined by plant culture

ARTICLES

technique often exceeds to that by the harvest method because of unavoidable plant respiratory promotion in response of plant physical scathe in the process of removing plant from soil^[17]. Our experiment indicated that the plant dark respiratory coefficient determined by the culture method was increased by 20%—65% compared with that by the harvest method. This experiment was conducted in the main developmental stages of winter wheat. It is generally believed that the harvest method is more suitable to determine plant autotrophic respiration. In fact, substrate for plant respiration is protoplasm or protein. The temporal pattern of plant respiratory coefficient was pronounced over the growing season (Fig. 2). Highest respiratory coefficient occurred at the early stage of seedling and stepped down with plant growth and development. Seasonal variation of plant respiratory coefficient associated with plant N content is consistent with that of plant relative growth rate (RGR)^[18], which was also certificated from our result that the shoot dark respiratory coefficient is dependent on plant N content or RGR (Fig. 3). Plant N content was measured by the spectrum technique, and RGR was derived from the logistic equation of plant growth (Fig. 1(a)). Relationships in Fig. 3 provide wonderful possibilities that the shoot dark respiration can be quantified with several parameters including temperature, biomass, and plant N content.

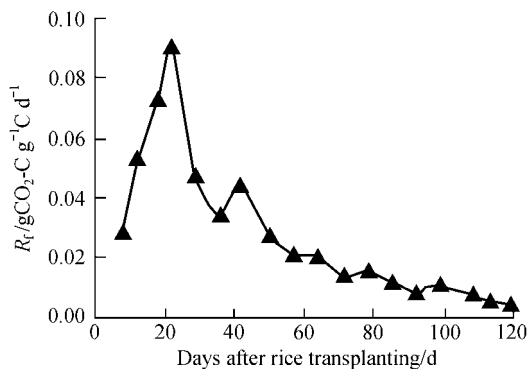


Fig. 2. Seasonal pattern of rice shoot dark respiratory coefficient (R_r).

(iv) Root respiration. Soil respiration, i.e. total soil respiration or apparent soil respiration, is often determined through three approaches: direct measurement, deduction of shoot dark respiration from the total respiration of ecosystem, and simulation by linking abiotic factors with biotic components. Results from these approaches have different interpretations. Strictly speaking, soil respiration represents an overall metabolic process of CO_2 formation, including root autotrophic respiration, soil microbe respiration and soil herbivores respiration, and an abiological process of the chemical oxidization of carbon compounds^[19]. Generally, soil microbe and root respiration account for the main constitutions of soil respiration and

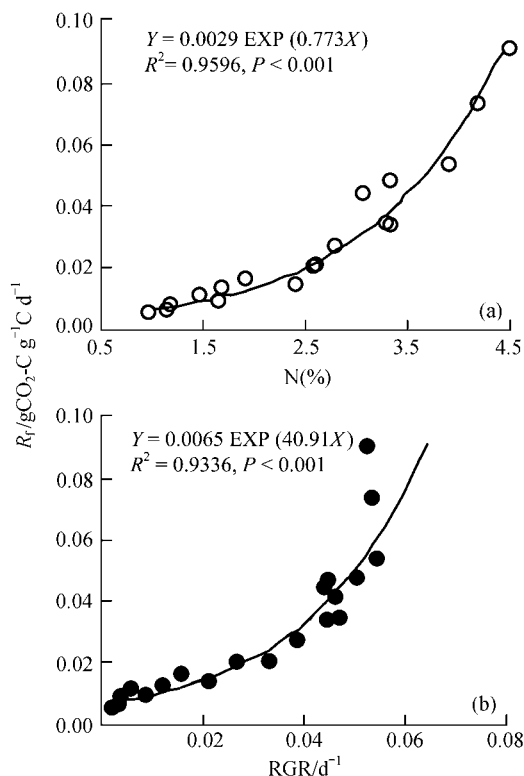


Fig. 3. Correlations of rice shoot dark respiratory coefficient (R_r) with plant nitrogen content (N) and plant relative growth rate (RGR).

the two-latter is often negligible. According to carbon origins, soil respiration is usually divided into four components: root autotrophic respiration (R_{AR}), rhizodeposition carbon heterotrophic decomposition (R_E), organic litter (R_L) and soil organic matter (R_O) heterotrophic decomposition. Over the last 30 years, many research techniques have been developed to partition root respiration from soil CO_2 effluxes^[20–24]. These techniques include two categories. One is that root respiration is directly measured, for example, root sterilized by germicide is cultured to measure respiratory coefficient. However, the natural metabolism process in the plant might be disturbed due to the sterilization. Moreover, CO_2 evolved from root respiration could be excluded in the total fluxes of ecosystem when it combines with other compounds during the transportation of CO_2 from soil to atmosphere. The other is subtractive approach that R_E , R_L and R_O subtracted from R_S gives R_{AR} . The R_L can be measured in lab incubation, field burying, or chamber method *in situ*^[25–28]. Either R_S or R_O can be monitored in field plots with or without plants, respectively^[14]. Simultaneously, rhizosphere soil is incubated in lab to detect CO_2 efflux (R_E). Investigation conducted by Kelting et al. showed that the root respiration determined by these two categories yielded approximately 30% difference^[29]. Based on the pulse labeling technique, Kuzyakov investigated R_{AR} and root-derived CO_2 efflux under similar experimental conditions with four methods,

namely, the isotope dilution method, the model rhizodeposition technique, modeling of $^{14}\text{CO}_2$ efflux dynamics, and the exude elution procedure. Results from his investigation indicated that R_{AR} contributes about 40%–50% to the root-derived CO_2 efflux^[30]. Up to date, Kuzyakov's result is thought to be more reliable than others although it showed a wide range and the assumptions and principles were different for each method.

3 NEE determination

Assuming that the contribution of R_{AR} to the root-derived CO_2 efflux is denoted as β , the root-derived CO_2 efflux was quantified by the difference of CO_2 emissions from the plots with and without plant^[14]. In light of the results obtained by Kuzyakov^[30] and Kuzyakov et al.^[31] and the case of mostly waterlogged periods in rice paddy, the β was taken values ranging from 0.1 to 0.3 before drainage. Thereafter it was 0.4. NEE was therefore determined by eq. (6) as

$$\text{NEE} = (1 - \beta) (M - R_{\text{AS}}) - \text{NPP} \quad (6)$$

Based on the measurements of several relevant components, net exchange of CO_2 between rice-based ground and the atmosphere was calculated by eq. (6). Fig. 4 and Table 1 show the seasonal changes in NPP, R_{H} and NEE for 2001 and 2002 seasons, respectively. Water regime in the rice paddy over an entire season was characterized as a course of flooding–drainage–alteration of dry and wet. Field drainage was initiated from 35 days and 37 days after rice transplanting, and lasted one week and 5 days in 2001 and 2002 seasons, respectively. Synthetic nitrogen fertilizer was applied at the rate of 333 kgN hm^{-2} in 2001 season and 450 kgN hm^{-2} in 2002 season, respectively. Local agricultural practices were accepted in the two seasons. Results of Fig. 4 and Table 1 suggested that the seasonal pattern of NPP, R_{H} and NEE was similar for the two seasons with the exception of the period before drainage. Within 3 weeks after rice transplanting, net carbon emissions occurred in 2001 season and fractional net carbon was fixed in 2002 season. Field drainage resulted in the descent of the net carbon fixation for the two seasons. Higher net carbon fixation appeared in rice developmental period from elongating to heading, 50–80 days after rice transplanting. A decline trend in the fixation was documented after rice heading (Fig. 4). Drainage events shifted rice paddy from anaerobic to aerobic condition and aggressively fomented soil CO_2 effluxes. As soil CO_2 effluxes increase, the net carbon fixed by the ecosystem dropped down (e.g. Fig. 4). Microorganism accommodation to the reflooded condition led to soil respiration decrease. The difference of NEEs between the two seasons within first 3 weeks was mostly ascribed to temperature. Too higher air temperature with an average of 29.1°C in 2001 season was answerable for R_{H} exceeding NPP. On the contrary, lower air temperature with an average of 25.6°C in 2002 season was beneficial to rice adaptation

and tillering, which induced higher NPP and lower R_{H} . Seasonal amounts of R_{H} , NPP and NEE were 2.10 ± 0.05 , 9.31 ± 0.56 and $-7.21 \pm 0.26 \text{ t hm}^{-2}$ in 2001 rice season, and 1.38 ± 0.10 , 10.84 ± 0.25 , $-9.46 \pm 0.15 \text{ t hm}^{-2}$ in 2002 rice season, respectively. In a word, NEE in rice ecosystem is influenced by abiotic and biotic factors such as temperature, soil water state, plant N and growth. An integrated effect of these factors is responsible for the inter-annual variation in NEE.

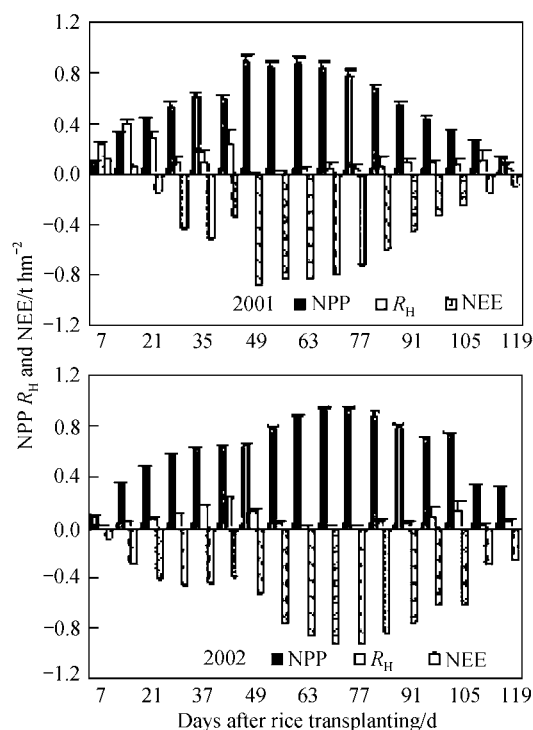


Fig. 4. Seasonal changes in NPP, R_{H} and NEE in 2001 and 2002 rice seasons.

Table 1 Comparison of NEE ($\text{gC m}^{-2} \text{d}^{-1}$) of rice ecosystem determined by static opaque chamber method (Nanjing, China) with that based on Bowen ratio-energy balance technique (Texas, USA)

Days after transplanting/d	Nanjing, China		Texas, USA ^{b)}		
	NEE ^{a)}		Days after seedling/d	NEE	
	2001	2002		1998	1999
0–21	0.23	-3.81	0–24	0.63	0.22
22–42	-6.25	-6.18	25–40	-1.53	-1.69
43–63	-11.96	-10.17	41–56	-9.16	-7.85
64–77	-10.91	-13.10	57–84	-13.62	-13.34
78–98	-6.65	-10.52	85–110	-6.82	-9.85
99–119	-2.40	-5.65	111–121	-1.15	-14.43

a) The negative NEE means net carbon fixation of rice ecosystem and the positive means net carbon effluxes. b) Data were derived from [32].

Table 1 shows net efflux of CO_2 emissions in this study and that measured by Campbell et al. with Bowen

ARTICLES

ratio-energy balance technique^[32]. Measurements by Campbell et al. were made in an irrigated rice field in EI Campo (29°12' N, 96°30' W), Texas, USA^[32]. Average air temperature over the rice season was 24.9°C in Nanjing and 24.2°C in EI Campo, respectively. There was a significant difference in precipitation between the two sites, 375 mm in Nanjing and 185 mm in EI Campo, respectively. The precipitation intensively happened within the first 3 weeks of rice growing due to monsoonal climate in Nanjing. Results in Table 1 indicated that NEEs determined by two methods were comparable with the same seasonal pattern. The mean daily NEE in Nanjing was -6.06 gC m^{-2} in 2001 season and -7.95 gC m^{-2} in 2002 season, and that in EI Campo was -6.05 gC m^{-2} in 1998 season and -7.68 gC m^{-2} in 1999 season, respectively. With the eddy covariance method, Miyata et al.^[33] measured NEE in a Japanese rice field located at Hachihama (34° 32' N, 133° 56' E). Their measurements demonstrated that mean daily NEE in drainage course was -3.95 gC m^{-2} , which accounts for 49% of that (ca. -8.13 gC m^{-2}) from waterlogged periods. On average of the two seasons, daily NEE in this study was -5.38 gC m^{-2} during drainage period and -11.01 gC m^{-2} for the following two waterlogged weeks, respectively. The former value also accounts for 49% of the latter. Clearly, NEE determined by the static opaque chamber method in this study is comparable and in agreement with those measured by Bowen ratio-energy balance and eddy covariance methods, though there are some uncertainties such as partitioning R_H from R_S and identifying rhizodeposition C from NPP.

4 Discussion and conclusions

Determination of NEE based on the static opaque chamber technique needs to simultaneously measure CO_2 fluxes of ecosystem, NPP and root/shoot ratio over an entire season. In addition, variables and components should be measured with enough replicates to reduce errors of NEE calculation. The reasonable estimations of plant respiratory coefficient and its associated temperature coefficient are the keys to quantifying plant respiration.

Determination of NEE with static opaque chamber method should focus on (1) reasonable deduction of shoot autotrophic respiration from the total CO_2 fluxes of ecosystem, (2) partition of root autotrophic respiration from soil CO_2 efflux, and (3) quantification of rhizodeposition C from NPP. Shoot autotrophic respiration has been well documented while root autotrophic respiration and rhizodeposition C are less to be identified. These two components involve in carbon cycle in the rhizosphere microecological system. Unfortunately, there is still lack of the effective method to measure carbon flow in the rhizosphere microecological system *in situ*^[34].

As Chapin and Ruess pointed out, the below ground

carbon issue has constituted the most scientific challenge to terrestrial carbon cycling^[35]. Quantification of rhizodeposition carbon is merely circumscribed by nutrient solution culture and isotope labeling approaches^[36]. Some literatures suggested that about 20%—50% of plant photosynthetic products is transferred into soil and establishes carbon flow and distribution in rhizosphere microecological system^[37–39]. Although there are many mechanistic and process-oriented models about rhizosphere carbon flow and rhizodeposition carbon^[40–42], modeling parameters have much uncertainties^[43]. Furthermore, the different definition of rhizodeposition also incurs comparison among results with great difficulties^[44]. Since the 1970s, many methods^[45] have been developed to investigate rhizosphere CO_2 effluxes such as soil sterilization and fumigation techniques^[46], isotope labeling techniques^[47], soil component integration method^[48], and plant girdling method^[49]. Estimations indicated that the contribution of root respiration to total CO_2 efflux from soil ranges from 10% to 90%, with methodological uncertainties accounting for most of this variation^[24,35]. Moreover, both root respiration and microorganism respiration are regulated by several soil environmental factors, which further instigates difficulties in study^[48,49]. Although there was a report that root autotrophic respiration is associated with root growth^[50], the universal adaptability of this relationship still needs to be extensively examined. It is noteworthy that the study on carbon cycle in rhizosphere microecological system is lack of integrality, and hence it is necessary to pay more attention to this issue in China.

With an understanding of the processes involved in the CO_2 exchange between terrestrial and the atmosphere, we estimated NEE of rice ecosystem in Nanjing. Results from this study indicated that NEE determined by the static opaque chamber method is comparable and in agreement with those measured by Bowen ratio-energy balance and eddy covariance methods. It is concluded that NEE could be quantified through CO_2 fluxes measured by the static opaque static chamber method and the measurements of relevant biotic components and abiotic factors.

Acknowledgements We thank Professors Liu Guangren and Zhang Wen with the Institute of Atmospheric Physics and Professor Zong Li-anggang with Nanjing Agricultural University for their help. This work was supported by the Knowledge Innovation Program of the Chinese Academy of Sciences (Grant No. KZCX1-SW-01-13) and the National Key Basic Research Development Foundation (approved # 2002CB412500), China.

References

1. IPCC, Atmospheric Chemistry and Greenhouse Gases (eds. Houghton, J. T., Ding, Y., Griggs, D. J. et al.), Climate Change 2001: the Scientific Basis, Cambridge: Cambridge University Press, 2001, 183—238.

2. Chen, Y. Y., Global change and social sustainable development, *Advance in Earth Sciences* (in Chinese), 2003, 18(1): 1—3.
3. Huang, Y., Study on carbon budget in terrestrial and marginal sea ecosystems of China, *Bulletin of the Chinese Academy of Sciences* (in Chinese with English abstract), 2002, 17(2): 104—107.
4. Wang, Y. S., Ji, B. M., Wang, Y. F. et al., Measurements of exchange rates of greenhouse gases between soil and atmosphere in semiarid grasslands, *Environmental Sciences* (in Chinese with English abstract), 2000, 21(3): 6—10.
5. Dong, Y. S., Zhang, S., Qi, Y. C. et al., Fluxes of CO₂, N₂O and CH₄ from a typical temperature grassland in inner Mongolia and its daily variation, *Chinese Science Bulletin*, 2000, 45(17): 1590—1594. [[Abstract](#)] [[PDF](#)]
6. Zou, J. W., Jiao, Y., Wang, Y. S. et al., GC-based technique for determination of CO₂, CH₄ and N₂O emissions from rice paddy, *Journal of Nanjing Agricultural University* (in Chinese with English abstract), 2002, 25(4): 45—48.
7. IGBP, The terrestrial biosphere and global change: Implication for nature and managed ecosystems, *A Synthesis of GCTE and Related Research*, 1997, 1—32.
8. Zhu, Z. H., Model for estimation of net primary production (NPP) of natural vegetation, *Chinese Science Bulletin* (in Chinese), 1993, 38(15): 1422—1426.
9. Zhou, G. S., Zhang, X. S., Study on NPP of natural vegetation in China under global climate change, *Acta Phytoecologica Sinica* (in Chinese with English abstract), 1996, 20(1): 11—19.
10. Huang, Y., Gao, L. Z., Jin, Z. Q. et al., Simulating the optimal growing season of rice in the Yangtze River valley and its adjacent area, China, *Agricultural and Forest Meteorology*, 1998, 91: 251—262. [[DOI](#)]
11. Domanski, G., Kuzyakov, Y., Siniakina, S. et al., Carbon fluxes in the rhizosphere of *Lolium perenne*, *Journal of Plant Nutrition and Soil Science*, 2001, 164: 381—387. [[DOI](#)]
12. Coombes, J., Hall, D., Long, S. et al., *Biological Production and Plant Photosynthesis Measurements Technique* (in Chinese), Beijing: Science Press, 1986, 78—96.
13. Wang, Z., Gao, Y. Z., Study on relationship between photorespiration and photosynthesis III, Wheat leaf CO₂ post-illumination burst and its related with photosynthesis, *Acta Phytophysiology Sinica* (in Chinese), 1983, 9(4): 421—435.
14. Zou, J. W., Huang, Y., Zong, L. G. et al., Field study on CO₂, CH₄ and N₂O emissions from rice paddy and impact factors, *Acta Scientiae Circumstantiae* (in Chinese with English abstract), 2003, 23: 758—764.
15. Zheng, X. H., Xu, Z. J., Wang, Y. S. et al., Determination of net exchange of CO₂ between paddy fields and atmosphere with static opaque chamber-based measurements, *Chinese Journal of Applied Ecology* (in Chinese with English abstract), 2002, 13(10): 1240—1244.
16. Pan, R. Z., Dong, Y. D., *Plant Physiology*, 2nd ed. (in Chinese), Beijing: Higher Education Press, 1995, 246—253.
17. Salisbury, F., Ross, C., *Plant Physiology* (in Chinese), Beijing: Science Press, 1979, 87—96.
18. Penning de Vries, F., van Laar, H., Chardon, M., Bioenergetics of growth of seeds, fruits, and storage organs. In *Potential productivity of field crops under different environments*, IRRI, Los Banos, Philippines, 1983, 37—59.
19. Singh, J., Gupta, W., Plant decomposition and soil respiration in terrestrial ecosystems, *Bot. Rev.*, 1977, 43: 449—529.
20. Van der Werf, A., Kooijman, A., Welschen, R., Respiratory energy costs for the maintenance of biomass, for growth and for ion uptake in roots of *Carex diandra* and *Carex acutiformis*, *Physiol. Plant*, 1988, 72: 483—491.
21. Bouma, T., Broekhuysen, A., Veen, B., Analysis of root respiration of *Solanum tuberosum* as related to growth, ion uptake and maintenance biomass, *Plant Physiol. Biochem.*, 1996, 34: 795—806.
22. Fang, C., Moncrieff, J., An improved chamber technique for measuring CO₂ efflux from the surface soil, *Funct. Ecol.*, 1996, 10: 297—305.
23. Epron, D., Farque, L., Lucot, E. et al., Soil CO₂ efflux in a beech forest: The contribution of root respiration, *Ann. For. Sci.*, 1999, 56: 289—295.
24. Högberg, P., Nordgren, A., Buchman, N. et al., Large-scale forest gridling shows that current photosynthesis drives soil respiration, *Nature*, 2001, 411: 789—792. [[DOI](#)]
25. Chen, S. Q., Chui, X. Y., Zhou, G. S. et al., Study on the CO₂ release rate of soil respiration and litter decomposition in *Stipa grandis* Steppe in Xilin River Basin, Inner Mongolia, *Acta Botanica Sinica* (in Chinese), 1999, 41(6): 645—650.
26. Huang, Y., Liu, S. L., Shen, Q. R. et al., Model establishment for simulating soil organic carbon dynamics, *Agricultural Sciences in China*, 2002, 1(3): 307—312.
27. Huang, Y., Liu, S. L., Shen, Q. R. et al., Influence of environmental factors on the decomposition of organic carbon in agricultural soils, *Chinese Journal of Applied Ecology* (in Chinese with English abstract), 2002, 13(6): 709—714.
28. Wang, W., Guo, J. X., Contribution of CO₂ emission from soil respiration and from litter decomposition in *Lymus chinensis* Community in northeast Songnen grassland, *Acta Ecologica Sinica* (in Chinese with English abstract), 2002, 22(5): 655—660.
29. Kelting, D., Burger, J., Edwards, G., Estimating root respiration, microbial respiration in the rhizosphere, and root-free soil respiration in forest soils, *Soil Biol. Biochem.*, 1998, 30(7): 961—968. [[DOI](#)]
30. Kuzyakov, Y., Separating microbial respiration of exudates from root respiration in non-sterile soils: a comparison of four methods, *Soil Biol. Biochem.*, 2002, 34: 1621—1631. [[DOI](#)]
31. Kuzyakov, Y., Kretschmar, A., Stahr, K., Contribution of *Lolium perenne* rhizodeposition to carbon turnover of pasture soil, *Plant and Soil*, 1999, 213: 127—136. [[DOI](#)]

ARTICLES

32. Campbell, C., Heilman, J., McInnes, K. et al., Diel and seasonal variation in CO₂ flux of irrigated rice, *Agricultural and Forest Meteorology*, 2001, 108: 15—27. [\[DOI\]](#)
33. Miyata, A., Leuning, R., Denmead, T. et al., Carbon dioxide and methane fluxes from an intermittently flooded paddy field, *Agricultural and Forest Meteorology*, 2000, 102: 287—303. [\[DOI\]](#)
34. Lin, W. H., Zhang, F. S., Bai, K. Z., Responses of plant rhizosphere to atmospheric CO₂ enrichment, *Chinese Science Bulletin*, 1999, 45(2): 97—101.
35. Chapin, F. S. III, Ruess, R., The roots of the matter, *Nature*, 2001, 411: 749—752. [\[DOI\]](#)
36. Meharg, A., A critical review of labeling techniques used to quantify rhizosphere carbon flow, *Plant and Soil*, 1994, 166: 55—62.
37. Lambers, H., Growth, respiration, exudation and symbiotic associations: the fate of carbon translocated to the roots (eds. Gregory, P. et al.), *Root Development and Function*, Cambridge: Cambridge University Press, 1987, 125—146.
38. Peng, S., Eissenstal, D., Graham, J. et al., Growth depression of mycorrhizal citrus at high phosphorus supply: Analysis of carbon costs, *Plant Physiol.*, 1993, 101: 1063—1071.
39. Bloom, A., Sukrapanna, S., Warner, R., Root respiration associated with ammonium and nitrate absorption and assimilation by barley, *Plant Physiol.*, 1992, 99: 1294—1301.
40. Blagodatsky, S., Richter, O., Microbial growth in soil and nitrogen turnover: a theoretical model considering the activity rate of microorganisms, *Soil Biol. Biochem.*, 1998, 30(13): 1743 — 1755. [\[DOI\]](#)
41. Blagodatsky, S., Yevdokimov, I., Larionova, A. et al., Microbial growth in soil and nitrogen turnover: model calibration with laboratory data, *Soil Biol. Biochem.*, 1998, 30(13): 1757—1764. [\[DOI\]](#)
42. Davidson, K., Modeling microbial food webs, *Mar. Ecol. Prog. Ser.*, 1996, 145: 279—296.
43. Toal, M., Yeomans, C., Killham, K. et al., A review of rhizosphere carbon flow modeling, *Plant and Soil*, 2000, 222: 263—281. [\[DOI\]](#)
44. Shen, J. B., Zhang, F. S., Mao, D. R., Carbon cycling in rhizosphere microecological system, *Plant Nutrition and Fertilizer Science (in Chinese)*, 2001, 7(2): 232—240.
45. Hanson, P., Edwards, N., Garten, C. et al., Separating root and soil microbial contributions to soil respiration: a review of methods and observations, *Biogeochemistry*, 2000, 48: 115—146. [\[DOI\]](#)
46. Barber, D., Martin, J., The release of organic substances by cereal roots in soil, *New Physiologist*, 1976, 76: 69—80.
47. Cheng, W., Coleman, D., Carroll, C. et al., Investing short-term carbon flows in the rhizospheres of different plant species, using isotopic trapping, *Agronomy Journal*, 1994, 86: 782—788.
48. Killham, K., Yeomans, C., Rhizosphere carbon flow measurement and implications: from isotope to reporter genes, *Plant and Soil*, 2001, 232: 91—96. [\[DOI\]](#)
49. Tjeerd, J., David, R., On the assessment of root and soil respiration for soils of different textures: interactions with soil moisture contents and soil CO₂ concentrations, *Plant and Soil*, 2000, 277: 215—221.
50. Szaniawski, R., Kielkiewicz, M., Maintenance and growth respiration in shoots and roots of sunflower plants grown at different root temperatures, *Physiol. Planta.*, 1982, 54: 500—504.

(Received June 27, 2003; accepted December 1, 2003)