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ORIGINAL ARTICLE

Phenophases alter the soil respiration–temperature relationship in an oak-dominated forest

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Abstract Soil respiration (SR) represents a major component of forest ecosystem respiration and is influenced seasonally by environmental factors such as temperature, soil moisture, root respiration, and litter fall. Changes in these environmental factors correspond with shifts in plant phenology. In this study, we examined the relationship between canopy phenophases (pre-growth, growth, pre-dormancy, and dormancy) and SR sensitivity to changes in soil temperature (T_S). SR was measured 53 times over 550 days within an oak forest in northwest Ohio, USA. Annual estimates of SR were calculated with a Q_{10} model based on T_S on a phenological (PT), or annual timescale (AT), or T_S and soil volumetric water content (VWC) on a phenological (PTM) or annual (ATM) timescale. We found significant ($p<0.01$) difference in apparent Q_{10} from year 2004 (1.23) and year 2005 (2.76) during the growth phenophase. Accounting for moisture-sensitivity increased model performance compared to temperature-only models: the error was −17% for the ATM model and −6% for the PTM model. The annual models consistently underestimated SR in summer and overestimated it in winter. These biases were reduced by delineating SR by tree phenophases and accounting for variation in soil moisture. Even though the bias of annual models in winter SR was small in absolute scale, the relative error was about 91%, and may thus have significant implications for regional and continental C balance estimates.

Keywords Oak openings · Oak phenology · Soil respiration · Soil temperature · Temperature sensitivity (Q_{10})

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Introduction

Soil respiration (SR) is a major component of the global carbon (C) cycle and can represent 50–75% of terrestrial ecosystem respiration (Schlesinger 1997; Hanson et al. 2000). Small changes in SR could greatly affect the amount of C added to the atmosphere because the global soil C pool contains twice as much C as the atmospheric pool (Schimel et al. 1990; Jenkinson et al. 1991). However, SR is a large source of uncertainty in terrestrial C budgets due to a lack of understanding of the environmental factors regulating SR on seasonal, annual, or interannual timescales. For example, Hanson et al. (2004) compared 13 ecosystem process models and found that the r^2 of measured versus modeled SR ranged from 0.67 to 0.04 between these models. One of the significant contributions to the high inter-model SR variation (i.e., low confidence in estimating SR) was related to the phenological changes of species in an ecosystem. Growing season length has a large influence on ecosystem C flux (Goulden et al. 1996; Chen et al. 1999), and thus influences plant impact on the annual SR budget (Högberg et al. 2001). Since the variability of inter-annual start of the growing season is increasing and occurring sooner due to climate change (Menzel and Fabian 1999; Schwartz et al. 2006), the timing when plants have the most influence on

SR would follow, and thus may have a profound effect on inter-annual SR budgets.

Efforts to scale up SR from the plot level to the stand level commonly use a constant empirical temperature-based regression (Raich et al. 1991; Potter et al. 1993; Schimel et al. 2000). The limitations of these models are generally recognized (Qi et al. 2002; Gu et al. 2004; Hanson et al. 2004), as other environmental factors also influence SR. For example, soil moisture may exercise a dominate control over SR in some ecosystems (Davidson et al. 1998; Ma et al. 2005, Concilio et al. 2005). The availability of C substrate for heterotrophic metabolism may dominate SR in other ecosystems (Kelting et al. 1998; Högberg et al. 2001; Janssens et al. 2001; Vance and Chapin 2001; Campbell et al. 2004). Even though soil temperature (T_S) frequently explains less than 50% of the growing season variation in SR in forest soils (Toland and Zak 1994; Morén and Lindroth 2000; Euskirchen et al. 2003; Curiel-Yuste et al. 2004), the simplicity of the temperature-based SR models, and availability of T_S data for different ecosystems, make T_S the first choice for scaling up estimates of SR.

The dynamics of environmental factors like T_S and soil moisture that mediate SR are coupled to seasonal climatic patterns, and this relationship has fueled the development of temperature response models with dynamic Q_{10} (Janssens and Pilegaard 2003; Curiel-Yuste et al. 2004; Hanson et al. 2004). On a seasonal timescale, changes in temperature often coincide with changes in water availability, plant activity, and the amount of C input into the soil across temperate regions. The degree to which these factors mediate SR can vary seasonally. For example, water would most likely limit summertime SR when T_S is high (Ma et al. 2005) or T_S could be the rate-limiting factor in the winter when temperatures are their lowest (Curiel-Yuste et al. 2004). However, SR can increase even with declining T_S in the autumn due to an influx of labile C from fallen leaves and decomposing fine roots (Davidson et al. 1998; Lee et al. 2003). The possibility for these environmental factors to confound with the apparent temperature sensitivity (Davidson et al. 1998; Gu et al. 2004) increases as the temporal and spatial extent of observations increase.

We hypothesized that the limiting environmental factors mediating SR can be delineated using changes in plant phenology. Plant phenophases often correspond with changes in T_S and soil moisture, and can indicate plant inputs of C to the soil. For example, during the growing season, SR rates strongly reflect plant activity and the availability of C allocated belowground (Högberg et al. 2001), whereas during the winter, T_S would likely limit SR regardless of C availability. We hypothesized those seasonal changes in plant phenophases will result in a shift in the SR–T_S relationship due to the relative changes in the importance of other limiting environmental factors that mediate SR. Therefore, we expected T_S to have more influence on SR during plant dormancy than during the growing season. To test this hypothesis, we measured SR rates, T_S, and soil moisture throughout the year to capture differences in SR responding to phenological changes in an oak-dominated forest. Our specific objectives were to: (1) account for the seasonal environmental changes in the regulation in SR; and (2) compare estimates of annual SR budget derived from a Q_{10} model with fixed parameters and variable parameters based on oak phenophases.

Materials and methods

Study site

Our study site was located in an oak (*Quercus* spp.)-dominated forest within the Oak Openings Region located in northwest Ohio, USA (41°33'17"N, 8°50'36"W). Oak Openings supports a mosaic of oak savanna, oak woodland, and wet prairie communities that developed on a series of post-glacial beach ridges and swales (Moseley 1928; Brewer and Vankat 2004). This 15-km^2 forested area is within the Oak Openings Preserve where parts of this ecosystem are subjected to prescribed burns. The topography is flat, and the forest is dominated by *Q. rubra* (red oak; 32%), *Q. alba* (white oak; 27%), *Q. velutina* (black oak; 14%), *Acer rubra* (red maple; 20%) in the understory with the remaining 7% *Prunus serotina* (black cherry) and *Sassafras albidum* (sassafras). There are two distinct age classes in the forest, the majority of trees are between 40 and 50 years old and a minor component ~80 years. The younger cohort represents regrowth after fire suppression from this historically oak savanna area. The basal area of this stand is 26 m^2 ha^{-1}. The sandy soils are mixed, mesic Spodic Udipsamments. Soil C content has 28.1 g C kg^{-1} (0–20 cm) and the soil N has 1.6 g N kg^{-1} (0–20 cm), with about 82% of both C and N in the top 10 cm. The soil is udic (i.e. moist) even during periods of low precipitation, because a perched (~2 m) water table is prevalent throughout this area.

Within the oak forest landscape, 13 plots were arranged over a 100-ha area using the USDA Forest Service Forest Inventory and Analysis plot layout design, http://www.fia.fs.fed.us/library/). Each plot contained four circular 154-m^2 subplots 36.5 m apart. These plots were used to quantify stand phenology, stand density, tree species composition, and soil C and N. SR was measured on 8 of the 13 plots. Each soil respiration plot contained six plastic collars (10×5 cm) that were arranged on the circumference of a 10-m diameter circular plot. Soil collars were spaced 5 m apart. Thirty-minute mean T_S was recorded with HOBO temperature data loggers (Onset Computer, Mass.), installed

next to four of the SR collars on each soil respiration plot. Precipitation above the canopy and soil volumetric water content (VWC; 0–30 cm) were measured in the center of the study site using a tipping bucket rain gauge (TE525MM; Campbell Scientific, Logan, Utah) and a water content reflectometer (CS616; Campbell Scientific).

Phenological phases

The phenology was recorded on four major phases (i.e., pre-growth, growth, pre-dormancy, and dormancy) of *Quercus* spp. based on visual ground observations of the canopy (Table 1). Observations were made at least every 4 days around changes in phenophases. The start of the pre-growth (i.e., spring) phase is defined by *Quercus* spp. flowering and bud break, and is also considered a period of high root production and the start of acorn production. The start of the growth phase (i.e., summer) is defined by 95% leaf flush for *Quercus*. The start of pre-dormancy phase (i.e., autumn) was visually determined by the start of leaf discoloration of the *Quercus* spp., but leaves were still on the branches. The start of dormancy phenophase (i.e., winter) was defined by the loss of 95% loss of foliage from the *Quercus* spp. Oak phenology was used as a metric of total ecosystem phenophases because oaks are the dominant genus and represent 73% of tree biomass and canopy cover at the study site.

Field measurements

SR was measured with a EGM-4 (PP Systems, Hertfordshire, UK) and LI-6400 (Licor, Lincoln, Neb.) portable infrared gas analyzers with a matching soil respiration chambers (SRC-1 and 6400-09, respectively). The EGM-4 was primarily used in 2004 and the LI-6400 was used in 2005. The two soil respiration systems were compared over several sampling dates and provided similar estimates of SR, with no detectable systematic differences (p=0.85). SR was measured 53 times from 12 May 2004 to 7 November 2005 (Table 2). The measurements were made at least every 2 weeks from April to October and every 4 weeks from November to March. The less frequent SR measurement in the pre-dormancy and dormancy phase was due to frequent adverse weather conditions. Respiration was not measured when it was raining and measurements were postponed 48 h after a major rain event (15 mm day^{-1}) to minimize the effect of extreme precipitation on SR. Rainfall over 15 mm day^{-1} was infrequent and represented only 5% of all precipitation events in 2004 and 11% of all precipitation events in 2005. SR measurements were also not taken if the collars contained ice or were filled with more than 2.5 cm of snow, because this altered the collar area and the diffusion of gases leading to unrealistic SR rates. Fallen leaf litter was allowed to remain where it fell (i.e., in or out of the soil collars). During measurements, T_S was recorded at a depth of 5 cm within 15 cm of the collar center. Soil VWC was measured within 30 cm of the collar center to a depth of 15 cm using a time domain reflectometer unit (TDR100; Model 6050XI Soil Moisture Equipment, Santa Babbra, Calif.; and Turkey TDR-Kit 2004; Prenart Equipment APS, Fredericksberg, Denmark). Within a sampling time and plot, readings of SR, T_S and VWC were averaged across the six SR collars.

Data analysis

The dependence of SR (mg C m^{-2} h^{-1}) on T_S (°C) was estimated with a first-order exponential model:

$$SR = R_{ref} * e((ln(Q_{10})/10) * T_S) \quad (1)$$

where SR is measured soil respiration rate (mg C m^{-2} h^{-1}), R_{ref} is base soil respiration (mg C m^{-2} h^{-1}), normalized to 0°C, Q_{10} is temperature sensitivity of SR (i.e., change in SR per increase in T_S by 10°C), and T_S is the measured soil temperature (°C) at 5 cm depth. The R_{ref} and Q_{10} were estimated with non-linear least squares regression (PROC NLIN, SAS) for each of the four phenological phases (i.e., dormancy, pre-growth, growth, and pre-dormancy; hereafter referred to as PT model) and annually (AT model) from 10 May 2004 to 10 November 2005. The residuals from Eq. 1 were regressed against soil VWC because incorporating VWC into the non-linear analysis produced unreal-

Table 1 Day of the year for the major phenological events for *Quercus* spp.,the dominant tree genera at Oak Openings Preserve in northwest Ohio, USA. Dates are approximate and based on visual observation of the phenological event

Year	Phenophase	Day of year	Starting event	*Quercus* spp.
2004	Pre-growth	97–130	Flowering and bud swelling	6 April
2004	Growth	131–277	95% Leaf flush	10 May
2004	Pre-dormancy	278–315	Leaf discoloration	4 October
2004	Dormancy	316–366	95% Leaf drop	10 November
2005	Dormancy	1–102	Continuation	
2005	Pre-growth	103–150	Flowering and bud swelling	13 April
2005	Growth	151–290	95% Leaf flush	31 May
2005	Pre-dormancy	291–314	Leaf discoloration	17 October
2005	Dormancy	315–365	95% Leaf drop	10 November

Table 2 The apparent temperature sensetivity (Q_{10}) of soil respiration (SR) and the basal SR at 0°C estimates calculated for the four phenophase models and the annual model.Correlation coefficient (r^2) and p-value of the non-linear regression, mean SR and mean, range of soil temperature (T_s),mean soil volume water content (VWC), and mean daily precipitation are listed. Each plot represents six measurements. Values in parentheses represent standard error of the mean (n=number of sampling times)

Variable/year	Pre-growth	Growth		Pre-dormancy		Dormancy	Entire period
	2005	2004	2005	2004	2005	2004–2005	
Time period (days)	48	147	140	38	24	153	550
No. of plots	32	105	83	25	20	31	296
No. of sampling times	5	15	19	4	5	5	53
Apparent Q_{10}	2.00 (0.17)	1.23 (0.12)	2.76 (1.09)	8.12 (3.91)	5.54 (2.76)	2.97 (0.32)	2.97 (0.10)
R_{ref} (mg C m^{-2} h^{-1})	46.1 (4.8)	197.4 (35.4)	47.7 (2.8)	9.9 (5.1)	19.5 (10.5)	19.5 (2.2)	38.5 (2.5)
r^2	0.89	0.81	0.84	0.77	0.76	0.79	0.81
p-value	<0.01	<0.01	<1.01	<0.01	<0.01	<0.01	<0.01
Mean SR (mg C m^{-2} h^{-1})	99.7 (19.8)	285.7 (35.6)	303.7 (37.9)	83.2 (26.0)	116.3 (31.4)	40.3 (14.4)	212.1 (22.0)
Mean T_s (°C)	3.4 (1.5)	18.0 (0.5)	17.8 (0.7)	9.9 (0.8)	10.3 (0.5)	5.6 (2.1)	14.4 (0.8)
Range TS (°C)	4.7–17.6	13.0–22.6	10.6–24.8	7.8–11.9	7.7–12.4	0.1–14.7	0.4–24.8
Mean VWC (%)	19.4	18.4	17.7	18.8	17.6	19.6	18.6
Mean precip.(mm day^{-1})	1.0	2.4	2.0	1.6	0.8	1.9	1.9

istic results. The product from this analysis was incorporated into Eq. 1 to form an equation that takes into account both temperature and soil moisture:

$$SR = R_{ref} * e((ln(Q_{10})/10) * T_S) + (\theta * m + b) \quad (2)$$

where θ is soil VWC (%), m is the slope of the residuals versus VWC relationship, and b is the intercept. Eq. 2 was applied as a phenophase modeled (PTM model) and annual modeled (ATM model) timescale. We used Eq. 2 only for the growth and per-dormancy periods because the residuals of Eq. 1 were significant (p<0.05). For the growth phase, m was 60.1±6.1 (mean±SE) in 2004 and 59.6±10.7 in 2005, whereas b was −817.4±83.0 and −787.5±140.9 for 2004 and 2005, respectively. During the pre-dormancy phase, m was 23.4±5.1 in 2004 and −45.2±21.7 in 2005, whereas b was −319.8±70.6 and 585.0±280.9 for 2004 and 2005, respectively. We did not apply Eq. 2 to the dormancy and pre-growth phenophases since the residuals of Eq. 1 exhibited no significant relationship with VWC during these periods (p>0.10). The temperature sensitivity of SR was also expressed with an Arrhenius expression (data not presented). However, the results from this analysis produced similar trends and results to Eq. 1 and Eq. 2. Continuous estimates of SR from the 2004 growth phase to 2005 pre-dormancy phase were estimated using Eq. 1 and Eq. 2 and the continuous T_S collected at each of the soil respiration plots and VWC data at the center of the stand (Table 2). While using an independent data set seemed the best method to evaluate the models against measured SR, we found setting aside half the observations for an independent data set produced similar parameters (p>0.50), but errors increased. Therefore, the performance of each of the models was evaluated with the same observations used to parameterize the models using a linear regression.

Results

Variation in phenophases

The timing and duration of phenophases in 2004 and 2005 were different. The pre-growth phase started 6 days later in 2005 than 2004 and lasted 35 days in 2004, but 48 days in 2005. Bud break started when mean daily T_S reached 10°C, but continued even when T_S fell below this threshold (Fig. 1). The growth phase started 20 days later in 2005 than 2004, but was only 7 days shorter in 2005 when compared to 2004 (140 vs 147 days; Table 2). The observed start in the growth phenophase corresponded exactly with T_S exceeding 15°C, which occurred on day 130 in 2004, and day 150 in 2005 (Fig. 1). The start of the pre-dormancy phase was 13 days later in 2005 when compared to 2004 and corresponded with declining T_S below 15°C (Fig. 1). The length of the pre-dormancy was shorter in 2005 at 24 days when compared to the 38 days in 2005 (Table 2), but the start of the dormancy was similar between the two years (Table 1).

Soil respiration, temperature, and water content

The rate and variation in SR increased with increases in T_S (Fig. 2). The T_S recorded during the dormancy phase generally ranged from 0°C to 10°C, while pre-growth or pre-dormancy T_S ranged from 5°C to 15°C, and the growth phenophase T_S was over 15°C. VWC throughout the entire

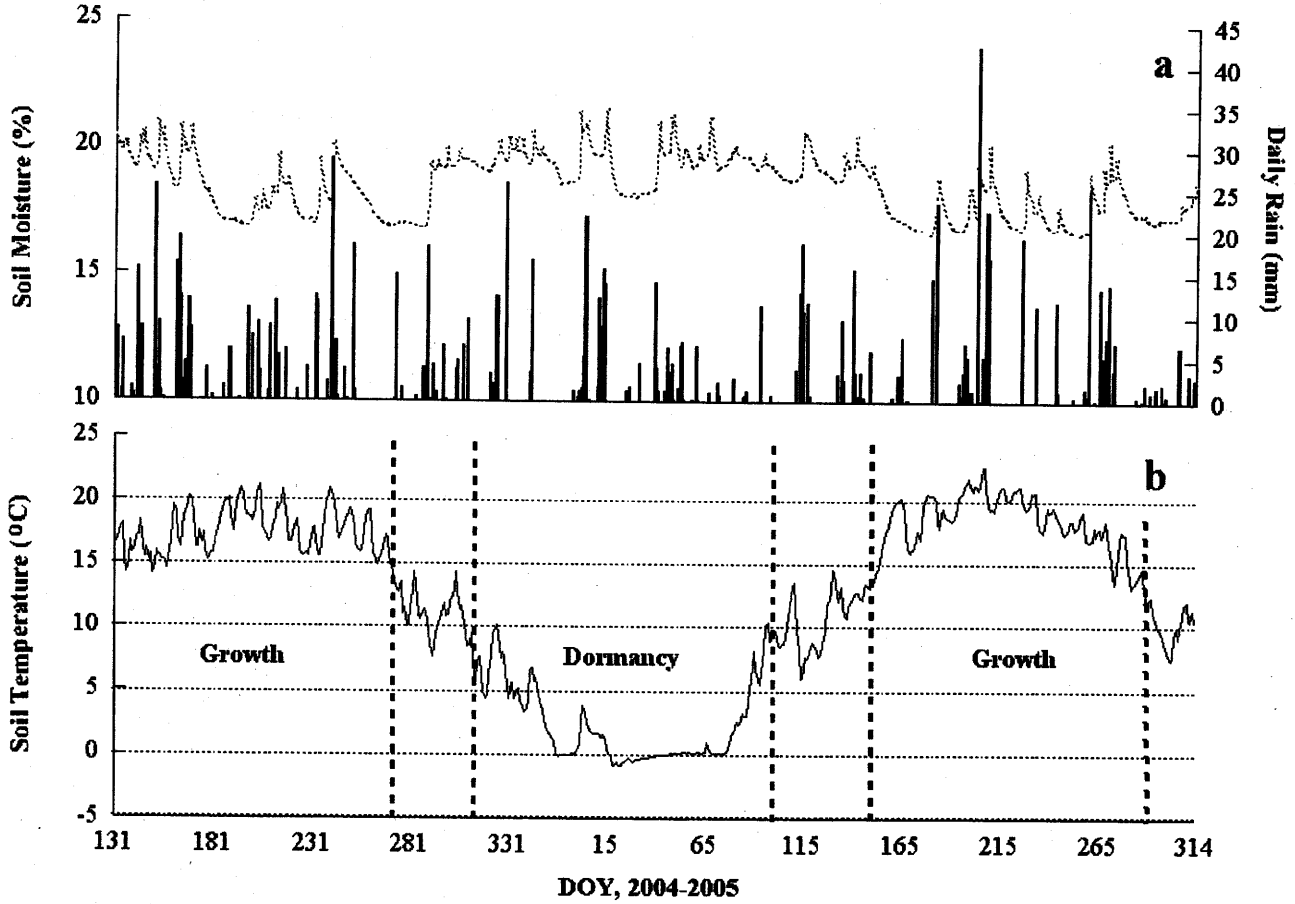

Fig. 1 **a** Seasonal variation in soil volume moisture content (*line*) and daily sums of rain fall (*bars*). **b** Seasonal variation in mean daily soil temperature 5 cm in the mineral soil. *Vertical dashed lines* distinguish phenophases

study period was from 16.7% to field capacity at 22.3%. VWC was the highest and changed the least during the dormancy and pre-growth phase, and it was the lowest and varied the most during the growth phenophase (Table 2). Soil was significantly drier ($p<0.01$) during the 2005 growth phenophase, with mean VWC at 17.7%, compared to 18.4% in 2004 (Table 2). The precipitation was 280 mm for growing phase in 2005 and 353 mm in 2004.

The sensitivity of SR to T_S varied significantly between the different phenological phases. During the 2004 growth phase, SR was insensitive to changes in T_S evidenced by a Q_{10} of 1.23. However, during the 2005 growth phase, the Q_{10} was 2.76 (Table 2). There were no significant differences in apparent Q_{10} during the pre-dormancy phase between the 2 years, because of the large uncertainty in the Q_{10} estimates (Table 2). Overall, the annual Q_{10} for all SR and T_S, regardless of phenophase, was 2.97, which was similar to that during dormancy (Table 2). The base SR at 0°C (R_{ref}) of AT model was 4 times higher in 2004 than in 2005 (197 vs 48 mg C m^{-2} h^{-1}; $p<0.01$). R_{ref} during the pre-dormancy phase was similar between 2004 and 2005

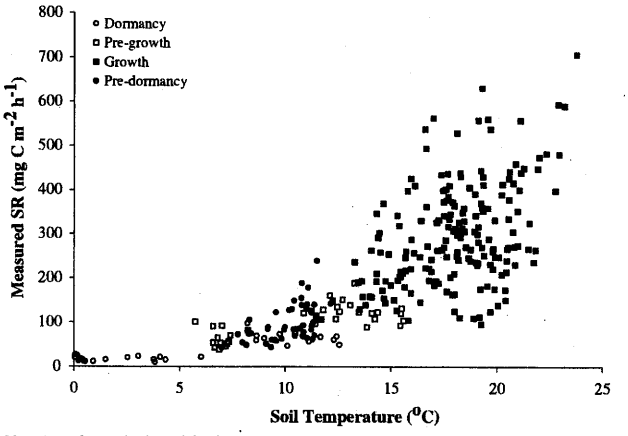

Fig. 2 The relationship between soil respiration and soil temperature during four oak phenophases; post-dormancy, growth, pre-dormancy, and dormancy. Post-dormancy begins at oak flowering, the growth phase begins at 95% leaf flush, pre-dormancy is hallmarked by leaf discoloration, and dormancy is after 95% leaf drop. Each *data marker* represents soil respiration rate from a plot averaged from six measurements scattered across a 100-ha area of the Oak Openings region

(Table 2). The mean R_{ref} for the entire study period was 39 mg C m^{-2} h^{-1} (Table 2).

The fit of modeled SR with measured values increased significantly during the growth and pre-dormancy for both years when the effects of moisture were incorporated into the model Eq. (2). Variation in VWC appeared to have little influence on SR during the dormancy and pre-growth phases for both years. While the use of Eq. 2 did not significantly increase the correlation coefficient (r^2) of the models, it did decrease the model bias compared to Eq. 1 (Fig. 3). The r^2 between the phenological timescale Eq. 1 and Eq. 2 and measured SR were 0.82 and 0.83, respectively. SR estimated from Eq. 1 was generally 23% lower than measured SR and 6% lower from SR estimated from Eq. 2 (Fig. 3). When compared to measured SR, the products from Eq. 1 underestimated at high SR and overestimated at low SR, a bias which was reduced in Eq. 2 (Fig. 3).

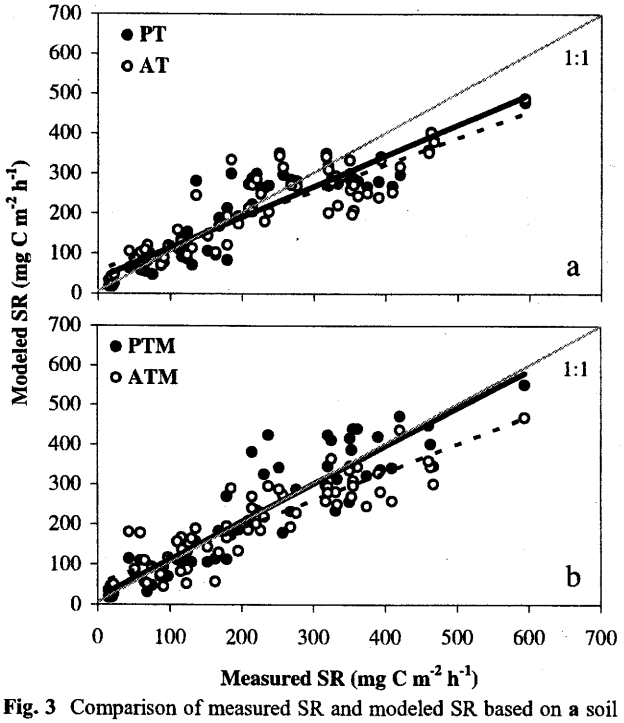

Fig. 3 Comparison of measured SR and modeled SR based on **a** soil temperature for the phenology (PT) and annual (AT) models and **b** soil temperature and moisture content for phenology (PTM) and annual (ATM) models. **a** *Solid line* indicates the significant ($p<0.01$, $r^2=0.82$) fitted function where modeled SR (PT)=0.77 × measured SR+37.3. *Dashed line* indicates the significant ($p<0.01$, $r^2=0.77$) where modeled SR (AT)=0.66 × measured flux+57.5. **b** *Solid line* indicates the significant ($p<0.01$, $r^2=0.83$) fitted function where model SR (PTM)= 0.94 × measured flux+17.6. *Dashed line* indicates the significant ($p<0.01$, $r^2=0.80$) fitted function where modeled SR (ATM)=0.70 × measured flux+50.2. *Gray line* indicates a perfect fit with a 1:1 ratio

Comparing phenological and annual timescales

For both years and both temperature-only and moisture-inclusive models (Eqs. 1 and 2, respectively), those partitioned at phenological timescale explained more variation in SR than annual models (Figs. 3, 4). For example, the modeled/measured SR ratio was 0.70 for the ATM model, but 0.94 for the PTM model. This improvement in model performance occurred primarily during the growth phenophase where the modeled / measured SR ratio increased by 46% and 23% for both the phenological and annual models, respectively (Fig. 4). Overall, using an annual timescale often underestimated SR during the growth phase (~145 days) and overestimated during the other phenophases (~220 days), whereas the SR model estimates were more consistent with measurements on phenology timescales (Fig. 3). The cumulative SR on annual timescale was 7% and 19% lower during growth phase for 2004 and 2005, respectively, using Eq. 2 than based on phenological timescales. The cumulative SR during the dormancy phase was 97% higher (197 vs 100 g m^{-2} $season^{-1}$) with the AT than with the PT models (Fig. 4). Likewise, during the pre-growth phase, cumulative SR was 23% higher on AT (148 g C m^{-2} $season^{-1}$) than the PT model (114 g C m^{-2}). During the pre-dormancy phase, the ATM model overestimated SR by 35% in 2004, but underestimated by 20% in 2005 compared to the PTM model. Overall, annual soil C budget estimated with ATM model was 1,383 (g C m^{-2} y^{-1}), which is 6% higher than with PTM model (1,294 g C m^{-2} y^{-1}) from 11 November 2004 to 12 November 2005.

Discussion

VWC and T_S explained 76-89% of variation in observed SR indicating strong environmental control on SR in this forest ecosystem. Although year 2005 was drier than 2004, the increase in model fit upon incorporating VWC increased more in 2004 than in 2005, which we attribute to more pronounced temperature dynamics in 2005 (Fig. 1). Nevertheless, our results are consistent with the observation of Davidson et al. (1998) who emphasized the confounding influences of T_S and VWC on SR. In addition, our results suggested that changes in VWC could influence the apparent temperature sensitivity of SR. For example, the apparent Q_{10} of SR during the growth phase was less sensitive to changes in T_S during the wetter 2004 (Q_{10}=1.23) when compared to the drier 2005 (Q_{10}=2.76; Fig. 1). Thus, SR was less strongly controlled by the 4% higher VWC in 2004 compared to the VWC of 2005 (Fig. 1). This result appeared to conflict with Qi et al. (2002) who reported that the apparent Q_{10} of soil increased

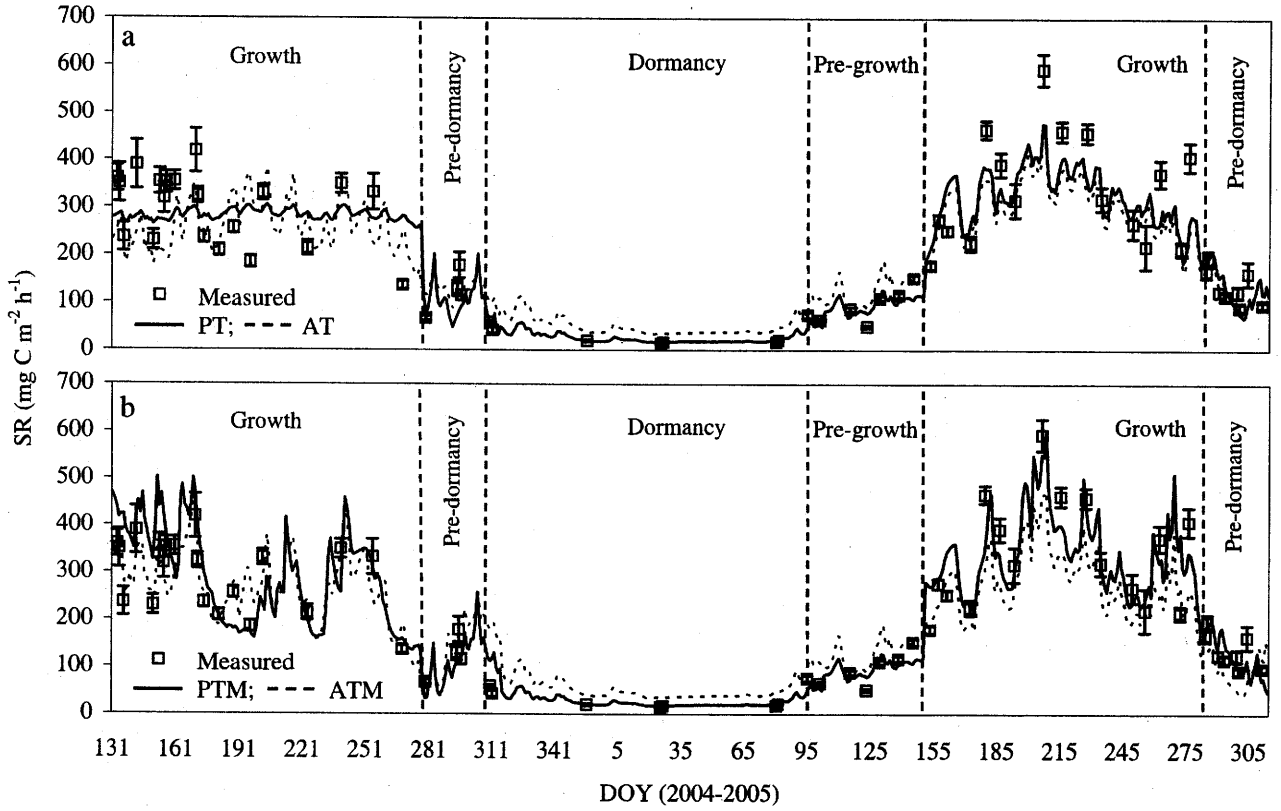

Fig. 4 **a** Seasonal and annual variation in measured soil respiration rates (*squares*), estimated flux from phenological changes in the Q_{10} and R_{ref} parameters (*solid line*) and estimated flux from a constant Q_{10} and R_{ref} parameters (*dashed line*) based on soil temperature. **b** Seasonal and annual variation in measured soil respiration rates (*squares*), estimated flux from phenological changes in the Q_{10} and R_{ref} parameters (*solid line*) and estimated flux from a constant Q_{10} and R_{ref} parameters (*dashed line*) based on soil temperature and soil water content

with soil moisture (VWC=10 to 24%) in a high elevation young pine forest. However, as mentioned above, in the current study the range of T_S was broader in the drier 2005 than wetter 2004, whereas the range of VWC differed little (Fig. 1). The relative constancy of T_S in 2004 and relatively small VWC range compared to that reported by Qi et al. (2002) are most plausible reasons for the observed difference in mechanistic regulation. These results show that moisture-limitation does not depend only on water availability, but can be modified by the dynamics of other parameters, in this case the dynamics of T_S. Although much more complex situations could be speculated, including pressure pumping of CO_2-rich air from soil pore space (Takle et al. 2003), rain-induced short-term SR pulses (Lee et al. 2004), or O_2 limitation to root respiration due to soil pores filling with water (Davidson et al. 1998), our current data do not suggest that any of them affected the measurements nor do we have the data to test these possibilities.

Our results support the hypothesis that changes in phenophases can alter the apparent Q_{10} of SR. The apparent Q_{10} varied according to phenophase and was highest during pre-dormancy and dormancy and lowest during pre-growth and growth phenophases (Table 2). This pattern has been commonly observed (Janssens et al. 2001; Curiel-Yuste et al. 2004), and is attributed to factors other than T_S being rate-limiting during non-dormant seasons, and may include other environmental factors such as soil moisture, its proxy air humidity (Ekblad et al. 2005), or biotic factors affecting C availability for auto- and heterotrophic respiration (Högberg et al. 2001; Janssens et al. 2001; Campbell et al. 2004). These additional factors can easily confound with the effects of temperature on SR (Davidson et al. 1998). During dormancy, however, when root respiration is minimal (Lee et al. 2003) and the allocation of C belowground is minimal, microbial activity is suppressed more by temperature than anything else (Zogg et al. 1997). The change in the environmental factor most mediating SR can explain the high sensitivity of SR to T_S observed during the pre-dormancy and dormancy phenophase. It is possible that higher T_S may increase the Q_{10} of soil by increasing the availability of C substrate in soil organic matter (Zogg et al. 1997). Likewise, an increase in the availability of C in

soil often causes an increase in respiration independent of temperature (Vance and Chapin 2001, Gu et al. 2004; Brooks et al. 2004). At 15°C T_S, SR was higher (120–400 mg C m^{-2} h^{-1}) during the growth than the pre-growth phase (95–150 mg C m^{-2} h^{-1}), and could be related to greater belowground allocation of newly assimilated C during the growth than pre-growth phase (Davidson et al. 1998; Vance and Chapin 2001; Fig. 2). Large inputs of easily decomposable carbon in leaf litter during the pre-dormancy phenophase are also likely to be the cause of the high apparent Q_{10} values in this study (Table 2). Even though the average T_S is lower during pre-dormancy than during growth phenophase, the decomposition of the fresh input of C can rapidly respond to brief warm periods and result in high apparent Q_{10}.

Alternatively, the apparent differences in the Q_{10} of SR may be caused by temperature thresholds of different microbial communities, which has been hypothesized to occur between 0 and 5°C (Davidson et al. 1998; Janssens et al. 2001; Law et al. 1999). Our results showed that the apparent Q_{10} of SR was the highest during the transition phenophases when T_S was from 5 to 15°C, and much lower when T_S was either greater than 15°C or lower than 5°C (Fig. 2). The relative impact of temperature and phenophase on SR is difficult to determine as changes in phenophases are induced by temperature (Menzel and Fabian 1999). This study showed that the start of the pre-growth phase (i.e., oak bud break) in 2004 and 2005 began when T_S exceeded 10°C. The start of the growth phase (i.e., 95% leaf flush) occurred when T_S reached 15°C (Fig. 2). However, the rapid changes in SR during the pre-growth and pre-dormancy phenophases suggest that the contribution of autotrophic respiration and/or the plant-derived newly assimilated C were more important for the seasonal dynamics of SR than the hypothetical differential activation of different microbial groups. However, both of these scenarios refer to a similar phenomenon; in the current study, it is the shifts in plant activity as identified by oak phenophases, whereas in the studies of Davidson et al. (1998), Janssens et al. (2001) and Law et al. (1999) cited above it is the shifts in microbial activity (i.e., microbial phenophases).

Our results indicated that, compared to the annual model, phenophase-specific models of SR provided less biased estimates by accounting for driving variables that were not explicitly in the model. The PTM model had an average bias of −6% whereas the ATM model underestimated by 30% (Fig. 3). The PT and AT models performed poorer (−33% and −44%, respectively) than the PTM and ATM models. The tendency for simple regression models to underestimate long-term SR has been discussed in more detail by Hanson et al. (2004) and Del Grosso et al. (2005). In contrast to the annual pattern, the model bias was minimal when only growth phase was analyzed, and the ATM and PTM models explained similar amount of variation. Based on the model r^2 the relationships between modeled and observed SR during different phenophases, we noticed that the error of annual models (both ATM and PTM) was greatest during the pre-growth and pre-dormancy phases (Fig. 4). We attribute this to the drastic biological changes that occur during these periods, as they affect SR through belowground C allocation, root respiration and litter fall, while the concomitant changes in temperature may be very small. The lower bias of PTM model indicates that by partitioning the model for individual phenophases indirectly accounts for the biological source of variation, even though model error remains greatest during the transition periods when these sources dominate.

Our results also demonstrated that scaling SR from short-term measurements to an annual scale is difficult and requires detailed understanding of the controlling factors at the particular ecosystem. For example, our models are unable to capture short-term pulses in SR that might occur during and shortly after precipitation which results in an underestimation of the annual budget (Hanson et al. 2003). The mechanisms of regulation changed significantly between different seasons and winter SR (41% of the entire year) were particularly easy to bias. The AT model overestimated winter SR by 91%, whereas the phenophase-specific parameterization of the PT model resulted only in 1% overestimation. The annual SR budget using the AT model resulted in a 6% higher cumulative SR than the PT model. These results demonstrated the need to measure SR throughout the year, and not just during the growing season, and across a wide range of temperatures when scaling SR up to an annual budget.

Conclusions

There is mounting evidence to suggest that climate change is increasing the variability of the start and the duration of the growth phenophase (Menzel and Fabian 1999; Wolfe et al. 2005; Schwartz et al. 2006). Even within a 2-year period of this study, we observed a 20-day difference in the start of the growth phase and a 7-day difference in its duration. Our results indicated that using phenology to partition seasonal time periods of similar conditions helped to significantly reduce bias in SR estimation. The phenophase differences in the environmental regulation of SR also had implications for annual SR estimates; in this case, the traditional annual model overestimated annual SR by about 6%, mostly because of overestimating winter SR by 91%. We reason that incorporating phenology into SR models indirectly accounted for changes in environmental and/or biological

factors that were not explicitly defined in the model. Ideally, though, the component fluxes should be modeled independently, or at least grouped according to time windows and environmental conditions when common regulatory mechanisms, like phenology, can be applied.

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