

# Soil temperature and biotic factors drive the seasonal variation of soil respiration in a maize (*Zea mays* L.) agricultural ecosystem

Guangxuan Han · Guangsheng Zhou ·  
Zhenzhu Xu · Yang Yang · Jingli Liu ·  
Kuiqiao Shi

Received: 29 May 2006 / Accepted: 22 November 2006 / Published online: 23 December 2006  
© Springer Science+Business Media B.V. 2006

**Abstract** The diurnal and seasonal variation of soil respiration (SR) and their driving environmental factors were studied in a maize ecosystem during the growing season 2005. The diurnal variation of SR showed asymmetric patterns, with the minimum occurring around early morning and the maximum around 13:00 h. SR fluctuated greatly during the growing season. The mean SR rate was  $3.16 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , with a maximum of  $4.87 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  on July 28 and a minimum of  $1.32 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  on May 4. During the diurnal variation of SR, there was a significant exponential relationship between SR and soil temperature ( $T$ ) at 10 cm

depth:  $\text{SR} = \alpha e^{\beta T}$ . At a seasonal scale, the coefficient  $\alpha$  and  $\beta$  fluctuated because the biomass ( $B$ ) increased  $\alpha$ , and the net primary productivity (NPP) of maize markedly increased  $\beta$  of the exponential equation. Based on this, we developed the equation  $\text{SR} = (aB + b)e^{(c\text{NPP} + d)T}$  to estimate the magnitude of SR and to simulate its temporal variation during the growth season of maize. Most of the temporal variability (93%) in SR could be explained by the variations in soil temperature, biomass and NPP of maize. This model clearly demonstrated that soil temperature, biomass and NPP of maize combined to drive the seasonal variation of SR during the growing season. However, only taking into account the influence of soil temperature on SR, an exponential equation over- or underestimated the magnitude of SR and resulted in an erroneous representation of the seasonal variation in SR. Our results highlighted the importance of biotic factors for the estimation of SR during the growing season. It is suggested that the models of SR on agricultural sites should not only take into account the influence of soil temperature, but also incorporate biotic factors as they affect SR during the growing season.

G. Han · G. Zhou (✉) · Z. Xu  
Laboratory of Quantitative Vegetation Ecology,  
Institute of Botany, The Chinese Academy of  
Sciences, Beijing 100093, P.R. China  
e-mail: gszhou@ibcas.ac.cn

G. Han  
Graduate School of the Chinese Academy of  
Sciences, Beijing 100039, P.R. China

G. Zhou  
Institute of Atmospheric Environment, China  
Meteorological Administration, Shenyang 110016,  
P.R. China

Y. Yang · J. Liu · K. Shi  
Meteorological Bureau of Jinzhou, Jinzhou 121001,  
P.R. China

**Keywords** Biomass · Net primary productivity ·  
Soil respiration · Soil temperature · Temporal  
variation

## Abbreviations

SR	Soil respiration
<i>T</i>	Soil temperature
<i>B</i>	Biomass
NPP	Net primary productivity
SWC	Soil water content
<i>C</i>	Total carbon of soil
<i>N</i>	Soil nitrogen

## Introduction

Soil respiration (SR) is a major CO<sub>2</sub> flux from ecosystems to the atmosphere and is therefore an important component of the global carbon balance (Schimel 1995; Raich and Tufekcioglu 2000). Due to the high order of magnitude of this flux, relatively small climatically-induced changes in SR may have a great effect on atmospheric CO<sub>2</sub> concentrations and the global carbon budget with potential feedbacks to climate change (Reichstein et al. 2003; Sánchez et al. 2003). Therefore, it is important to obtain good estimates of SR and to understand environmental factors controlling its variability across ecosystems.

Researchers rely on empirical models to simulate the magnitude and temporal variability of SR, while process-based models are rarely used because of the complexity of the soil environment (Michelsen et al. 2004). These empirical models typically use soil temperature (Fang et al. 1998; Buchmann 2000; Janssens and Pilegaard 2003), soil moisture (Davidson et al. 2000; Epron et al. 2004; Sotta et al. 2004) as well as their interaction (Tufekcioglu et al. 2001; Lee et al. 2002; Tang and Baldocchi, 2005) for large-scale SR estimates. For example, previous investigators proposed several different functions to describe the relationship between SR and soil temperature, including linear or sinusoidal regressions (Fan et al. 1995; O'Connell et al. 2003; Chimner 2004); exponential equations (Davidson et al. 1998; Buchmann 2000; Sánchez et al. 2003; Reth et al. 2004); Arrhenius equations (Lloyd and Taylor 1994; Thierron and Laudelout 1996); power models (Fang and Moncrieff 2001); and logistic models (Rodeghiero and Cescatti 2005). However, a number of field studies have clearly shown that none of these models appears to be consis-

tently better than the others. In the present study, we used exponential functions because this function is most widely used to simulate the temperature response of SR.

Soil respiration is a composite flux and includes respiration of soil organisms and plant roots, organic matter decomposition, and the subsequent release of CO<sub>2</sub> at the soil surface. Besides soil temperature and soil moisture, root biomass, net primary productivity (NPP), litter inputs, microbial populations, root nitrogen concentrations, soil texture, substrate quantity and quality have all been shown to have effects on SR (Boone et al. 1998; Buchmann 2000; Fang and Moncrieff 2001; Sánchez et al. 2003; Dilustro et al. 2005). Moreover, SR is not a pure physiological response to soil temperature, but an integration of several confounding ecosystem processes (Janssens and Pilegaard 2003). Thus, significant errors in predictions of SR may result from models based only on soil temperature and moisture, when changes in other biotic and abiotic factors, such as soil properties, root biomass and NPP, can confound the temperature or moisture dependence of SR (Janssens and Pilegaard 2003). Therefore, it is necessary to incorporate additional factors (biotic factors or soil properties) into these models for evaluating SR because the existing models based on environmental factors cannot accurately simulate the magnitude and variation of SR. For example, Reichstein et al. (2003) developed a general statistical nonlinear regression model to describe SR as dependent on soil temperature, soil water content (SWC), and site-specific maximum leaf area index. And, Reth et al. (2005) developed a regression model to describe SR as a function of soil temperature, soil moisture, pH-value and root mass.

Based on the measurements of SR, environmental factors, maize biomass, NPP and soil chemical properties (organic matter, total nitrogen) in a maize ecosystem during the growth season, the present work is intended to investigate the effect of biotic factors on the response of SR to soil temperature and to bridge some existing gaps in the study of modeling the magnitude and temporal variation of SR. Specifically, the objectives of this study were: (1) to quantify the effect of soil temperature on diurnal

variation in SR in a maize agricultural ecosystem; (2) to describe the effects of biotic factors on the response of SR to soil temperature; and (3) to determine the seasonal variation of SR during the growth season of maize.

## Materials and methods

### Study site

The study was conducted in a spring maize ecosystem located on Jinzhou Agricultural Ecosystem Research Station (41°09'N, 121°12'W), which belongs to Institute of Atmospheric Environment, China Meteorological Administration. The selected crop type is rainfed spring maize, which is the main crop type, and it was sown and harvested in early May and late September, respectively. Plants were planted 30 cm apart in rows. The distance between rows was 60 cm. The fields are under till management and N fertilizer is around 300 kg N ha<sup>-1</sup>.

The region has a temperate zone monsoon climate with a mean annual temperature of about 9.1°C and an annual precipitation of about 568.8 mm over the last 20 years. The average growing season temperature (May–September) is 20.1°C and the average temperature of other months is 0.5°C. The study site is relatively flat with slopes <3 and the elevation is 17 m. The soil type is a typical brown soil, and is composed of 45% of sand, 40% of silt, and 15% of clay with a pH value of 6.3. The organic matter content varies from 0.6% to 0.9% and total N is 0.069%. The data come from A<sub>p</sub> horizon at a depth of 0–30 cm.

### Soil respiration measurements

Soil respiration rates were measured twice monthly during the growing season (May–September) in 2005 using a SR chamber (LI-6400-09, Li-Cor, Inc., Lincoln, NE) connected to a portable infrared gas analyzer (IRGA, LI-6400, Li-Cor, Inc., Lincoln, NE). To minimize soil surface disturbances, the chamber was mounted on PVC soil collars sharpened at the bottom and inserted into the soil about 1 or 2 cm, and the soil collars were installed one day before the measurements. We inserted 15 soil collars, each with a height of

4.5 cm and a diameter of 11 cm, into the soil and SR was pooled over all 15 collars per plot. To catch the diurnal pattern, SR rates were measured every hour from 6:00 to 18:00 on May 4, June 5, June 28, July 28, August 28 and September 22.

### Measurements of environmental factors

Soil temperature was measured simultaneously with SR using a copper/constantan thermocouple penetration probe (LI-6400-09 TC, LiCor) inserted in the soil to a depth of 10 cm in the vicinity of the soil collars. SWC (0–12 cm and 0–20 cm depth, based on as soil volume) in the vicinity of the soil collars was monitored with a portable sensor (Diviner2000, Sentek, Australia). In addition, the microclimate data, including soil temperatures (at the depth of 10 cm, 20 cm and 30 cm) and profiles of soil moisture (0–10 cm and 10–20 cm depth), were logged continuously in the vicinity of a meteorological tower (HMP45C, Vaisala, Helsinki, Finland) located within the study area.

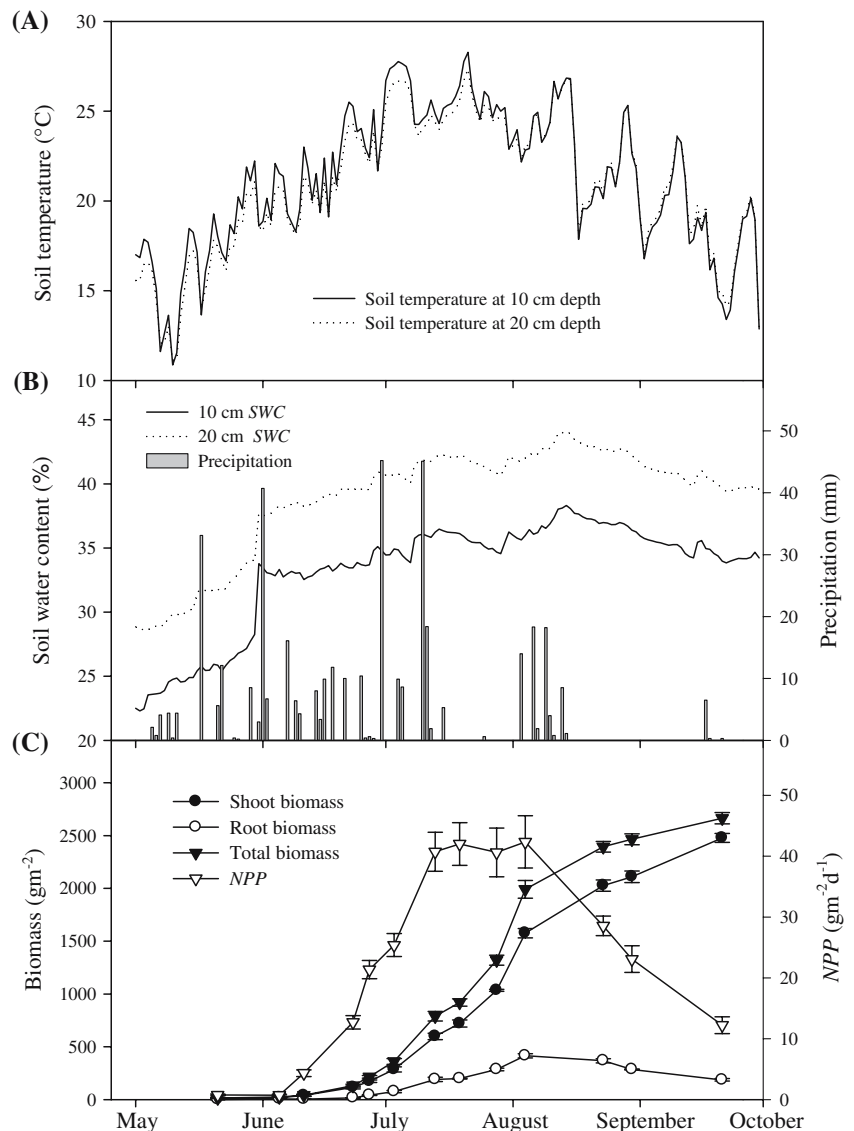
Aboveground biomass of maize plant was measured by clipping five maize plants at intervals of 20 days from the beginning of May to the end of September. At the same time, root biomass was measured by taking five soil blocks (15 cm wide × 30 cm long × 30 cm deep). The aboveground and belowground biomass was oven-dried at 80°C for 48 h and weighed. The weight difference of total biomass between the two sampling periods was considered to represent NPP.

$$\text{NPP} = \Delta B = \frac{B_2 - B_1}{t_2 - t_1} \quad (1)$$

where NPP is the net primary productivity (g m<sup>-2</sup> d<sup>-1</sup>), B<sub>1</sub> is the total biomass (g m<sup>-2</sup>) at t<sub>1</sub> sampling time (d), B<sub>2</sub> is the total biomass (g m<sup>-2</sup>) at t<sub>2</sub> sampling time(d).

For each measurement, SWC, total carbon and total nitrogen of 30 cm depth soil samples were analyzed. SWC was analyzed using oven-drying, total soil carbon was analyzed using the potassium dichromate oxidation method, and soil nitrogen was measured by the Kjeldahl method.

**Fig. 1** Seasonal courses of (A) soil temperature at 10 cm and 20 cm depth, (B) precipitation and soil water content (SWC) at 10 cm and 20 cm and (C) seasonal variations of averaged shoot biomass, root biomass, total biomass and NPP of maize during the growth season in 2005. Vertical bars indicate standard deviations of five sampling plants for every sampling day



## Statistical analysis

Correlation and exponential regressions were used to evaluate the relationship between SR rate and soil temperature. Correlation and linear regression analyses were used to describe the relationships between parameters in the equations and the environmental factors measured during the growing season. Significant differences for all statistical tests were evaluated at the level  $\alpha = 0.05$ . All statistical analyses were performed using the SPSS 11.0 package (SPSS, Chicago, IL, USA).

## Results

### Microclimate, plant biomass and net primary productivity

Measurements were conducted over a wide range of environmental conditions during the growing season (Fig. 1). The mean value of soil temperature at 10 cm depth was 20.7°C, ranging from a minimum of 8.1°C in May to a maximum of 28.3°C in July. The mean soil moisture at 10 cm and 20 cm from May to September were 34.4% and 40.1%, respectively. During the

measurement period, the total precipitation was 464.0 mm.

Maize plants had a very slow growth of shoots and roots in the young development stage. Shoot biomass increased intensively at the beginning of July and reached a maximum of 2,477 g m<sup>-2</sup> in September. Root biomass showed a different seasonal variation pattern compared with shoot biomass. It increased slightly from sowing and reached the seasonal peak value of 414 g m<sup>-2</sup> in August, and then decreased slightly towards the end of the growth season. The total biomass followed a seasonal pattern almost matching that of the shoot biomass, reaching the peak value of 2,664 g m<sup>-2</sup> at the harvesting stage. NPP of maize presented a single peak with the highest values occurring between mid-July and mid-August (Fig. 1).

#### Relationships between soil temperature and diurnal variations of soil respiration

The diurnal fluctuations of SR were relatively high and all showed asymmetric patterns, with the minimum appearing around early morning (06:00–7:00 h) and the maximum around 13:00 h (Fig. 2). The diurnal patterns of SR varied correspondingly with soil temperature each day. SR rates followed the increasing trend of soil temperature in the morning, and then decreased slightly when soil temperature decreased in the afternoon.

Correlation analysis revealed that SR was more significantly related to soil temperature at the depth of 10 cm than at the depths of 20 cm and 30 cm during its diurnal variations (Table 1). Thus, soil temperature at 10 cm depth was used to investigate the influence of temperature on SR. Regression analysis revealed that there were significant exponential relationships between SR and soil temperature at 10 cm depth for the six sampling dates (Fig. 3).

$$SR = \alpha e^{\beta T} \quad (2)$$

where SR is soil respiration rate ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ),  $T$  is soil temperature at 10 cm depth ( $^{\circ}\text{C}$ ),  $\alpha$  and  $\beta$  are parameters and they are showed in Table 2.

#### Effects of biotic factors on the response of soil respiration to temperature

It was clear that parameters  $\alpha$  and  $\beta$  in Eq. (2) fluctuated during the growing season of maize (Fig. 3, Table 2), and these fluctuations might be attributable to the seasonal changes in water-heat factors, biotic factors or soil properties. Regression analysis indicated that biomass of maize was the best predictor of parameter  $\alpha$  and NPP was a driving factor of parameter  $\beta$ . Biomass of maize markedly increased parameter  $\alpha$  of the exponential equation and NPP influenced SR by increasing its  $\beta$ .

$$\alpha = 0.001B + 0.051; R^2 = 0.715, P = 0.034, n = 6 \quad (3)$$

$$\beta = 0.0002\text{NPP} + 0.425; R^2 = 0.772, P = 0.021, n = 6 \quad (4)$$

Substituting Eqs. (3) and (4) into (2), a simplified equation for estimating seasonal variation of SR could be developed as

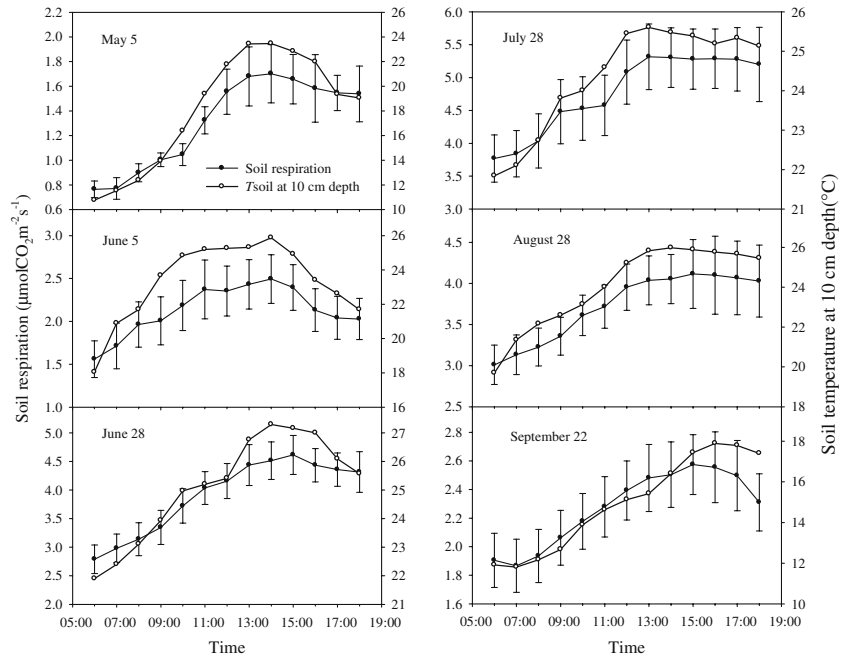
$$SR = (4 \times 10^{-5}B + 0.725) \exp[(7.5 \times 10^{-4}\text{NPP} + 0.046)T]; R^2 = 0.927, P < 0.001, n = 78 \quad (5)$$

where SR is the soil respiration rate ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ),  $T$  is soil temperature at 10 cm depth ( $^{\circ}\text{C}$ ), NPP is net primary productivity ( $\text{g m}^{-2}\text{d}^{-1}$ ),  $B$  is biomass of maize ( $\text{g m}^{-2}$ ).

Equation (5) showed that SR responded positively to changes in soil temperature. Furthermore, these responses were affected by changes in NPP and biomass of maize over the growing season. The equation gave a good agreement between observed and predicted SR rates at seasonal scale ( $R^2 = 0.929, n = 78$ ). Most of the temporal variability in SR could be explained by the variations in soil temperature and associated biomass and NPP of maize defined in Eq. (5) (Fig. 4a, b).

Only taking into account the influence of soil temperature, the relationship between SR and soil temperature during the growth season could be empirically fitted as:

**Fig. 2** Diurnal variations of soil respiration and soil temperature ( $T_{\text{soil}}$ ) at 10 cm depth on May 4, June 5, June 28, July 28, August 28 and September 22 during the growing season of maize in 2005. Data of soil respiration rate represent means  $\pm$  standard error ( $n = 15$ )



**Table 1** Correlation coefficients of soil respiration rate during daytime to soil temperatures ( $T$ )

Date	$T$ at 10 cm depth ( $^{\circ}\text{C}$ )	$T$ at 20 cm depth ( $^{\circ}\text{C}$ )	$T$ at 30 cm depth ( $^{\circ}\text{C}$ )
May 4	0.976**	0.475	0.145
June 5	0.955**	0.682*	0.483
June 28	0.980**	0.976**	0.826**
July 28	0.979**	0.923**	0.693**
August 28	0.986**	0.842**	0.695**
September 22	0.929**	0.877**	0.427

\* and \*\* are significant at the 0.01 level and the 0.05 level (2-tailed) respectively

$$\text{SR} = 0.52e^{0.076T}; R^2 = 0.527, P < 0.001, n = 78 \tag{6}$$

where SR is the soil respiration rate ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ),  $T$  is soil temperature at 10 cm depth ( $^{\circ}\text{C}$ ).

However, the exponential equation resulted in a lower  $R^2$  value (0.53) compared to Eq. (5) (Fig. 4a, c). Moreover, the residuals (measured values—modeled values) vs. measured SR were plotted (Fig. 4b, d). The residuals in Eq. (5) were much less than that using Eq. (6), which indicated Eq. (5) fitted better the measurement results.

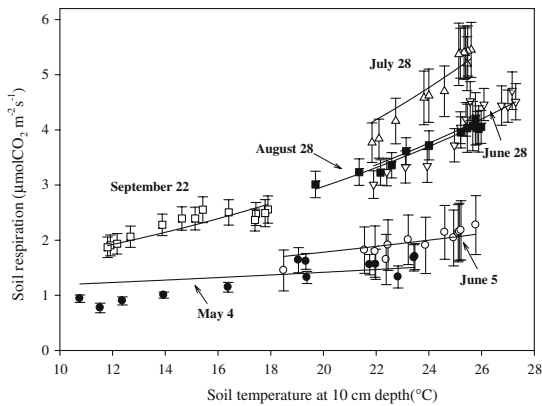
Nevertheless, soil moisture ( $R^2 = 0.563$ ,  $P = 0.146$ ) did not explain a significant amount

of the variation in SR rates, because it fluctuated from 22% to 38% during the growth season, and fluctuated from 32% to 38% from June to September (Fig. 1), and never seemed to reach either extremely high or extremely low limiting values at this site. Furthermore, soil organic matter ( $R^2 = 0.332$ ,  $P = 0.534$ ) and total N content ( $R^2 = -0.301$ ,  $P = 0.561$ ) were not significantly correlated with SR because they fluctuated only slightly during the growing season (Table 2).

### Seasonal variation of soil respiration

In this study, SR rates were based on an average produced from measurements made near and away from plants in order to take into account the spatial influence of respiring root biomass (Pangle and Seiler 2002). Furthermore, mean SR of sampling days was calculated by averaging all measured SR values during the diurnal variations. Thus, the seasonal variation of SR was characterized (Fig. 5). SR fluctuated greatly during the growing season. SR rate was about  $1.32 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  on May 4 when the maize sowed. The SR rate increased as the soil temperature increased and the crop grew, and it peaked at  $4.87 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  on July 28, and then





**Fig. 3** Relationships between soil respiration and soil temperature at 10 cm depth for each of the six measurement dates in a maize ecosystem. The solid lines represent the fitted exponential equations. Vertical bars represent standard errors of the mean

decreased until September, the harvest season. The mean SR rate was  $3.16 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  during the measurement period.

With the biomass and NPP every day estimated by interpolating between sampling dates and with soil temperature automatically measured, Eq. (5) fitted the seasonal changes in SR well (Fig. 5). However, Eq. (6) significantly overestimated the SR during the early growth stage, while underestimated SR during the middle and late growth stages of maize (Fig. 5). This indicated that it would result in an erroneous estimate of seasonal variation of SR only according to soil temperature because the NPP and biomass of maize varied simultaneously and combined to influence SR. Applying Eq. (5), the estimate of SR was  $476.12 \text{ g cm}^{-2}$  during the growing season in 2005. However, the estimate was reduced by 10.2% if Eq. (6) was used.

### Discussion

Soil temperature driving the diurnal variation of soil respiration

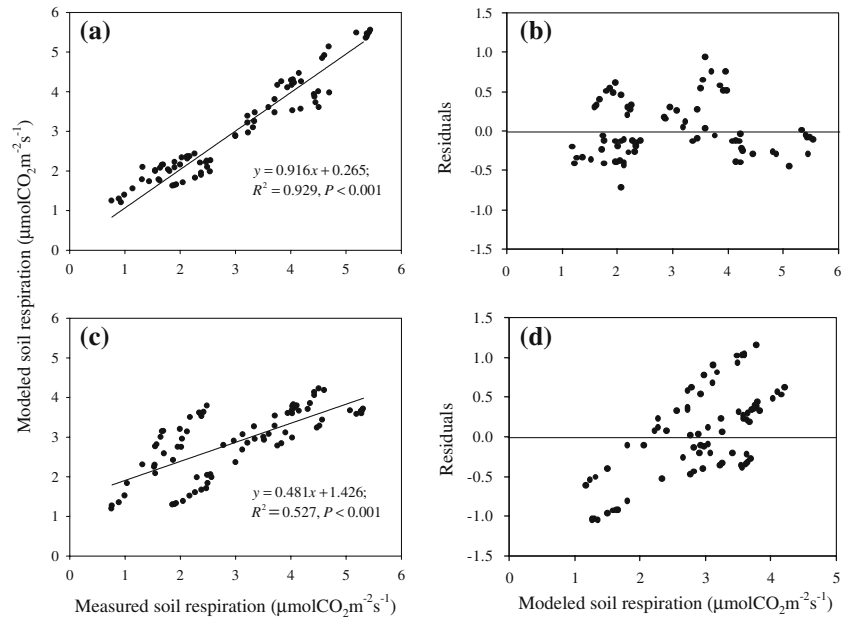
The diurnal variation of SR showed asymmetric patterns, with the minimum appearing around early morning and the maximum around 13:00 h. SR fluctuated during the daytimes following the trend of soil temperature (Fig. 2). These results

**Table 2** Values of coefficients  $\alpha$  and  $\beta$  of the Eq. ( $\text{SR} = \alpha e^{\beta T}$ ) and corresponding environmental factors including soil temperature ( $T$ ) at 10 cm depth, soil water content (SWC) at 10 cm depth, biomass ( $B$ ), net primary productivity (NPP) of maize, total carbon (C) and soil nitrogen (N) for each of the six measurement dates during a maize growth season in 2005

Date	Exponential function $\text{SR} = \alpha e^{\beta T}$			$T$ at 10 cm depth (°C)	SWC at 10 cm depth (%)	$B$ ( $\text{g m}^{-2}$ )	NPP ( $\text{g m}^{-2} \text{ d}^{-1}$ )	C (%)	N (%)
	$\alpha$	$\beta$	$R^2$						
May 4	0.4827	0.0536	0.84	18.2	23.6	0.0	0.0	7.84 (0.32)	0.86 (0.05)
June 5	0.4953	0.0583	0.89	23.3	33.1	17.4 (1.5)	0.7 (0.2)	8.61 (0.33)	0.91 (0.05)
June 28	0.5103	0.0814	0.91	25.1	34.8	174.3 (15.8)	21.3 (1.5)	8.44 (0.31)	0.93 (0.02)
July 28	0.4231	0.1000	0.97	24.4	34.7	1034.5 (35.1)	40.6 (3.2)	9.10 (0.12)	1.01 (0.02)
August 28	1.0448	0.0587	0.97	24.1	36.9	2110.1 (51.7)	23.1 (2.2)	7.98 (0.11)	0.70 (0.02)
September 22	1.1576	0.0552	0.80	14.8	33.8	2477.2 (53.8)	12.2 (1.4)	8.46 (0.24)	0.70 (0.03)

Numbers in brackets represent the standard error of the mean

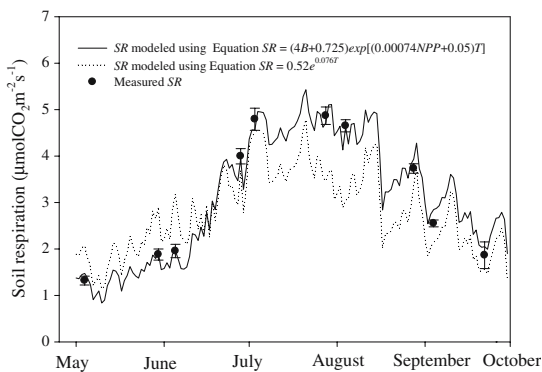
**Fig. 4** Relationships between measured soil respiration and the modeled soil respiration (a, c) and analysis of residuals (b, d) for all data combined during the growing season in the maize ecosystem, using Eq.  $SR = (4 \times 10^{-5}B + 0.725) \exp[(7.5 \times 10^{-4}NPP + 0.046)T]$  (a, b) and Eq.  $SR = 0.52e^{0.076T}$  (c, d), respectively. Both regressions are statistically significant at  $P < 0.001$ . The regression functions and the  $R^2$  of the regression are given.



are consistent with previous reports about diurnal variation of SR for terrestrial ecosystems (Fang et al. 1998; Elberling 2003; Cao et al. 2004).

In this study, soil temperature exerted the dominant control over the diurnal variation of SR, while other important variables such as soil moisture and soil properties varied relatively slightly in the same period. There was a significant exponential relationship between SR and soil temperature during its diurnal and seasonal

variations (Eq. (2)). Exponential regressions have often been used to describe the relationship between SR and soil temperature at seasonal scale when soil moisture or other factors are not limiting (Buchmann 2000; Janssens and Pilegaard 2003; Reth et al. 2004). It is clear that SR responds positively to temperature in a number of systems (Davidson et al. 2000; Fang and Moncrieff 2001; Richard et al. 2004; Wiseman and Seiler 2004). Increasing temperatures can activate dormant microbes and increase microbial species richness, which potentially broadened the mineralizable carbon pools (Andrews et al. 2000), thus promoting microbial respiration. At the same time, increasing temperature can also activate root respiration by influencing the photosynthesis of the plant and photosynthates translocated from the aboveground part of the plant (as explained below). Furthermore, increasing soil temperature advances gas transmission in soil and therefore accelerates gas exchange with the atmosphere (Tang et al. 2003).



**Fig. 5** Seasonal variations of measured and modeled soil respiration during the growth season of maize. Symbols represent mean and standard error of soil respiration on every sampling day. The solid line represents the equation  $SR = (4 \times 10^{-5}B + 0.725) \exp[(7.5 \times 10^{-4}NPP + 0.046)T]$  fit, and the dotted line is the Eq.  $SR = 0.52e^{0.076T}$

#### Biotic factors affecting the response of soil respiration to temperature

The temperature sensitivity of SR is a critical component of many ecosystem models (Raich and Schlesinger 1992), since small changes in



global temperature could have a large influence on the atmospheric carbon balance. At present, many ecosystem models use an exponential relationship to describe how respiration responds to temperature (Langley et al. 2005). There is increasing empirical evidence that the temperature sensitivity of SR is not a constant, but tends to be modified by seasonal changes in soil moisture, root biomass, litter inputs, microbial populations and other seasonally fluctuating conditions and processes (Davidson et al. 1998). During the growing season of maize, the coefficients  $\alpha$  and  $\beta$  in Eq. (2) fluctuated because biomass markedly increased  $\alpha$ , and NPP markedly increased  $\beta$  of the exponential Eq. (2). This demonstrated that biotic factors might affect the response of SR to soil temperature during the growing season of maize.

The strong positive relationship between  $\beta$  and NPP indicated that NPP ameliorated the temperature sensitivity of SR. At the ecosystem scale, NPP may be the most important factor controlling soil biota and belowground processes (Wardle 2002). There is strong evidence that rates of plant production and SR are linked processes (Raich and Tufekcioglu 2000). The effect of temperature on root respiration is likely to be constrained by the seasonal changes in NPP, because root respiration largely depends on the amount of photosynthates translocated from the aboveground part of the plant (Högberg et al. 2001; Janssens et al. 2001; Curiel-Yuste et al. 2004). Recent field experiments have shown that as much as half of the soil respiratory carbon release is derived from recent photosynthate (Högberg et al. 2001; Steinmann et al. 2004). An increase in the carbon availability to the root system often causes an increase in root respiration (Atkin et al. 2000). Kirschbaum (2006) reported that changes in substrate availability may confound the apparent temperature dependence of SR. Hence, a high NPP may contribute to a high temperature sensitivity of root respiration. In addition, NPP provides the inputs to the soil of aboveground litter and belowground organic detritus (Raich and Potter 1995). Schimel et al. (1994) reported that microbes preferably use the short-lived fractions of soil organic matter as an energy source and therefore depend primarily on new litter inputs. Any changes in the inputs of litter and

detritus to the soil are likely to affect rates of microbial respiration strongly (Rey et al. 2002). Thus, microbial respiration indirectly depends on ecosystem productivity (Janssens et al. 2001). Modeling exercises and field studies have shown that the availability of high quality substrate may drive the temperature sensitivity of heterotrophic respiration (Vance and Chapin 2001; Brooks et al. 2004; Eliasson et al. 2005). Therefore, high NPP in our study may have elevated heterotrophic temperature sensitivity. Besides, NPP may change the relative contribution of root respiration to total SR, consequently affecting the temperature sensitivity of SR. Boone et al. (1998) reasoned that higher temperature sensitivity should attribute to larger contribution of root respiration to total SR, because root respiration had higher temperature sensitivity than heterotrophic CO<sub>2</sub> efflux from decomposing soil organic matter.

During the growing season of maize, biomass was another factor influencing the response of SR to soil temperature since it markedly influenced parameter  $\alpha$  of the exponential equation (2). Roots below the measurement chambers probably influenced SR rates since root respiration is an integral part of SR (Hanson et al. 2000). Root respiration was thought to comprise 40–60% of total SR (Raich and Schlesinger 1992), although these values strongly depended on growth stage, especially in agricultural soils. In addition to the direct contribution of roots to total SR, roots can also affect soil microbial growth and activities by exuding organic substrates for microorganisms and by altering the soil physical and chemical environment, consequently controlling microbial respiration (Lohila et al. 2003; Kuzyakov and Cheng 2004). Therefore, biomass might promote the positive response of SR to temperature. The positive correlation between biomass and parameter  $\alpha$  indicated that biotic factors affected the response of SR to soil temperature.

Soil temperature, net primary productivity and biomass driving the seasonal variation of soil respiration

Biotic factors affect SR by influencing soil microclimate and structure, the quantity of detritus supplied to the soil, the quality of detritus, and

the overall rate of root respiration (Raich and Tufekcioglu 2000). Therefore, changes in biotic factors have the potential to modify the responses of soils to environmental change. With respect to temporal dynamics in biomass, NPP and soil properties, there is a need to extend the model with either temporal varying parameters or dynamic model formulation. In this study, the response of SR to soil temperature was influenced by biomass and NPP during the growing season of maize. Thus, we developed Eq. (5) to describe the seasonal variation of SR, which fitted the data well ( $R^2 = 0.93$ ). It clearly demonstrates that soil temperature, NPP and biomass of maize are important in determining the temporal pattern of SR through an interaction that can be captured by a model. The current study does not contradict the general positive response of SR to temperature, but indicates that temperature is not necessarily the single most important factor.

Soil respiration is a net flux derived from several different processes, and changes occurring in any single process can be masked by opposite changes in another (Buyanovsky and Wagner 1995). During the growing season, NPP and biomass changed rapidly on several days (Fig. 1), which might affect SR rates by influencing detritus production and root respiration rates (Raich and Tufekcioglu 2000). It may be impossible to determine the direct temperature response if such a confounding correlation exists (Janssens and Pilegaard 2003). For example, SR can increase even with declining SR in the autumn due to an influx of labile carbon from fallen leaves and decomposing fine roots (Davidson et al. 1998). In spring, when root respiration increases with increasing soil temperature and root growth increases the amount of respiring tissue at the same time, the exponential equation between SR and temperature no longer reflects just temperature sensitivity alone (Davidson et al. 2006). Therefore, Eq. (6) lacked a physiological basis and bore obvious limitations for extrapolations within physiological scales (Subke et al. 2003). Depending on seasonal changes in soil temperature, biomass and NPP, Eq. (5) was favored to describe the temporal variation of SR, and thus reflected community responses, which might differ from the temperature re-

sponses of the respiratory processes. Although this model may not be broadly applicable, our results suggest that biotic factors affect the response of SR to temperature during the growing season, so we should not only take into account the influence of temperature, but also incorporate biotic factors into the models in order to simulate the seasonal variation of SR on agricultural sites.

**Acknowledgements** We thank Dr Yuhui Wang, Dr Yanling Jiang, Dr Bingrui Jia, Dr Fengyu Wang, Dr Xu Wang, Dr Yijun Li, Dr Yunlong Wang, Dr Ensheng Weng and Ms Jian Song for their help during the experiments. This work was jointly supported by the National Key Project for Basic Research (2006CB400502) and the Knowledge Innovation Programs of the Chinese Academy of Sciences (KSCX2-SW-133) and the National Science Foundation of China (40625015).

## References

- Andrews JA, Matamala R, Westover KM, Schlesinger W (2000) Temperature effects on the diversity of soil heterotrophs and the  $\delta^{13}\text{C}$  of soil-respired  $\text{CO}_2$ . *Soil Biol Biochem* 32:699–706
- Atkin OK, Edwards EJ, Loveys BR (2000) Response of root respiration to changes in temperature and its relevance to global warming. *New Phytol* 147:141–154
- Boone RD, Nadelhoer KJ, Canary JD, Kaye JP (1998) Roots exert a strong influence on the temperature sensitivity of soil respiration. *Nature* 396:570–572
- Brooks PD, McKnight D, Elder K (2004) Carbon limitation of soil respiration under winter snowpacks: potential feedbacks between growing season and winter carbon fluxes. *Glob Change Biol* 11:231–238
- Buchmann N (2000) Biotic and abiotic factors controlling soil respiration rates in *Picea abies* stands. *Soil Biol Biochem* 32:1625–1635
- Buyanovsky GA, Wagner GH (1995) Soil respiration and carbon dynamics in parallel native and cultivated ecosystems. In: Lal R, Kimble J, Levine E, Stewart BA (eds) *Soils and Global Change* CRC Press, Boca Raton, FL, U.S.A., pp 209–217
- Cao GM, Tang YH, Mo WH, Wang YS, Li YN, Zhao XQ (2004) Grazing intensity alters soil respiration in an alpine meadow on the Tibetan plateau. *Soil Biol Biochem* 36:237–243
- Chimner RA (2004) Soil respiration rates of tropical peat lands in Micronesia and Hawaii. *Wetlands* 24:51–56
- Curjel-Yuste J, Janssens IA, Carrara A, Ceulemans R (2004) Annual  $Q_{10}$  of soil respiration reflects plant phenological patterns as well as temperature sensitivity. *Glob Change Biol* 10:161–169
- Davidson EA, Belk E, Boone RD (1998) Soil water content and temperature as independent or confounded factors controlling soil respiration in a

- temperate mixed hardwood forest. *Glob Change Biol* 4:217–227
- Davidson EA, Janssens IA, Luo Y-Q (2006) On the variability of respiration in terrestrial ecosystems: moving beyond  $Q_{10}$ . *Glob Change Biol* 11:1–11
- Davidson EA, Trumbore SE, Amundson R (2000) Soil warming and carbon content. *Nature* 408:789–790
- Dilustro JJ, Collins B, Duncan L, Crawford C (2005) Moisture and soil texture effects on soil  $CO_2$  efflux components in southeastern mixed pine forests. *Forest Ecol Manag* 204:85–95
- Elberling B (2003) Seasonal trends of  $CO_2$  dynamics in a soil subject to freezing. *J Hydrol* 276:59–15
- Eliasson PE, McMurtrie RE, Pepper DA, Strömrgren M, Linder S, Ågren GI (2005) The response of heterotrophic  $CO_2$  flux to soil warming. *Glob Change Biol* 11:167–181
- Epron D, Nouvellon Y, Rouspard O, Mouvondy W, Mabilalab A, Laurent SA, Joffre R, Jourdan C, Bonfond JM, Berbigier P, Hamel O (2004) Spatial and temporal variations of soil respiration in a Eucalyptus plantation in Congo. *Forest Ecol Manag* 202:149–160
- Fan SM, Goulden ML, Munger JW, Daube BC, Bakwin PS, Wofsy SC, Amthor JS, Fitzjarrald D, Moore KE, Moore TR (1995) Environmental controls on the photosynthesis and respiration of a boreal lichen woodland: a growing season of whole-ecosystem exchange measurements by eddy-correlation. *Oecologia* 102:443–452
- Fang C, Moncrieff JB (2001) The dependence of soil  $CO_2$  efflux on temperature. *Soil Biol Biochem* 33:155–165
- Fang C, Moncrieff JB, Gholz HL, Clark KL (1998) Soil  $CO_2$  efflux and its spatial variation in a Florida slash pine plantation. *Plant Soil* 205:135–146
- Hanson PJ, Edwards NT, Garten CT, Andrews JA (2000) Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogeochemistry* 48:115–146
- Högberg P, Nordgren A, Buchmann N, Taylor AF, Ekblad A, Hogberg MN, Nyberg G, Ottosson-Lofvenius M, Read DJ (2001) Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature* 411:789–792
- Janssens DI, Lankreijer H, Matteucci G, Kowalski AS, Buchannan N, Epron D, Pilegaard K, Kutsch W, Longdoz B, Grinwald T, Montagnani L, Dore S, Rebmann C, Moors EJ, Grelle A, Rannik U, Morgenstern K, Oltchev S, Clement R, Guomundsson J, Minerbi S, Berbigier P, Ibrom A, Moncrieff J, Aubinet M, Bernhofer C, Jensen NO, Vesala T, Granier A, Schulze ED, Lindroth A, Dolman AJ, Jarvis PG, Ceulemans R, Valentini R (2001) Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Glob Change Biol* 7:269–278
- Janssens IA, Pilegaard K (2003) Large seasonal changes in  $Q_{10}$  of soil respiration in a beech forest. *Glob Change Biol* 9:911–918
- Kirschbaum MUF (2006) The temperature dependence of organic-matter decomposition—still a topic of debate. *Soil Biol Biochem* 38:2510–2518
- Kuzyakov Y, Cheng W (2004) Photosynthesis controls of  $CO_2$  efflux from maize rhizosphere. *Plant Soil* 263:85–99
- Langley JA, Johnson NC, Koch GW (2005) Mycorrhizal status influences the rate but not the temperature sensitivity of soil respiration. *Plant Soil* 277:335–344
- Lee MS, Nakane K, Nakatsubo T, Mo Wh, Koizumi H (2002) Effects of rainfall events on soil  $CO_2$  flux in a cool temperate deciduous broad-leaved forest. *Ecol Res* 17:401–409
- Lloyd J, Taylor JA (1994) On the temperature dependence of soil respiration. *Func Ecol* 8:315–323
- Lohila A, Aurela M, Regina K, Laurila T (2003) Soil and total ecosystem respiration in agricultural fields: effect of soil and crop type. *Plant Soil* 251:303–317
- Michelsen A, Andersson M, Jensen M, Kjøller A, Gashew M (2004) Carbon stocks, soil respiration and microbial biomass in fire-prone tropical grassland, woodland and forest ecosystems. *Soil Biol Biochem* 36:1707–1717
- O’Connell KEB, Gower ST, Norman JM (2003) Net ecosystem production of two contrasting boreal black spruce forest communities. *Ecosystems* 6:248–260
- Pangle RE, Seiler JR (2002) Influence of seedling roots, environmental factors and soil characteristics on soil  $CO_2$  efflux rates in a 2-year-old loblolly pine (*Pinus taeda* L.) plantation on the Virginia Piedmont. *Environ Pollut* 116:B85–B96
- Raich JW, Schlesinger WH (1992) The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus* 44B:81–99
- Raich JW, Potter CS (1995) Global patterns of carbon-dioxide emissions from soils. *Global Biogeochem Cy* 9:23–36
- Raich JW, Tufekcioglu A (2000) Vegetation and soil respiration: correlations and controls. *Biogeochemistry* 48:71–90
- Reichstein M, Rey A, Freibauer A, Tenhunen J, Valentini R, Banza J, Casals P, Cheng YF, Grunzweig JM, Irvine J, Joffre R, Law BE, Loustau D, Miglietta F, Oechel W, Ourcival JM, Pereira JS, Peressotti A, Ponti F, Qi Y, Rambal S, Rayment M, Romanya J, Rossi F, Tedeschi V, Tirone G, Xu M, Yakir D (2003) Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices. *Global Biogeochem Cy* 17(4), Art. No. 1104
- Reth S, Göckede M, Falge E (2004)  $CO_2$  efflux from agricultural soils in Eastern Germany—comparison of a closed chamber system with eddy covariance measurements. *Theor Appl Climatol* 85:175–186
- Reth S, Reichstein M, Falge E (2005) The effect of soil water content, soil temperature, soil pH-value and the root mass on soil  $CO_2$  efflux—A modified model. *Plant Soil* 268:21–33
- Rey A, Pegoraro E, Tedeschi V, Parri ID, Jarvis PG, Valentini R (2002) Annual variation in soil respiration and its components in a coppice oak forest in central Italy. *Glob Change Biol* 8:851–866
- Richard TC, Dalla-Betta P, Klopatek CC, Klopatek JM (2004) Controls on soil respiration in semiarid soils. *Soil Biol Biochem* 36:945–951

- Rodeghiero M, Cescatti A (2005) Main determinants of forest soil respiration along an elevation/temperature gradient in the Italian Alps. *Glob Change Biol* 11:1024–1041
- Sánchez ML, Ozores MI, López MJ, Colle R, De Torre B, García MA, Pérez I (2003) Soil CO<sub>2</sub> fluxes beneath barley on the central Spanish plateau. *Agri For Meteo* 118:85–95
- Schimel DS (1995) Terrestrial ecosystem and the carbon-cycle. *Glob Change Biol* 1:77–91
- Schimel DS, Braswell BH, Holland EA, McKeown R, Ojima DS, Painter TH, Parton WJ, Townsend AR (1994) Climatic, edaphic, and biotic controls over storage and turnover of carbon in soils. *Global Biogeochem Cy* 8:279–293
- Sotta ED, Meir P, Malhi Y, Donatobre A, Hodnett M, Grace J (2004) Soil CO<sub>2</sub> efflux in a tropical forest in the central Amazon. *Glob Change Biol* 10:601–617
- Steinmann K, Siegwolf RTW, Saurer M, Körner Ch (2004) Carbon fluxes to the soil in a mature temperate forest assessed by <sup>13</sup>C isotope tracing. *Oecologia* 141:489–501
- Subke J-A, Reichstein M, Tenhunen JD (2003) Explaining Temporal variation in soil CO<sub>2</sub> efflux in a mature spruce forest in Southern Germany. *Soil Biol Biochem* 35:1467–1483
- Tang JW, Dennis DB, Qi Y, Xu LK (2003) Assessing soil CO<sub>2</sub> efflux using continuous measurement of CO<sub>2</sub> profiles in soils with small solid-state sensors. *Agri For Meteo* 118:207–220
- Tang JW, Baldocchi DD (2005) Spatial–temporal variation in soil respiration in an oak–grass savanna ecosystem in California and its partitioning into autotrophic and heterotrophic components. *Biogeochemistry* 73:183–207
- Thierron V, Laudelout H (1996) Contribution of root respiration to total CO<sub>2</sub> efflux from the soil of a deciduous forest. *Can J For Res* 26:1142–1148
- Tufekcioglu A, Raich JW, Isenhardt TM, Schultz RC (2001) Soil respiration within riparian buffers and adjacent crop fields. *Plant Soil* 229:117–124
- Vance ED, Chapin III FS (2001) Substrate limitations to microbial activity in taiga forest floors. *Soil Biol. Biochem* 33:173–188
- Wardle DA (2002) *Communities and Ecosystems, Linking the Above-ground and Belowground Components*. Princeton University Press, Princeton. 392 pp
- Wiseman PE, Seiler JR (2004) Soil CO<sub>2</sub> efflux across four age classes of plantation loblolly pine (*Pinus taeda* L.) on the Virginia Piedmont. *Forest Ecol Manag* 192:297–311