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Contrasting responses to drought of forest floor CO_2 efflux in a Loblolly pine plantation and a nearby Oak-Hickory forest

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Abstract

Forest floor CO_2 efflux (F_{ff}) depends on vegetation type, climate, and soil physical properties. We assessed the effects of biological factors on F_{ff} by comparing a maturing pine plantation (PP) and a nearby mature Oak-Hickory-type hardwood forest (HW). F_{ff} was measured continuously with soil chambers connected to an IRGA during 2001–2002. At both sites, F_{ff} depended on soil temperature at 5 cm (T_5) when soil was moist (soil moisture, $\theta > 0.20\,m^3\,m^{-3}$), and on both T_5 and θ when soil was drier. A model (F_{ff} (T_5, θ)) explained $\geqslant$92% of the variation in the daily mean F_{ff} at both sites. Higher radiation reaching the ground during the leafless period, and a thinner litter layer because of faster decomposition, probably caused higher soil temperature at HW compared with PP. The annual F_{ff} was estimated at 1330 and 1464 $g\,C\,m^{-2}\,yr^{-1}$ for a year with mild drought (2001) at PP and HW, respectively, and 1231 and 1557 $g\,C\,m^{-2}\,yr^{-1}$ for a year with severe drought (2002). In the wetter year, higher soil temperature and moisture at HW compared with PP compensated for the negative effect on F_{ff} of the response to these variables resulting in similar annual F_{ff} at both stands. In the drier year, however, the response to soil temperature and moisture was more similar at the two stands causing the difference in the state variables to impel a higher F_{ff} at HW. A simple mass balance indicated that in the wetter year, C in the litter–soil system was at steady state at HW, and was accruing at PP. However, HW was probably losing C from the mineral soil during the severe drought year of 2002, while PP was accumulating C at a lower rate because of a loss of C from the litter layer. Such contrasting behavior of two forest types in close proximity might frustrate attempts to estimate regional carbon (C) fluxes and net C exchange.

Keywords: belowground carbon allocation, chamber, conifer, hardwood, IRGA, litterfall, *Pinus taeda* L., *Quercus* ssp., soil respiration, temperate

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Introduction

The importance of soils in global carbon (C) accounting requires that soil C fluxes and stocks be accurately quantified across ecosystems and climates (Raich & Nadelhoffer, 1989; Raich & Schlesinger, 1992; Liski *et al.*, 2003; Reichstein *et al.*, 2003). At the ecosystem level, net ecosystem exchange (NEE) of carbon (C) is defined as the difference between gross primary production (GPP), the amount of C assimilated in photosynthesis, and ecosystem respiration (R_E), the amount of C re-emitted to the atmosphere from autotrophic and heterotrophic respiration. R_E utilizes a large proportion of GPP, with an average ratio for R_E/GPP of 0.82 for temperate coniferous forests and 0.77 for temperate broad-leaved deciduous forests (FluxNet sites; Falge *et al.*, 2002). Forest floor CO_2 efflux (F_{ff}), in turn, represents a large proportion of R_E, with an average F_{ff}/R_E ratio of 0.69 (EuroFlux sites; Janssens *et al.*, 2001).

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Consequently, accurate predictions of NEE responses to variation in climate depend on understanding and quantifying the responses of F_{ff} to climatic variables in different forest types.

Climate, net primary production (NPP), and F_{ff} are linked through the closely coupled C and nutrient cycles (Raich & Schlesinger, 1992). In most cases, warmer and wetter climates support higher productivity and, thus, higher litterfall and absolute amount of belowground C allocation. At the global scale, F_{ff} has been related to NPP and temperature (Raich & Schlesinger, 1992). However, other studies at large geographical scales have found that F_{ff} is unrelated to temperature (Janssens *et al.*, 2001; Reichstein *et al.*, 2003). In these studies F_{ff} was related to precipitation and productivity indices, such as leaf area index (LAI) and leaf production. The prevalence of studies that find a productivity measure to explain a large proportion of the variation in F_{ff} is not surprising. According to a simple mass balance, the sum of litterfall and belowground allocation equals F_{ff} if changes in soil and litter C stocks, and C transported off site are assumed negligible relative to the other fluxes (Raich & Nadelhoffer, 1989; Giardina & Ryan, 2002). A recent study by Davidson *et al.* (2002) suggested that, when averaged across biomes and stands of different ages, the annual release of C in F_{ff} is roughly four times the amount of C in the annual aboveground litterfall.

Forest floor CO_2 efflux reflects both the production of CO_2 and its transport to the surface of the litter layer, although integrated over long periods F_{ff} reflects primarily the production of CO_2 in respiration. The production of CO_2 is comprised of root and fungal respiration, and microbial decomposition of dead roots, root exudates, fungal hyphae, and leaf and woody litter (e.g., Hanson *et al.*, 2000). Thus, the production processes must be affected by vegetation type, which determines the quantity, quality, and timing of litter fall, root biomass and its turnover rate, and photosynthetic activity and allocation patterns of recent photosynthates (Hanson *et al.*, 2000; Hogberg *et al.*, 2001). The production of CO_2 in the soil creates a concentration gradient driving the gaseous transport, which is affected by the physical properties, temperature, and the water content of the soil–litter continuum (e.g., Nobel, 1999). Thus, temperature and precipitation greatly influence, directly or indirectly, all the component processes of F_{ff} (e.g., Singh & Gupta, 1977; Raich & Shlesinger, 1992; Lloyd & Taylor, 1994; Reichstein *et al.*, 2003).

Vegetation cover affects local soil temperature through intercepted radiation and local soil moisture through interception and transpiration. Although Raich & Tufekcioglu (2000) suggested that soil respiration is controlled primarily by climate factors with vegetation only having a secondary effect, soil respiration rates in coniferous forests were 10% lower, on average, than those in adjacent broad-leaved stands on the same soil type. The reasons underlying this finding remain largely unresolved (Raich & Tufekcioglu, 2000), and may relate to the effect of vegetation on the seasonal dynamics of soil respiration (Curiel Yuste *et al.*, 2004). The difference in magnitude of soil respiration between different forest types may have a large effect on NEE of the forests, particularly in regions with warm, moist temperate climate that support high rates of productivity and F_{ff}, such as the south-east US.

The forested area of the south-eastern US is a mosaic composed largely of pine forest (both naturally and artificially regenerated), mixed pine–hardwood forests, and hardwood forests (HW). Pine forests cover ~ 0.13 million km^2 (Wear, 2002) and can support very high GPP, NPP, NEE, and F_{ff} (Clark *et al.*, 1999; Moncrieff & Fang, 1999; Maier & Kress, 2000; Andrews & Schlesinger, 2001; Katul *et al.*, 2001; Finzi *et al.*, 2002; Butnor *et al.*, 2003; Schäfer *et al.*, 2003). Relative to pine forests, less has been published on this region's hardwood forests (Hanson *et al.*, 1993; Curtis *et al.*, 2001; Norby *et al.*, 2002; Lee & Jose, 2003; King *et al.*, 2004), which cover ~ 0.30 million km^2. However, the area under pine is projected to increase by 0.09 million km^2 by 2040 while the area under HW is projected to decrease by 0.11 million km^2 (Wear, 2002). Thus, our ability to quantify differences in F_{ff} between these forest types is critical for estimating current and future C budgets for the region.

The aim of this study was to quantify seasonal and annual F_{ff} in both forest types, and to separate the effect of forest type from that of climate or soil on the magnitude and dynamics of F_{ff}. To accomplish this we compared CO_2 efflux in a maturing loblolly pine plantation (PP) and a mature Oak-Hickory type forest (HW), representative of a large portion of south-eastern US forests, during a mild and severe drought years (2001 and 2002, respectively). The two experimental stands represent different developmental stages. Maximum tree height at HW was twice that at PP, and aboveground living biomass $\sim 27\%$ higher at HW, however, in 2001, peak one-sided LAI and litterfall were more similar at the two stands (Table 1). We present a unique combination of synchronous and near-continuous monitoring of F_{ff} at both HW and PP (in temporal scales from ~ 3 h to 2 years), large spatial coverage by the monitoring system, and close proximity of the two study stands (<1 km apart). HW and PP were, therefore, on a similar soil type, and experienced identical incident radiation and precipitation above the canopy. Hence, differences between the stands in the key forcing variables, such as soil temperature and moisture, are solely reflecting differences in the amount of leaf area and its dynamics, transpiration, and litter quality.

Table 1 Maximum height, total aboveground living biomass (in September 2002), peak one-sided leaf area index (LAI), and annual litterfall at the hardwood forest (HW) and the pine plantation (PP) located at Duke Forest

	Year	HW	PP
Height (m)*	2002	35	17
Total aboveground living biomass ($kg\,m^{-2}$)†	2002	14.1 (1.23)	10.8 (0.28)
Peak LAI	2001	6.9 (0.25)	5.6 (0.25)
Litterfall ($g\,C\,m^{-2}$)	2001	342 (36)	332 (16)
	2002	294 (42)	250 (15)

Standard error in parenthesis; $N = 3$ at HW and 5 at PP.
*In the beginning of 2002 at PP.
†Biomass equations from Brown *et al*. (1997) and Naidu *et al*. (1998).

Materials and methods

Site description

The PP, planted in 1983, and the 80–100-year-old uneven aged HW, are both AmeriFlux sites located at the Duke Forest C-H_2O Research Site, in Orange County, NC (35°58′N, 79°08′W). The soil is classified as Enon silt loam, a low fertility Hapludalf typical of the SE US Piedmont, with a transition to Iredell gravelly loam toward HW (Pataki & Oren, 2003). An impervious clay pan underlies the research sites at ca. 30 cm belowground. The topographic variations are small (<5% slopes). The region is characterized by warm summers and mild winters. The annual mean temperature is 15.5 °C and the 1140 mm of annual precipitation is evenly distributed throughout the year.

At PP, *Pinus taeda* L. is in the dominant canopy position together with fewer individuals of *Liquidambar styraciflua* L. The subcanopy contains ~40 woody species of which *Acer rubrum* L., *Ulmus alata* Michx., and *Cornus florida* L. are the most prevalent. The HW stand is composed mostly of *Liriodendron tulipifera* L., *Quercus alba* L., *Q. michauxii* Nutt., *Q. phellos* L., *L. styraciflua* L., and *Carya* ssp. The stand characteristics are given in Table 1.

Forest floor CO_2 efflux and litterfall

F_{ff} was measured with the automated carbon efflux system (ACES, US Patent 6692970) developed at USDA Forest Service, Southern Research Station Laboratory in Research Triangle Park, NC (Butnor *et al*., 2003). ACES is an open system where an IRGA is connected with 15 soil chambers (491 cm^2) equipped with air and soil (at 5 cm, T_5) thermocouples, pressure equilibration ports, and reflective covers. Forest floor CO_2 efflux was measured for 10 min from each chamber. ACES gives consistent responses regardless of differences in soil and litter properties and has been calibrated with known CO_2 efflux rates (Butnor & Johnsen, 2004).

An ACES unit with eight chambers was operating at PP from February 2001 until August 2001 and with six chambers until December 2002. At HW, a unit with 15 chambers was operating from June 2001 until December 2002. Chambers were placed randomly at PP and systematically at HW because of coordination with eddy covariance measurements at HW. To minimize the effect of precipitation and litterfall exclusion on the soil substrate within the chambers, they were moved every 3–4 days between two sample points (i.e., there were two locations, A and B, for each chamber). Metal collars attached to the chambers (and a collar only for the 'empty' location) were pushed 1–2 cm into the mineral soil. To minimize long-term disturbance caused by the experiment, the chambers at both stands were relocated on March 26–28, 2002. Starting in the fall of 2002, litter from litter collectors was used to replace the litter excluded while the chambers were in place. The litter was weighed in the field (wet weight), and distributed to each A and B location in proportion to the area covered by the chamber.

Litterfall collection began at both stands in September 2001. There were 20 traps (0.5 m^2) at PP and 48 at HW. These were emptied weekly or biweekly during the heaviest litterfall period and monthly or bimonthly otherwise. Leaf area of a subsample was measured with a leaf area meter (DIAS, Decagon Devices Inc., Pullman, WA, USA) and all the material (divided into leaves, woody material, seeds, and other) was dried ($\geq$ 3 days at 68 °C) and weighed. C content of 0.47 was used in dry-mass-to-C conversions (Hamilton *et al*., 2001). In 2001, the annual litterfall at PP was extrapolated using data from the free-air CO_2 enrichment (FACE) experiment (Finzi *et al*., 2002), and at HW by assuming that monthly litterfall, excluding leaves, is constant throughout the year. At HW, LAI was derived from plant area index measurements with LAI-2000 (Li-Cor Inc., Lincoln, NE, USA) scaled with the estimates of LAI obtained from the litterfall data. At PP, it was calculated as the balance between growth of new foliage (needle elongation measurements) and litterfall.

Environmental data

Environmental data were partially obtained from the nearby FACE experiment (Duke Forest FACE (FACTS I); http://face.env.duke.edu). Precipitation (mm) was measured with one tipping bucket (TI, Texas Instruments, Austin, TX, USA) above the canopy. At each of the six FACE plots at PP, volumetric soil moisture

content (θ, $m^3\,m^{-3}$) was measured with four frequency-domain reflectometry probes (CS615 Campbell Scientific, Logan, UT, USA) placed in the upper 30 cm of the mineral soil. Soil temperature (T_{10}, °C) was measured with one sensor (M 841/S1, Siemens, Germany) at 10–15 cm depth at each FACE plot. At HW, θ was measured with θ probes (ML1X/ML2X, Delta-T Devices, Cambridge, UK) placed at 10 cm (two probes) and 25 cm (two probes) in the mineral soil. The site mean θ for HW was obtained by averaging over the four ML1X/ML2X probes, and at PP by averaging over all CS615 probes located in the ambient FACE plots. Comparison of the θ probe measurements at HW with identical θ probe measurements at PP showed similar between site difference in θ to that suggested by the data used in this study (H. McCarthy, unpublished data). All sensors were sampled every 30 s, and data were averaged over 30 min and stored in a data logger (21X or CR23X, Campbell Scientific).

Data analysis

The response of F_{ff} ($\mu mol\,CO_2\,m^{-2}\,s^{-1}$) to temperature ($T_{soil}$, °C) and volumetric soil moisture content (θ, $m^3\,m^{-3}$) was described as

$$F_{ff}(T_{soil},\theta) = R_b e^{a\,T_{soil}}[1 - e^{(-b\theta+c)}], \qquad (1)$$

where R_b ($\mu mol\,m^{-2}\,s^{-1}$) is the intercept at 0 °C, the so-called base respiration, and a is the temperature sensitivity ($Q_{10} = e^{a\times 10}$) when soil moisture is not limiting, representing potential efflux F_{ff}^P. The function $1-e^{(-b\theta+c)}$, where b and c are fitting parameters, gives the reduction of F_{ff} from F_{ff}^P as soil moisture decreases (modified from Fang & Moncrieff, 1999). The threshold for 'nonlimiting soil moisture' was defined as the value of θ where F_{ff} reached 90% of the F_{ff} averaged over the range of θ within which F_{ff} was clearly insensitive to soil moisture ($\theta > 0.25\,m^3\,m^{-3}$). Very high values of soil moisture ($\theta > 0.4$) occurred for short periods only and no reduction in F_{ff} (because of oxygen limitation) was observed at either stand. The curve fitting was done using the nonlinear curve fitting procedure of Systat (Systat Software Inc., Richmond, CA, USA).

To study the relationship between R_b, a, and θ (i.e., the assumption that these parameters are independent of θ) the data were filtered for T_5 values ranging from 12 to 22 °C at PP, and from 12 to 24 °C at HW, and $\theta < 0.3\,m^3\,m^{-3}$ at both stands. Consequently, the conditions containing very few observations (low T_5 and θ, and high T_5 and θ) were excluded. The remaining data were stratified into soil moisture classes (10 at PP, and nine at HW) with approximately equal number of observations in each class, and the parameter values were estimated for each bin. To study the temperature dependence of the parameters of the F_{ff}–temperature response, the data were filtered for nonlimiting soil moisture. R_b and a were then estimated for five temperature bins at PP and six bins at HW. Although each chamber location (i.e., location A or B for each chamber) was considered a replicate, treating those separately would have resulted in too few observations within each class. Therefore, we used instantaneous data pooled over all the chamber locations (*pooled* data) in this analysis.

To test for differences between stands in the F_{ff}^P–temperature response, we quantified the within-stand spatial variability by estimating the parameters separately for each chamber position (*location* data). The number of chambers multiplied by two locations for each chamber allowed the generation of 12–16 and 30 relationships (replicates) at PP and HW, respectively. The normality of the distribution of the values of R_b and a (Eqn (1)) was tested using the Lilliefors modification of the Kolmogorov–Smirnov test (Systat Software Inc.). The differences between stands in the mean values of R_b and a were studied using ANOVA (Systat Software Inc.). The values of R_b and a, averaged for each stand, were used to calculate daily mean F_{ff}^P. The daily mean of the measured F_{ff} (*daily* data) was divided by the respective daily F_{ff}^P and this ratio was used in estimation of the parameter values of the F_{ff}–soil moisture reduction function. The between-stand difference in the parameter values of this response was tested by comparing a full model (with stand-specific parameters) to a reduced model (with a single set of parameters) based on F-test statistics for extra sum of squares (Ramsey & Schafer, 1997).

Daily averaging did not result in a considerable loss of information or introduction of bias because of the nonlinearity of the response functions. At both stands, the average daily range (max–min) in T_5 in 2002 was ~ 2 °C, and $>90\%$ of the observed ranges were <3.0 °C. The average daily range in θ was $\sim 0.016\,m^3\,m^{-3}$, and $>93\%$ of the observed ranges were $<0.05\,m^3\,m^{-3}$. A daily mean datum was included in the analysis if $\geq 50\%$ of the potential observations for the 24 h period were available. The number of days fulfilling this criterion was 467 at PP, and 409 at HW, and the proportion of gaps (in F_{ff} and T_5 data) was 36% at PP, and 44% at HW over the study period in 2001–2002. Soil temperature for the entire study period was available at ~ 10 cm (T_{10}) at the FACE site. In gap-filling, to avoid introducing an additional source of uncertainty when deriving T_5 from T_{10}, the model was reparameterized using T_{10}. The relationships between F_{ff}^P and T_{10}, and F_{ff}^P and T_5 were equally good at both stands. The data were gap-filled (using Eqn (1)) and monthly and annual estimates of F_{ff} for the two stands were compared.

Results

Daily mean soil temperature at 5 cm (T_5), volumetric soil moisture content (θ), and forest floor CO_2 efflux (F_{ff}) were higher at HW compared with PP most of the time over the study period (2001–2002) (Figs 1a, b and d). Precipitation was evenly distributed throughout the 2 years except for a drought period in the last quarter of 2001 and the second quarter of 2002. Peak one-sided LAI and annual litterfall were higher at HW than at PP (Fig. 1c, Table 1), and the differences increased with increasing drought severity in 2002.

Variation in F_{ff}*–temperature response*

The multiplicative model (Eqn (1)) assumes that the parameters of the F_{ff}–temperature response function (R_b and a) are independent of soil moisture. To test this assumption, the *pooled* data were stratified into soil moisture classes. Within the bins, the variation in T_5 explained more than 50% of the variation in F_{ff} ($P<0.001$) in all but the driest bin ($r^2=0.24$). Although soil moisture appeared to have influenced R_b and a, the effect was not clear and restricted to very low soil moisture ($\theta<0.15\,m^3\,m^{-3}$; Figs 2a and c), thus, giving support to our modeling approach.

To study the temperature dependence of the parameters of the F_{ff}–temperature response, the *pooled* data were filtered for nonlimiting soil moisture (representing F_{ff}^P). F_{ff} was considered as unlimited by soil moisture at $\theta \geq 0.2\,m^3\,m^{-3}$. The relationship between F_{ff} and T_5 was significant in all the temperature bins ($P<0.001$; $N>1000$), but the explained variation in F_{ff} was low ($\leqslant$%) reflecting high 'noise-to-signal ratio' over the narrow range in T_5 within each bin (3 °C). The values of R_b increased and those of a decreased with increasing temperature (Figs 2b and d). The inverse relationship between the two parameters obtained from Figs 2b and d is shown in Fig. 3a.

To quantify the spatial variation of the parameters of the F_{ff}^P–temperature response, R_b and a were estimated for each chamber location (i.e., using *location* data). In addition, based on a subsequent analysis of residuals, we partitioned the data into two periods, representing conditions before and after drought-breaking rains in 2002. From August 27, θ remained $\geq 0.20\,m^3\,m^{-3}$

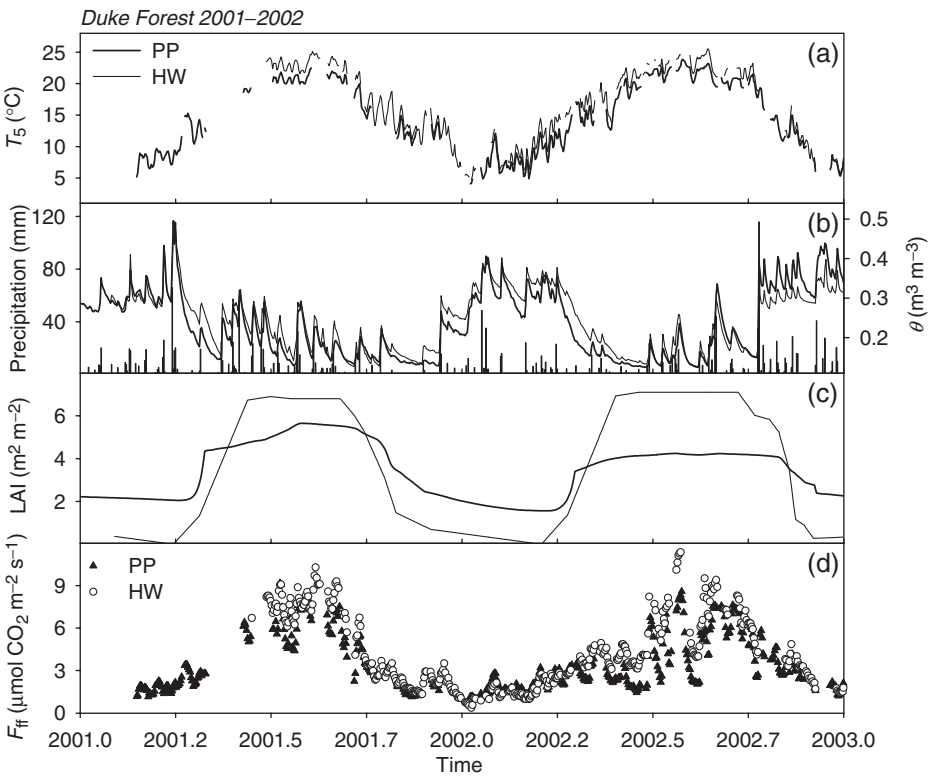

Fig. 1 Daily mean soil temperature at 5 cm (T_5) (a), precipitation (bars) and mean soil volumetric water content (θ) (b), leaf area index (LAI) (c), and daily mean forest floor CO_2 efflux (F_{ff}) (d) over time (in fractions of year). Thick lines and triangles stand for the pine plantation (PP) and thin lines and circles the hardwood forest (HW). Daily values were averaged over $\geq$ 36 and $\geq$ 68 instantaneous observations at PP and HW, respectively.

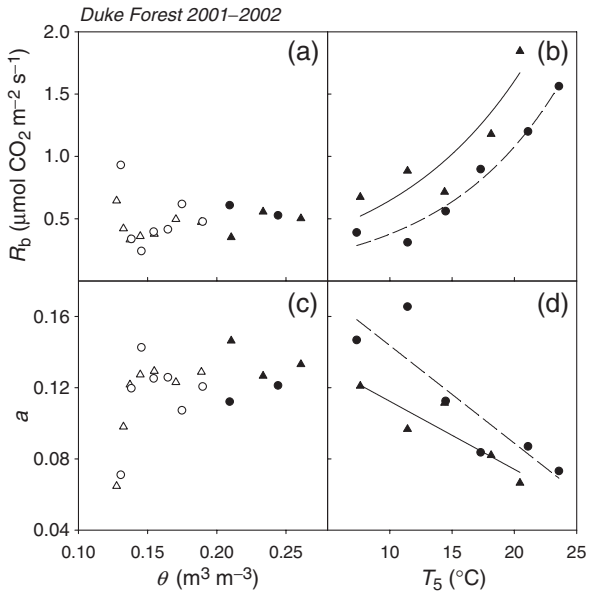

Fig. 2 Base respiration (R_b, F_{ff} at $T_5 = 0\,°C$) and temperature sensitivity of F_{ff} (a) as a function of soil volumetric water content (θ) (a, c), and of soil temperature (T_5) (b, d). Triangles stand for the pine plantation (PP) and circles the hardwood forest (HW). Each point represent mean values over >1000 instantaneous measurements, filled symbols data at $\theta \geq 0.20\,m^3\,m^{-3}$ and open symbols data at $\theta < 0.20\,m^3\,m^{-3}$. All nonlinear regressions were statistically significant ($P < 0.05$). PP: $R_b = 0.2604 \times 1.095^{T_5}$, $r^2 = 0.76$, $a = 0.1506 - 0.0038T_5$, $r^2 = 0.73$; HW: $R_b = 0.1315 \times 1.109^{T_5}$, $r^2 = 0.96$, $a = 0.1986 - 0.0055\ T_5$, $r^2 = 0.73$.

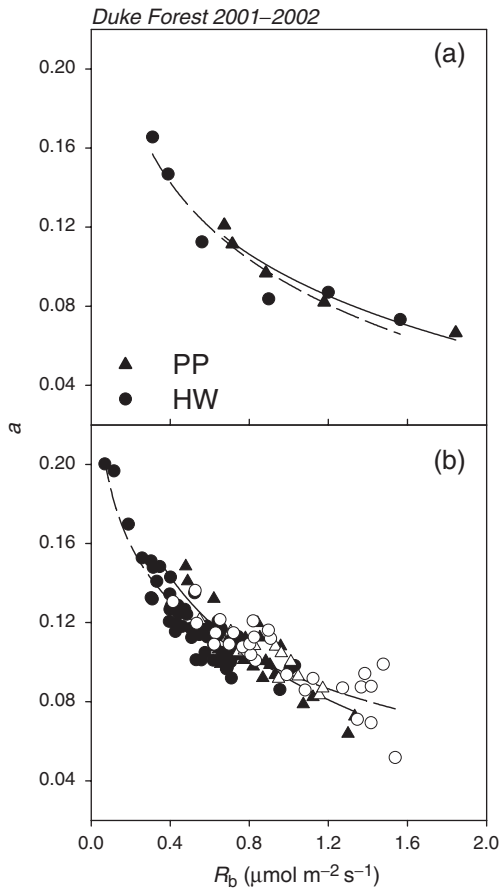

Fig. 3 Temperature sensitivity of F_{ff} (a) as a function of base respiration (R_b) from the temperature bins (data from Figs 2b and d) (a), and from the *location* data, where R_b and a are estimated for each chamber location ($N = 12$ at the pine plantation (PP), and 30 at the hardwood forest (HW)) (b). Filled symbols represent data prior and open symbols after drought-breaking rains. All nonlinear regressions were statistically significant ($P < 0.001$). (a) PP: $a = 0.0947 - 0.0519\ \ln(R_b)$, $r^2 = 0.96$; HW: $a = 0.0910 - 0.0564\ \ln(R_b)$, $r^2 = 0.93$. (b) PP: $a = 0.0913 - 0.0566\ \ln(R_b)$, $r^2 = 0.74$; HW: $a = 0.0939 - 0.0406\ \ln(R_b)$, $r^2 = 0.84$.

for most of the year after staying below that value for ~120 consecutive days. The distribution of the sampled values of R_b and a at both stands and periods were normal ($P > 0.10$). A two-way ANOVA with stand and period as main effects was used to test for differences in R_b and a. The time interval before and after the relocation of the chambers in March 2002 was incorporated as a nested effect in the period main effect, and was found insignificant ($P > 0.20$). The effects of both stand and period, and their interaction effect were significant ($P < 0.01$). The mean value of R_b was lower and of a higher at HW compared with PP during the first period (Tukey's pairwise comparison, $P < 0.05$; Table 2).

An inverse relationship, similar to that found in analysis of the temperature bins (Fig. 3a), emerged when R_b and a were estimated for each chamber location (Fig. 3b). The comparison of a full model (stand- or period-specific parameters) to a reduced model (single set of parameters) suggested that parameter values of this relationship were different between the stands ($P < 0.001$), but not between the two periods within each stand ($P > 0.20$). Analysis of the least-squares problem of estimating the parameter values for the Q_{10} function showed that increases in R_b indeed must result in decreases in a (see Appendix A).

To overcome the uncertainty in the estimates of R_b and a obtained from the temperature bins (*pooled* data, Fig. 3a), we used the more robust parameters obtained from the *location* data that covered the entire temperature range (Fig. 3b). The estimates of F_{ff}^{P} (with T_5 ranging from 5 to 23 °C) calculated using the mean values of R_b and a from the *location* data deviated <2% from the estimates calculated using temperature-bin-specific parameterization. At PP, one set of parameters was sufficient to describe the F_{ff}^{P}–temperature response (Table 2). At HW, the parameter values changed following the drought-breaking rains.

Table 2 Parameters of the responses of the forest floor CO_2 efflux (F_{ff}) to soil temperature at 5 cm under nonlimiting soil moisture conditions F_{ff}^{P} (T_5, R_b, a) and of the reduction function of soil moisture reduction function F_{ff}^{P} to account for the effect of soil moisture F_{ff} (θ, b, c) using daily mean θ.

	Period	R_b	a	Q_{10}	b	c	RMSE	r^2
PP	1	0.840^{Ba} (0.044)	0.103^{Aa} (0.004)	2.80	32.04^{B} (2.509)	3.64^{B} (0.337)	0.490	0.92
	2	0.902^{Aa} (0.054)	0.102^{Aa} (0.003)	2.77				
HW	1	0.534^{Aa} (0.026)	0.121^{Bb} (0.003)	3.35	28.82^{A} (3.239)	2.89^{A} (0.453)	0.535	0.93
	2	0.952^{Ab} (0.062)	0.102^{Aa} (0.004)	2.77				

Parameter values for the F_{ff}^{P}–T_5 function are means over chamber locations. R_b is F_{ff}^{P} at $T_5 = 0\,°C$ in $\mu mol\,CO_2\,m^{-2}\,s^{-1}$, where T_5 is soil temperature at 5 cm. Parameters a, $Q_{10} = e^{(a\times 10)}$, b, and c are dimensionless. Residual mean squared error (RMSE) and r^2 refer to the model $f(T_5)f(\theta)$. Periods 1 and 2 refer to data before and after drought-breaking rains (08/27/02). For R_b and a, the standard error (SE, in parentheses) is that of the mean over the chamber positions ($N = 12$ at PP, and 30 at HW), and for b and c it is SE of the estimate from the nonlinear regression analysis (*daily* data, $N > 50$). Data is from the hardwood forest (HW) and the pine plantation (PP) located at Duke Forest. Capital letters refer to statistically significant differences between stands within a year, and lower case letters to between years within a stand; $P < 0.05$.

Effect of soil moisture on F_{ff}

To assess the effect of low soil moisture on reducing the flux from its potential we analyzed the daily means of F_{ff} because soil moisture measurements were available for the site but not for each chamber. Under nonlimiting soil moisture conditions changes in F_{ff} were explained by an exponential function of temperature ($r^2 > 0.96$, filled symbols in Figs 4a and c). When soil moisture dropped to $\theta < 0.20\,m^3\,m^{-3}$, F_{ff} dropped below F_{ff}^{P} (open symbols in Figs 4a and c). There was a more pronounced decrease in F_{ff} with decreasing soil moisture at PP than at HW (insets, Figs 4a and c). The parameters (b and c in Eqn (1)) were statistically different between the sites ($P < 0.001$; Table 2).

In addition, frequently after major rain events (and when $\theta < 0.20\,m^3\,m^{-3}$) the estimates of daily F_{ff} were slightly smaller than the measured means for up to 5 days following the event (data not shown). Thus, the observed individual pulses in the measured F_{ff} seemed related to rewetting of litter and soil. We modeled these patterns using $Y = 1 + d_1 \times D \times e^{d_1 D}$, where Y is the ratio of measured F_{ff} to F_{ff} (T_{soil}, θ), and D is number of days from the rain event (modified from Liu *et al.*, 2002). The model explained reasonably well the residuals from values predicted based on Eqn (1) ($r^2 > 0.80$, $P < 0.001$).

Differences in monthly and annual F_{ff}

The multiplicative model F_{ff} (T_5, θ) with the mean values of R_b and a for the temperature response of F_{ff}^{P} (with parameters representing pre- and postdrought-breaking rains), with the soil moisture reduction function, and with the correction for the effects of rain events, explained 92% and 93% of the variation in the measured daily mean F_{ff} at PP and HW, respectively (Table 2, Figs 4b and d). There were no trends in the residuals of the model with respect to T_5, θ, or time (data not shown).

There were 304 days where F_{ff} data were available concurrently at both stands. Over these days, the cumulative F_{ff} was greater at HW ($1409\,g\,C\,m^{-2}$) than at PP ($1140\,g\,C\,m^{-2}$). The mean T_5 was 17.2 °C at HW, and 15.6 °C at PP. The average daily minimum T_5 was 0.5 °C higher and maximum 2.3 °C higher at HW compared with PP. Although the average value of θ was similar at PP ($0.21\,m^3\,m^{-3}$) and HW ($0.23\,m^3\,m^{-3}$), the frequency of low values of θ ($<< 0.20\,m^3\,m^{-3}$) was higher at PP. At both stands, the modeled cumulative F_{ff} during this period deviated <1% from the measured value. Using the model, we found that of the difference of $+269\,g\,C\,m^{-2}$ (Δ = HW–PP) $-133\,g\,C\,m^{-2}$ was attributable to differences in the F_{ff}^{P}–temperature response between the two stands, $+206\,g\,C\,m^{-2}$ to the soil temperature difference, $+120\,g\,C\,m^{-2}$ to the soil moisture response of F_{ff}, and $+76\,g\,C\,m^{-2}$ to soil moisture difference.

The monthly estimates of F_{ff} suggested that F_{ff} was higher at HW than at PP during the growing season in both years (Fig. 5). During the rest of the year, it was slightly higher at PP compared with HW or similar at the two stands. The intra-annual differences were roughly associated with differences in T_5 between the stands, while the interannual variation resulted from different responses to drought. The annual estimates of F_{ff} obtained using gap-filled data (Table 3) were similar to those based on only the model. Uncertainty around the estimates of F_{ff} at each stand was obtained using the model results from each chamber location. Based on these, the annual F_{ff} was not statistically different between years at each stand, or between stands in 2001, but was lower at PP than at HW in 2002 ($P < 0.05$).

We separated the effects of parameter differences on mean annual F_{ff} between the stands from those caused

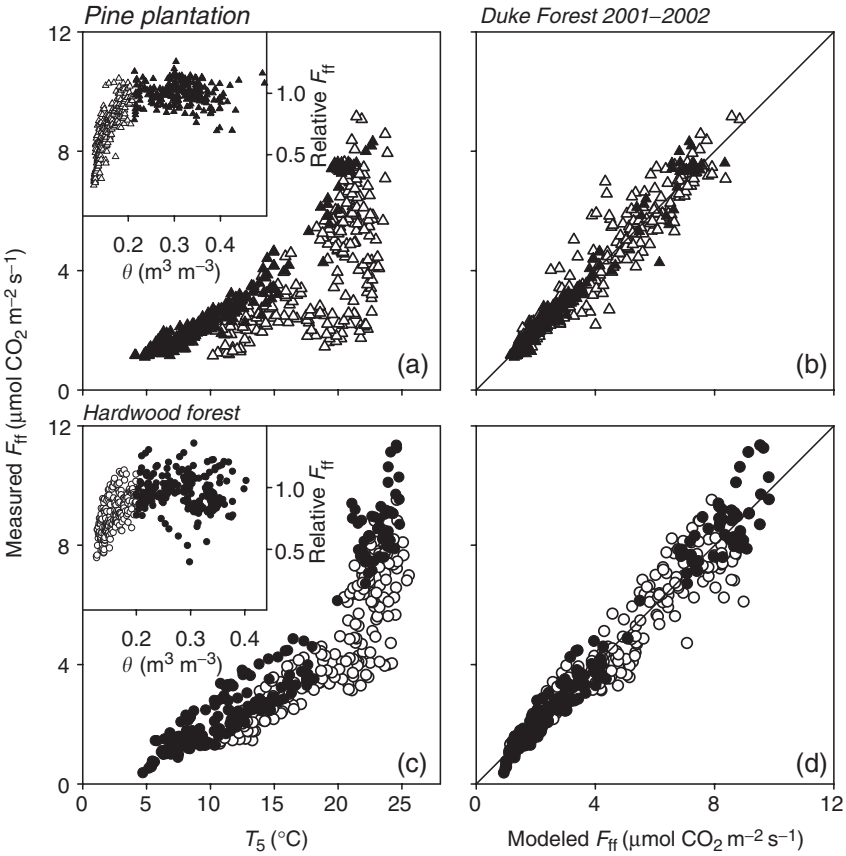

Fig. 4 Daily mean forest floor CO_2 efflux (F_{ff}) as a function of soil temperature at 5 cm (T_5). The ratio of measured F_{ff} to F_{ff} (T_5) as a function of soil volumetric water content (θ) in the insets (a, c). Measured F_{ff} vs. modeled F_{ff} (T_5, θ) and a 1 : 1 line (b, d). Filled symbols represent data at $\theta \geqslant 0.20\,m^3\,m^{-3}$ and open symbols at $\theta < 0.20\,m^3\,m^{-3}$. Daily values averaged as in Fig. 1. Parameter values for the fitted functions are given in Table 2.

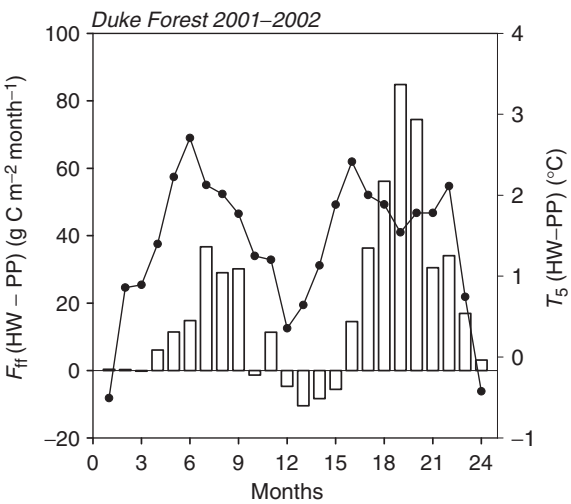

Fig. 5 Difference in the monthly sums of gap-filled forest floor CO_2 efflux (F_{ff}) and the monthly mean soil temperature (T_5, circles) between the hardwood forest (HW) and the pine plantation (PP).

by differences in the state variables (i.e., separating the effect of R_b, a, b, and c from the effect of θ and T_{soil}) using the chain rule (see Appendix B). For 2001, the parameter difference ($-0.18\,\mu mol\,CO_2\,s^{-1}\,m^{-2}$) was nearly entirely compensated by a $+0.17$ difference in the state. For 2002, the parameter difference (–0.07) was overwhelmed by the difference in state ($+0.16$). This analysis indicated that differences in F_{ff} between the stands, estimated for average conditions using average parameters, were relatively small in 2001 and larger in 2002. This was a result of a decrease (from 2001 to 2002) in the relative difference between the parameter values of stands, thus, allowing the compensatory effect of the state variables to become dominating in 2002.

Discussion

Our study demonstrated that, under certain conditions, evergreen pine and deciduous broadleaf forest on similar soils and affected by the same climate, can emit different quantities of CO_2 from the forest floor. The

Table 3 Annual estimates of F_{ff} ($g\,C\,m^{-2}\,yr^{-1}$) calculated using gap-filled data and standard deviation (in parentheses) obtained from the modeled estimates using each chamber location ($N = 12$–30).

	Year	F_{ff}	T_5	θ
PP	2001	1330^{Aa} (237)	13.9	0.22
	2002	1231^{Aa} (120)	14.3	0.23
HW	2001	1464^{Aa} (230)	15.2	0.23
	2002	1557^{Ba} (254)	15.8	0.25

Data is from the hardwood forest (HW) and the pine plantation (PP) located at Duke Forest. T_5 is soil temperature (°C) at 5 cm and θ is volumetric soil moisture (in $m^3\,m^{-3}$ measured over 0–30 cm at PP, and averaged over measurements at 10 and 25 cm at HW). Capital letters refer to statistically significant differences between stands within a year, and lower case letters to between years within a stand; $P < 0.05$.

difference was traceable to dissimilar F_{ff}–soil temperature and F_{ff}–moisture responses, and the effect that each vegetation type has on soil temperature and moisture. In the drought year of 2002, the annual F_{ff} was higher at HW compared with that at PP. This was because before the drought-breaking rains higher growing season temperature and moisture were coupled with lower sensitivity to drought at HW, and following the rains the response of F_{ff} to temperature at HW changed to be similar to that at PP.

F_{ff}^P–*temperature and* F_{ff}–*moisture response*

Because it was estimated from measurements of F_{ff}, the temperature sensitivity of the efflux (Q_{10}) represents both CO_2 production and transport. Nevertheless, the Q_{10} function describes F_{ff} reasonably well, even with parameters that do not vary with soil temperature, moisture, and season (e.g., Hanson *et al.*, 1993; Davidson *et al.*, 1998; Maier & Kress, 2000; Lee *et al.*, 2002; Rey *et al.*, 2002; Kang *et al.*, 2003; Pumpanen *et al.*, 2003). This is surprising because an invariant base respiration (R_b) implies constant substrate pool size, and because Q_{10} has been shown to decrease with temperature in plant tissues (e.g., Tjoelker *et al.*, 2001) and Q_{10} to depend on soil moisture (Borken *et al.*, 1999; Qi *et al.*, 2002; Reichstein *et al.*, 2002a, b).

In this study, very low soil moisture might have affected R_b and a at both stands, but the effect was unclear and inconsistent, supporting the assumption of independent effects of soil temperature and moisture on F_{ff}. On the other hand, the temperature sensitivity a ($= \ln(Q_{10})/10$) of F_{ff}^P, i.e., F_{ff} under nonlimiting soil moisture decreased with temperature at both stands, consistent with results from previous studies (Lloyd & Taylor, 1994; Qi *et al.*, 2002; Janssens & Pilegaard, 2003). The changes in a with temperature are rooted in the sensitivity of the underlying respiration processes to temperature, but F_{ff} is de-coupled to some extent from belowground metabolism (e.g., Curiel Yuste *et al.*, 2004). Thus, the temperature dependence of a is probably a reflection of the form of the Q_{10} function. An inherent mathematical property of the Q_{10} function is that a is related to R_b (see Appendix A). Nevertheless, the simple Q_{10} model performed equally well or better than the commonly used alternative, the modified Arrhenius model (Lloyd & Taylor, 1994) and was used in this study.

Except for conditions near soil saturation, F_{ff} is commonly found to be insensitive to soil moisture down to the moisture below which F_{ff} declines steeply as metabolic activity decreases (e.g., Hanson *et al.*, 1993; Davidson *et al.*, 1998; Fang & Moncrieff, 1999; Mielnick & Dugas, 2000). Although chamber-to-chamber variation in θ was not monitored in our study, it has been suggested that soil moisture is more important in explaining temporal variation than spatial variation in F_{ff} (Yim *et al.*, 2003). Using the site mean θ for our stands explained reasonably well the reduction of F_{ff} from F_{ff}^P at $\theta < 0.20\,m^3\,m^{-3}$.

The increase in CO_2 efflux after rewetting is widely reported (e.g., Birch, 1958; Anderson, 1973; Borken *et al.*, 1999; Borken *et al.*, 2002; Lee *et al.*, 2002; Rey *et al.*, 2002; Curiel Yuste *et al.*, 2003). The suggested causes include rapid evacuation of CO_2 from the soil pore space, increase in CO_2 production resulting from increase in substrate availability and microbial activity, and stimulation of root respiration. The effects of rewetting on annual soil CO_2 efflux in forests has, however, rarely been quantified. In a temperate spruce stand, rewetting after a simulated drought had no effect on the annual soil respiration during the first year, but increased it by 51% during the second year (Borken *et al.*, 1999). In a cool temperate deciduous forest, postrainfall increases in soil respiration accounted for 16–21% of the annual F_{ff} (Lee *et al.*, 2002). Our estimate of rain-induced increases in F_{ff} following droughts that reduced soil moisture to $< 0.20\,m^3\,m^{-3}$, amounted to $\sim 20\,g\,C\,m^{-2}\,yr^{-1}$ annually at both stands. This is likely to be an underestimation because the chambers were covered. The direct short-term effects of rewetting on F_{ff} could only be detected when the chambers were moved.

Differences in F_{ff} *between HW and PP*

Higher mean F_{ff} in oak-dominated than pine-dominated stands has been linked to a greater annual Q_{10} (Curiel Yuste *et al.*, 2004). Curiel Yuste *et al.* (2004) demonstrated correlations between annual Q_{10} and variables that reflect the seasonality of the stand, defined as the amplitude between the minimum and

maximum values of such variables. Among six sites varying in deciduousness, the amplitude of F_{ff} increased with the amplitude of LAI. Higher annual Q_{10} in stands with greater LAI dynamics was assumed to reflect root phenology, implying that the variability in Q_{10} among stands reflects differences in both temperature sensitivity and root phenology. Root phenology should be reflected to some extent in root biomass, presumably reaching maximum with LAI and resulting in high R_b at the height of the growing season. Our analysis showed that variability in R_b is predictably associated with variability in Q_{10}. Indeed, when data from the pine and oak stands were analyzed in 2 months intervals, R_b was highest and Q_{10} lowest in the middle of the growing season (Curiel Yuste *et al.*, 2004).

Our results also showed that the inverse relationships between R_b and Q_{10} were only slightly different between the two stands. Consequently, if two stands show large difference in seasonality, and their R_b and Q_{10} are similar during the nongrowing season, the R_b of the stand with greater seasonality should be higher and its Q_{10} lower than the stand with lesser seasonality during the growing season. As predicted, R_b at the oak stand studied by Curiel Yuste *et al.* (2004) tended to be higher than at the pine stand during the summer, but the temperature sensitivity was similar at both stands. Thus, the effect of root phenology on F_{ff} can be accounted for by analyzing R_b. However, R_b can change for reasons unrelated to root phenology. In this study, R_b at HW changed immediately following the drought-breaking rains in 2002, with no time lag necessary for increases in either LAI or root biomass. Our results suggested an alternative explanation to the intra-annual variability in F_{ff} that is also associated with the deciduousness of the forest, namely the effect LAI and thickness of the litter layer on soil temperature.

In the wetter of the 2 years, F_{ff} was statistically similar at the two stands. This was supported by the analytical evaluation of the controls over F_{ff} (Appendix B). The combined response to soil temperature and moisture at HW would have caused F_{ff} there to be lower compared with PP. However, this effect was compensated for by higher soil temperature and moisture at HW. Higher temperature throughout most of the year at HW was driven by differences in LAI dynamics and litter quality. While the peak LAI was somewhat higher at HW, the higher decomposition rate of broadleaf leaf litter (Finzi & Schlesinger, 2002) reduced the insulating litter layer at HW, bringing soil temperature in the uppermost layers closer to air temperature as has been shown elsewhere (Paul *et al.*, 2004). In the nongrowing (leafless) season, a greater proportion of incoming radiation was reaching the ground resulting in a higher soil temperature at HW than that at PP, except when the radiative forcing was very low.

Although not significant, the difference in F_{ff} between the stands (10% in 2001) was consistent with the differences found between six broad-leaved forests and their adjacent coniferous counterparts, even though our data extended twofold the range of the published data (Raich & Tufekcioglu, 2000, Fig. 6a). (Adding the data from Curiel Yuste *et al.*, 2004 did not change the overall relationship appreciably.) We evaluated the potential contributions of various C fluxes at each stand

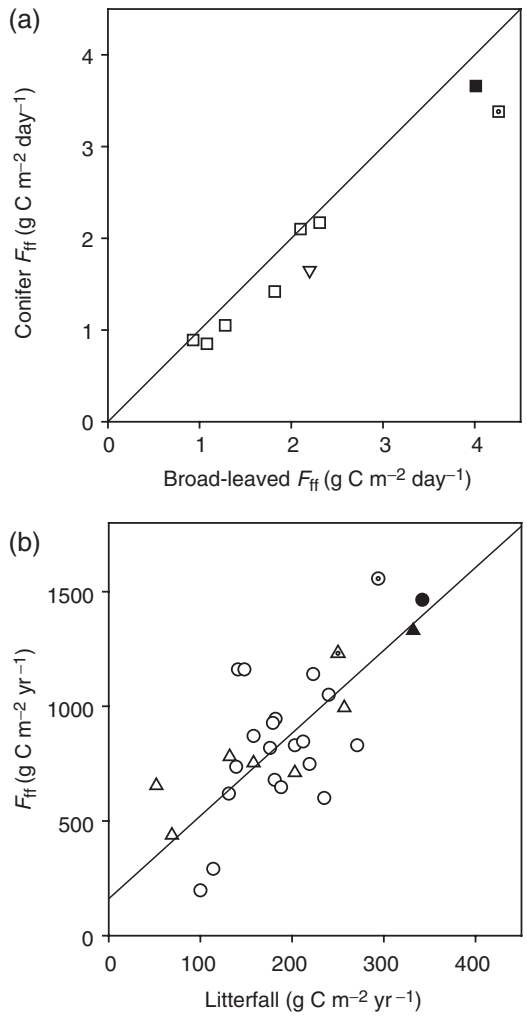

Fig. 6 Mean (annual or over growing season) daily forest floor CO_2 efflux (F_{ff}) in coniferous vs. nearby broad-leaved forests (a). Open squares represent data from Raich & Tufekcioglu (2000) and triangle down represents data from Curiel Yuste *et al.* (2004). Annual estimates of F_{ff} as a function of annual litterfall (b). Open symbols represent temperate stands and fitted line the regression for all stands ($y = 3.61x + 161$) from Davidson *et al.* (2002). Circles stand for hardwood forests and triangles coniferous stands. Data from this study are presented as closed symbols for 2001, and dotted symbols for 2002.

to this difference based on a simple mass balance approach. The sum of the litterfall C and allocation of C belowground, adjusted for changes in C stocks and the transport of C off site, should equal to the amount of C lost in F_{ff} (Raich & Nadelhoffer, 1989; Giardina & Ryan, 2002). Annual F_{ff} and litterfall across forest types are positively correlated (Davidson *et al*., 2002; Fig. 6b). Although Davidson *et al*. (2002) found no correlation when mature temperate HW were analyzed separately, our HW data extended the range of the published data and, for the wetter of the 2 years, fell near the line of the overall correlation between F_{ff} and litterfall.

Assuming a steady state of C storage in the litter–soil system and averaging across biomes and age classes, Davidson *et al*. (2002) showed that belowground processes contribute the equivalence of $\sim 75\%$ of F_{ff}, and the value is somewhat greater in young than mature stands. Our data suggested that in 2001, these processes accounted for $\sim 76\%$ of F_{ff} at both stands. Because we observed little leaf litter on the soil surface at HW just prior to leaf abscission in the autumn, we assumed that C is not accumulating in the litter–soil system, and the difference between F_{ff} and litterfall ($1122\,g\,m^{-2}\,yr^{-1}$ in 2001) represented C allocation belowground and belowground contribution to F_{ff} at this stand. In contrast, it is certain that PP was accumulating C in the litter–soil system. Averaged over the last few years, the PP accumulated C in both the litter layer ($44\,g\,m^{-2}\,yr^{-1}$; Schlesinger & Lichter, 2001) and the upper 30 cm of the mineral soil ($138\,g\,m^{-2}\,yr^{-1}$; Lichter *et al*., in press). Using these annual C accumulation rates together with litterfall and F_{ff} data for 2001, the mass balance showed that C allocation belowground at PP was $\sim 1180\,g\,m^{-2}\,yr^{-1}$. Thus, in 2001, C input belowground was somewhat higher at PP, and the lower F_{ff} at PP was related to it being in the C accumulation stage, in contrast to HW that reached a steady state of C storage.

During the drought year of 2002, the large difference in F_{ff} between the stands (26%) resulted from a relatively smaller difference in the response of F_{ff} to soil temperature and moisture and a larger effect of the difference in those state variables (see Appendix B). The difference in the response of F_{ff} to soil temperature decreased following the drought-breaking rains in August 2002. The value of R_b at HW increased to a value similar to that at PP, indicating an increase in substrate availability related to cessation of the drought. Results of girdling studies, terminating the supply of recently assimilated C to roots, have suggested that recent C contributes a significant amount to F_{ff} (Hogberg *et al*., 2001; Bhupinderpal-Singh *et al*., 2003). Previous studies at our stands have showed that the canopy conductance at PP is more sensitive to soil moisture than that at HW (Oren *et al*., 1998; Pataki & Oren, 2003). This may have resulted in smaller impact of the drought on C assimilation at HW, and continued allocation of recent C to belowground where it accumulated in the soil to a greater extent than at PP. In summary, the similar responses to soil temperature and moisture at the two stands in the latter half of 2002 allowed the differences in soil temperature and moisture to yield much higher F_{ff} at HW compared with PP.

We repeated the mass balance calculation to assess the contribution of belowground processes to F_{ff} in 2002. At PP, we assumed that the decomposition of litter contributed to F_{ff} the same amount of C as it did in the wetter year of 2001 ($\sim 288\,g\,C\,m^{-2}\,yr^{-1}$), $38\,g\,C\,m^{-2}\,yr^{-1}$ in excess of the litterfall in 2002. This would eliminate C accumulation in the litter layer maintaining the C storage there unchanged ($998\,g\,m^{-2}$; Lichter *et al*., in press). If annual C accumulation in the mineral soil remained the same as the annual average, allocation of C belowground ($= F_{ff}$–litter decomposition + accumulation) would have been $\sim 1081\,g\,m^{-2}\,yr^{-1}$. If the greater sensitivity of canopy conductance to drought at PP (Oren *et al*., 1998; Pataki & Oren, 2003) translates to a reduced belowground allocation, annual C accumulation in the mineral soil would have to decrease accordingly. Even though HW might be less sensitive to drought than PP, it is unlikely that it would be able to allocate belowground larger quantities of C in 2002 than in 2001 (~ 1263 vs. $\sim 1122\,g\,m^{-2}\,yr^{-1}$, respectively). A better assumption may be that allocation was similar to that in 2001. If so, this represents a loss of $\sim 141\,g\,C\,m^{-2}\,yr^{-1}$ from the mineral soil of HW in 2002, more than the estimated loss from the litter layer at PP ($\sim 38\,g\,C\,m^{-2}\,yr^{-1}$).

Conclusions

The aim of this study was to assess the role of vegetation in affecting seasonal and annual F_{ff} in a maturing loblolly PP and a mature Oak-Hickory type forest. The results showed that with the exception of the winter months, F_{ff} was higher at HW compared with the adjacent PP. The higher F_{ff} at HW resulted from the combined effects of stand differences in the responses to soil temperature and moisture, and the frequency distribution of soil temperature and moisture. The cumulative effect of the different responses was reflected in the interannual variation in F_{ff} at the two stands. Our results showed that predictions of F_{ff} under climate change scenarios, including changes in soil temperature and drought severity, are complicated by the differential effect of drought on litter production and belowground C allocation, and by the likelihood

that a series of drought years would generate responses that are quite different from the response of one severe drought year among normal years. Although these results indicate that C accumulation in litter and soil of PPs in this region is likely to be higher than in mature HW, it is essential to consider the fate of soil C already stored in broad-leaved forests as these undergo large-scale conversion to Pine Plantations.

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Appendix A: Theoretical relationship between a and R_b

Given an independent variable x and a dependent variable y, the least-squares problem of determining the slope (m) and intercept (b) of $y = mx + b$ from n (>3) observations of x and y (hereafter referred to as x_i, y_i)

can be formulated as the solution to the system of two equations with two unknowns:

$$\frac{1}{n}\sum_{i=1}^{n} y_i = m\frac{1}{n}\sum_{i=1}^{n} x_i + b, \tag{A.1}$$

$$\frac{1}{n}\sum_{i=1}^{n} x_i y_i = m\frac{1}{n}\sum_{i=1}^{n} x_i^2 + b\frac{1}{n}\sum_{i=1}^{n} x_i. \tag{A.2}$$

Letting $\overline{\Psi} = (1/n)\sum_{i=1}^{n}\Psi_i$, where Ψ is either x, y and adopting this notation in Eqn (A.1) yields a relationship between b and m as

$$b = \overline{y} - m\overline{x}. \tag{A.3}$$

The parameter estimation for R_b and a in Eqn (1) with no soil moisture limitations (or at specified moisture or temperature bins) can be formulated as a linear regression problem if $b = \ln(R_b)$, $y = \ln(F_{ff})$, $m = a$, and $x = T_{soil}$. Replacing these equalities into Eqn (A.3) yields

$$R_b = e^{[\overline{\ln(F_{ff})}]} e^{[-a\overline{T_{soil}}]}. \tag{A.4}$$

Note, $\overline{\ln(\Psi)} \neq \ln(\overline{\Psi})$. Because F_{ff} ranges between 2 and 4 μmol CO_2 m^{-2} s^{-1} for most of the times with maximum excursions to about 12 μmol CO_2 m^{-2} s^{-1}, the variability in $\ln(F_{ff})$ becomes much smaller (i.e., at least one order of magnitude) than the variability in F_{ff}. Hence, to a first approximation $e^{[\overline{\ln(F_{ff})}]}$becomes approximately a constant, γ. Upon replacing in Eqn (A.4), the relationship between R_b and a becomes

$$R_b = \gamma e^{[-a\overline{T_{soil}}]}. \tag{A.5}$$

It is evident from the above model that increases in a must result in decreases in R_b. Eqn (A.5) can be inverted to obtain a as a function of R_b:

$$a = \frac{1}{\overline{T_{soil}}}\ln\left(\frac{\gamma}{R_b}\right). \tag{A.6}$$

In Fig. 7, the values of a calculated based on Eqn (A.6) (a') are shown to be in close agreement with those obtained from the curve fitting of data in Fig. 3b.

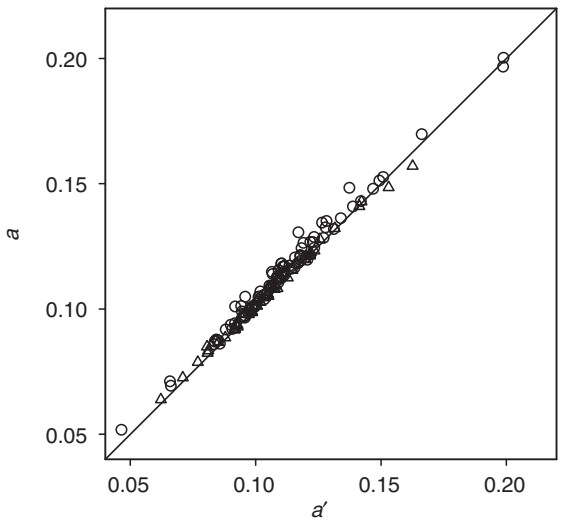

Fig. 7 Relationship (in Appendix A) between the values of a obtained from the curve fitting (data from Fig. 3b) and those calculated using Eqn (A.6) (a'). Triangles stand for the pine plantation (PP) and circles the hardwood forest (HW).

Appendix B: Parameter vs. state effects on F_{ff}

When comparing differences in F_{ff} between HW and PP, the genesis of the potential differences can be attributed to two types: state differences (i.e., the state variables θ and $T_{soil}T_s$) and parameter differences (i.e., R_b, a, b, and c). To separate these two effects, we start with Eqn (1) and proceed to quantify the variability in F_{ff} as state and/or parameter using the chain rule

$$dF_{ff} = \underbrace{\left[\frac{\partial F_{ff}}{\partial R_b}dR_b + \frac{\partial F_{ff}}{\partial_a}da + \frac{\partial F_{ff}}{\partial_b}\partial b + \frac{\partial F_{ff}}{\partial_c}\partial c\right]}_{\text{Parameter change}} + \underbrace{\left[\frac{\partial F_{ff}}{\partial T_s}dT_s + \frac{\partial F_{ff}}{\partial\theta}d\theta\right]}_{\text{State change}}, \tag{B.1}$$

where

$$\left.\frac{\partial F_{ff}}{\partial R_b}\right|_{a,b,c,T_s,\theta} = e^{aT_s}\left[1 - e^{(-b\theta+c)}\right], \tag{B.2}$$

$$\left.\frac{\partial F_{ff}}{\partial a}\right|_{R_b,b,c,T_s,\theta} = R_b T_s e^{aT_s}\left[1 - e^{(-b\theta+c)}\right], \tag{B.3}$$

$$\left.\frac{\partial F_{ff}}{\partial b}\right|_{R_b,a,c,T_s,\theta} = \theta R_b e^{aT_s}\left[e^{(-b\theta+c)}\right], \tag{B.4}$$

$$\left.\frac{\partial F_{ff}}{\partial c}\right|_{R_b,a,b,T_s,\theta} = R_b e^{aT_s}\left[e^{(-b\theta+c)}\right], \tag{B.5}$$

$$\left.\frac{\partial F_{ff}}{\partial T_s}\right|_{R_b,a,b,c_s,\theta} = R_b a e^{aT_s}\left[1 - e^{(-b\theta+c)}\right], \tag{B.6}$$

$$\left.\frac{\partial F_{ff}}{\partial \theta}\right|_{R_b a,b,c,T_s} = bR_b e^{aT_s}\left[1 - e^{(-b\theta+c)}\right]. \tag{B.7}$$

With these estimates and assuming that d $\Psi \approx \Delta\Psi$ (i.e., a first-order linear Taylor series expansion), where Ψ is any of the five variables (θ, T_{soil}, R_b, a, b, and c) the relative change is given by

$$\frac{\Delta F_{ff}}{F_{ff}} = \underbrace{\left[\frac{\Delta R_b}{R_b} + T_s\Delta a + \frac{\theta e^{-b\theta+c}}{1-e^{-b\theta+c}}\Delta b + \frac{-e^{-b\theta+c}}{1-e^{-b\theta+c}}\Delta c\right]}_{\text{Parameter change}} + \underbrace{\left[a\Delta T_s + \frac{b e^{(-b\theta+c)}}{1-e^{-b\theta+c}}\Delta\theta\right]}_{\text{State change}}, \tag{B.8}$$

where the annual values of θ, T_{soil}, R_b, a, b, and c, averaged for the two stands, represented a 'reference stand', and Δ referred to the differences between HW and PP (Δ = HW−PP).