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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 $\theta$ when soil was drier. A model ($F_{ff}$ ($T_5$, $\theta$)) 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 $\sim 0.13$ 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 $\sim 0.30$ 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 $\sim 3$ 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 ($\theta$, 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, $\theta$ was measured with theta 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 $\theta$ 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 theta probe measurements at HW with identical $\theta$ probe measurements at PP showed similar between site difference in $\theta$ 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 $F_{\mathrm{ff}}$ (μmol CO$_2$ m$^{-2}$ s$^{-1}$) to temperature ($T_{\mathrm{soil}}$, °C) and volumetric soil moisture content ($\theta$, m$^3$ m$^{-3}$) was described as

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

where $R_{\mathrm{b}}$ (μmol 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 $F_{\mathrm{ff}}^{\mathrm{P}}$. The function $1 - e^{(-b\theta + c)}$, where $b$ and $c$ are fitting parameters, gives the reduction of $F_{\mathrm{ff}}$ from $F_{\mathrm{ff}}^{\mathrm{P}}$ as soil moisture decreases (modified from Fang & Moncrieff, 1999). The threshold for 'nonlimiting soil moisture' was defined as the value of $\theta$ where $F_{\mathrm{ff}}$ reached 90% of the $F_{\mathrm{ff}}$ averaged over the range of $\theta$ within which $F_{\mathrm{ff}}$ 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 $F_{\mathrm{ff}}$ (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 $R_{\mathrm{b}}$, $a$, and $\theta$ (i.e., the assumption that these parameters are independent of $\theta$) 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 $\theta$, and high $T_5$ and $\theta$) 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 $F_{\mathrm{ff}}$–temperature response, the data were filtered for nonlimiting soil moisture. $R_{\mathrm{b}}$ 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 $F_{\mathrm{ff}}^{\mathrm{P}}$–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 $R_{\mathrm{b}}$ and $a$ were studied using ANOVA (Systat Software Inc.). The values of $R_{\mathrm{b}}$ and $a$, averaged for each stand, were used to calculate daily mean $F_{\mathrm{ff}}^{\mathrm{P}}$. The daily mean of the measured $F_{\mathrm{ff}}$ (*daily* data) was divided by the respective daily $F_{\mathrm{ff}}^{\mathrm{P}}$ and this ratio was used in estimation of the parameter values of the $F_{\mathrm{ff}}$–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 $\theta$ was ~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 ≥ 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 $F_{\mathrm{ff}}$ 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 $F_{\mathrm{ff}}^{\mathrm{P}}$ and $T_{10}$, and $F_{\mathrm{ff}}^{\mathrm{P}}$ and $T_5$ were equally good at both stands. The data were gap-filled (using Eqn (1)) and monthly and annual estimates of $F_{\mathrm{ff}}$ for the two stands were compared.

## Results

Daily mean soil temperature at 5 cm ($T_5$), volumetric soil moisture content ($\theta$), 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 ($\theta<0.15\,\mathrm{m^3\,m^{-3}}$; 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 $\theta \geq 0.2\,\mathrm{m^3\,m^{-3}}$. 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 ($\leqslant 24\%$) 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, $\theta$ remained $\geq 0.20\,\mathrm{m^3\,m^{-3}}$

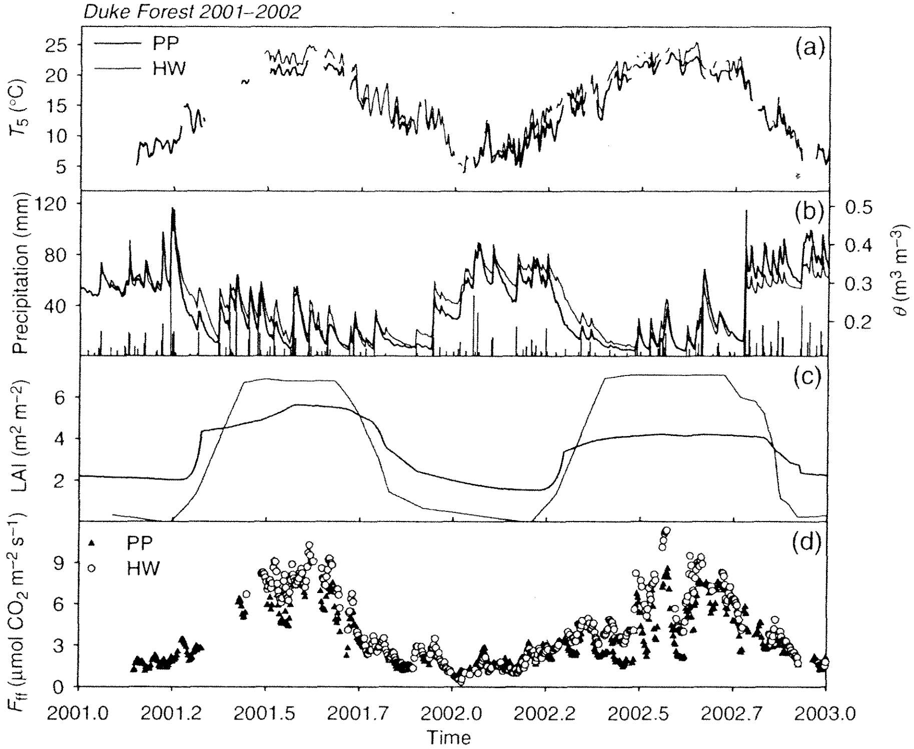

**Fig. 1** Daily mean soil temperature at 5 cm ($T_5$) (a), precipitation (bars) and mean soil volumetric water content ($\theta$) (b), leaf area index (LAI) (c), and daily mean forest floor CO$_2$ efflux ($F_{ff}$) (d) over time (in fractions of year). Thick lines and triangles stand for the pine plantation (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.

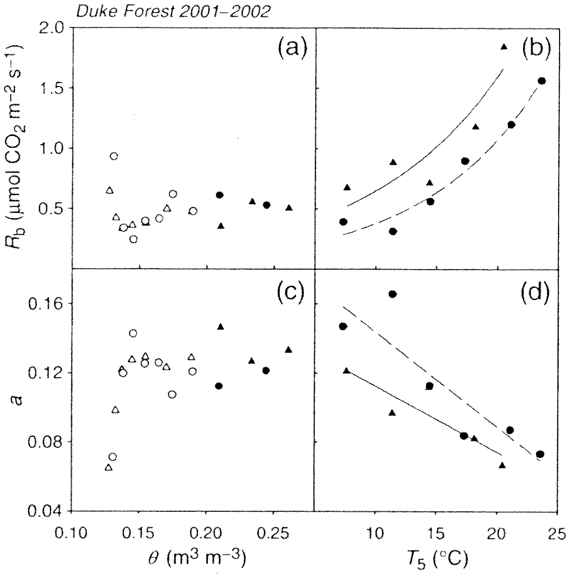

**Fig. 2** Base respiration ($R_\mathrm{b}$, $F_\mathrm{ff}$ at $T_5 = 0\,^\circ\mathrm{C}$) and temperature sensitivity of $F_\mathrm{ff}$ ($a$) as a function of soil volumetric water content ($\theta$) (a, c), and of soil temperature ($T_5$) (b, d). Triangles stand for the pine plantation (PP) and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

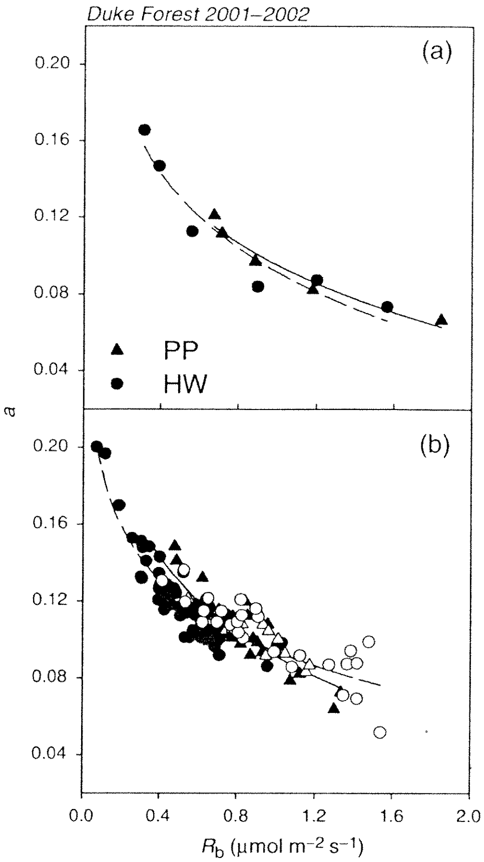

**Fig. 3** Temperature sensitivity of $F_\mathrm{ff}$ ($a$) as a function of base respiration ($R_\mathrm{b}$) from the temperature bins (data from Figs 2b and d) (a), and from the *location* data, where $R_\mathrm{b}$ and $a$ are estimated for each chamber location ($N = 12$ at the pine plantation (PP), 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: $a = 0.0947 - 0.0519\ln(R_\mathrm{b})$, $r^2 = 0.96$; HW: $a = 0.0910 - 0.0564\ln(R_\mathrm{b})$, $r^2 = 0.93$. (b) PP: $a = 0.0913 - 0.0566\ln(R_\mathrm{b})$, $r^2 = 0.74$; HW: $a = 0.0939 - 0.0406\ln(R_\mathrm{b})$, $r^2 = 0.84$.

for most of the year after staying below that value for ~ 120 consecutive days. The distribution of the sampled values of $R_\mathrm{b}$ 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 $R_\mathrm{b}$ 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 $R_\mathrm{b}$ 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 $R_\mathrm{b}$ 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 $R_\mathrm{b}$ indeed must result in decreases in $a$ (see Appendix A).

To overcome the uncertainty in the estimates of $R_\mathrm{b}$ 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 $F_\mathrm{ff}^\mathrm{P}$ (with $T_5$ ranging from 5 to 23 °C) calculated using the mean values of $R_\mathrm{b}$ 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 $F_\mathrm{ff}^\mathrm{P}$–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 $F_{ff}$ ($\theta$, $b$, $c$) using daily mean $\theta$.

| | 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 $T_5 = 0\,^{\circ}\mathrm{C}$ 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 are 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 $\theta < 0.20\,\mathrm{m^3\,m^{-3}}$, $F_{ff}$ 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 $\theta < 0.20\,\mathrm{m^3\,m^{-3}}$) 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 $F_{ff}$ ($T_{soil}$, $\theta$), 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 $F_{ff}$ ($T_5$, $\theta$) 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 $T_5$, $\theta$, 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 $\theta$ was similar at PP (0.21 m$^3$ m$^{-3}$) and HW (0.23 m$^3$ m$^{-3}$), the frequency of low values of $\theta$ ($<<$ 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$^{-2}$ ($\Delta$ = 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

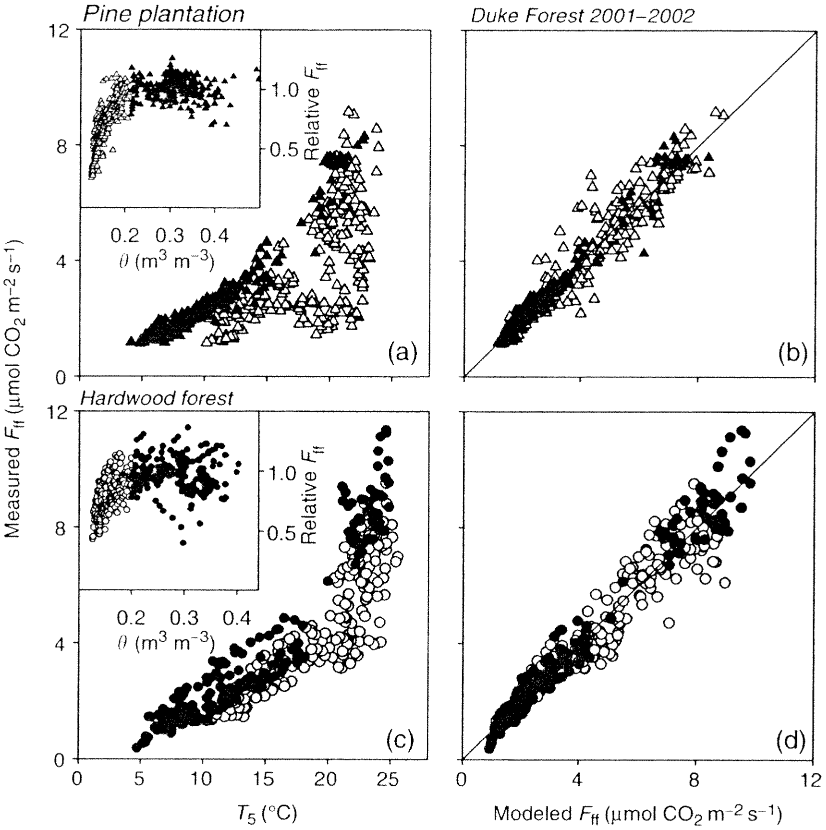

**Fig. 4** Daily mean forest floor CO$_2$ efflux ($F_{ff}$) as a function of soil temperature at 5 cm ($T_5$). The ratio of measured $F_{ff}$ to $F_{ff}$ ($T_5$) as a function of soil volumetric water content ($\theta$) in the insets (a, c). Measured $F_{ff}$ vs. modeled $F_{ff}$ ($T_5$, $\theta$) and a 1 : 1 line (b, d). Filled symbols represent data at $\theta \geq 0.20\,\mathrm{m^3\,m^{-3}}$ and open symbols at $\theta < 0.20\,\mathrm{m^3\,m^{-3}}$. Daily values averaged as in Fig. 1. Parameter values for the fitted functions are given in Table 2.

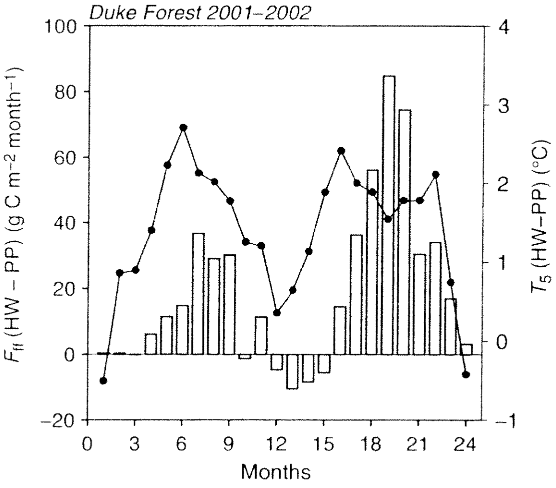

**Fig. 5** Difference in the monthly sums of gap-filled forest floor CO$_2$ efflux ($F_{ff}$) and the monthly mean soil temperature ($T_5$, circles) between the hardwood forest (HW) and the pine plantation (PP).

by differences in the state variables (i.e., separating the effect of $R_b$, $a$, $b$, and $c$ from the effect of $\theta$ and $T_{soil}$) using the chain rule (see Appendix B). For 2001, the parameter difference ($-0.18\,\mu\mathrm{mol\,CO_2\,s^{-1}\,m^{-2}}$) 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 | $F_{ff}$ | $T_5$ | $\theta$ |
|---|---|---|---|---|
| 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 are from the hardwood forest (HW) and the pine plantation (PP) located at Duke Forest. $T_5$ is soil temperature (°C) at 5 cm and $\theta$ 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 $\theta$ 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 $\theta$ 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

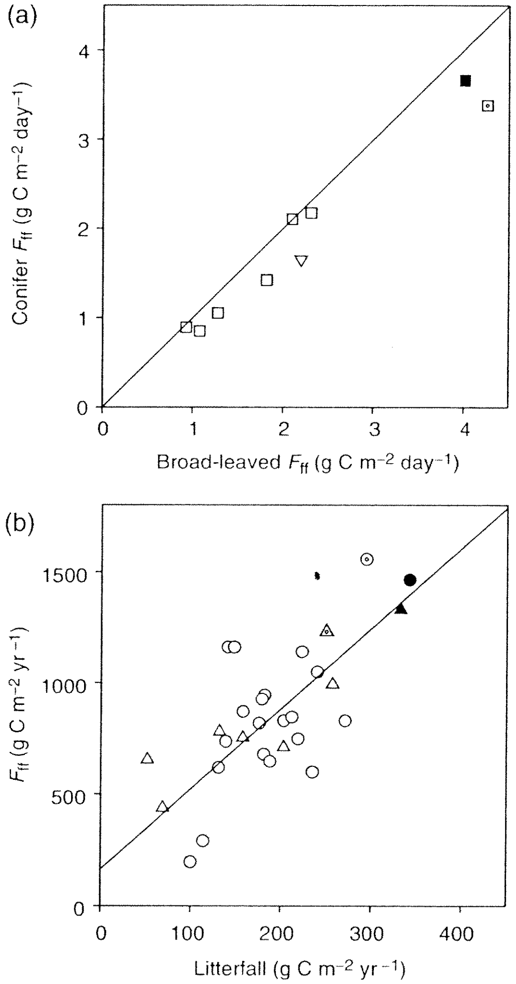

**Fig. 6** Mean (annual or over growing season) daily forest floor $CO_2$ efflux ($F_{ff}$) in coniferous vs. nearby broad-leaved forests (a). Open squares represent data from Raich & Tufekcioglu (2000) and triangle down represents data from Curiel Yuste *et al.* (2004). Annual estimates of $F_{ff}$ 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 ($1122\,\mathrm{g\,m^{-2}\,yr^{-1}}$ 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 ($44\,\mathrm{g\,m^{-2}\,yr^{-1}}$; Schlesinger & Lichter, 2001) and the upper 30 cm of the mineral soil ($138\,\mathrm{g\,m^{-2}\,yr^{-1}}$; 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 $\sim 1180\,\mathrm{g\,m^{-2}\,yr^{-1}}$. 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 ($\sim 288\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$), $38\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ in excess of the litterfall in 2002. This would eliminate C accumulation in the litter layer maintaining the C storage there unchanged ($998\,\mathrm{g\,m^{-2}}$; 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 $\sim 1081\,\mathrm{g\,m^{-2}\,yr^{-1}}$. 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 ($\sim 1263$ vs. $\sim 1122\,\mathrm{g\,m^{-2}\,yr^{-1}}$, respectively). A better assumption may be that allocation was similar to that in 2001. If so, this represents a loss of $\sim 141\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ from the mineral soil of HW in 2002, more than the estimated loss from the litter layer at PP ($\sim 38\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$).

## 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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## References

Anderson JM (1973) Carbon dioxide evolution from two temperate deciduous woodland soils. *Journal of Applied Ecology*, **10**, 361–378.

Andrews JA, Schlesinger WH (2001) Soil $CO_2$ dynamics, acidification, and chemical weathering in a temperate forest with experimental $CO_2$ enrichment. *Global Biochemical Cycles*, **15**, 149–162.

Bhupinderpal-Singh, Nordgren A, Ottoson Löfvenious M *et al.* (2003) Tree root and soil heterotrophic respiration as revealed by girdling of boreal Scots pine forest: extending observation beyond the first year. *Plant, Cell, and Environment*, **26**, 1287–1296.

Birch H (1958) The effect of soil drying on humus decomposition and nitrogen availability. *Plant and Soil*, **10**, 9–31.

Borken W, Xu Y-J, Brumme R *et al.* (1999) A climate change scenario for carbon dioxide and dissolved organic carbon fluxes from a temperate forest soil: drought and rewetting effects. *Soil Science Society of America Journal*, **63**, 1848–1855.

Borken W, Xu Y-J, Davidson EA *et al.* (2002) Site and temporal variation of soil respiration in European beech, Norway spruce, and Scots pine forests. *Global Change Biology*, **8**, 1205–1216.

Brown S, Schroeder P, Birdsey R (1997) Aboveground biomass distribution of US eastern hardwood forests and the use of large trees as an indicator of forest development. *Forest Ecology and Management*, **96**, 37–47.

Butnor JR, Johnsen KH (2004) Calibrating soil respiration measures with a dynamic flux apparatus using artificial soil media of varying porosity. *European Journal of Soil Science*, **55**, 639–647.

Butnor JR, Johnsen KH, Oren R *et al.* (2003) Reduction of forest floor respiration by fertilization on both carbon dioxide-enriched and reference 17-year-old loblolly pine stands. *Global Change Biology*, **9**, 849–861.

Clark KL, Gholz HL, Moncrieff JB *et al.* (1999) Environmental controls over net exchanges of carbon dioxide from contrasting Florida ecosystems. *Ecological Applications*, **9**, 936–948.

Curiel Yuste J, Janssens IA, Carrara A *et al.* (2003) Interactive effects of temperature and precipitation on soil respiration in a temperate maritime pine forest. *Tree Physiology*, **23**, 1263–1270.

CurielYuste J, Janssens IA, Carrara A *et al.* (2004) Annual $Q_{10}$ of soil respiration reflects plant phenological patterns as well as temperature sensitivity. *Global Change Biology*, **10**, 161–169.

Curtis PS, Hanson PJ, Bolstad P *et al.* (2001) Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests. *Agricultural and Forest Meteorology*, **113**, 3–19.

Davidson EA, Belk E, Boone RD (1998) Soil water content and temperature as independent and confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biology*, **4**, 217–227.

Davidson EA, Savage K, Bolstad P *et al.* (2002) Belowground carbon allocation in forests estimated from litterfall and IRGA-based soil respiration measurements. *Agricultural and Forest Meteorology*, **113**, 39–51.

Falge E, Baldocchi D, Tenhunen J *et al.* (2002) Seasonality of ecosystem respiration and gross primary production as derived from fluxnet measurements. *Agricultural and Forest Meteorology*, **113**, 53–74.

Fang C, Moncrieff JB (1999) A model for soil $CO_2$ production and transport 1. Model development. *Agricultural and Forest Meteorology*, **95**, 225–236.

Finzi AC, DeLucia EH, Hamilton JG *et al.* (2002) The nitrogen budget of a pine forest under free-air $CO_2$ enrichment. *Oecologia*, **132**, 567–578.

Finzi AC, Schlesinger WH (2002) Species control variation in litter decomposition in a pine forest exposed to elevated $CO_2$. *Global Change Biology*, **8**, 1217–1229.

Giardina CP, Ryan MG (2002) Total belowground carbon allocation in a fast growing Eucalyptus plantation estimated using carbon balance approach. *Ecosystems*, **5**, 487–499.

Hamilton JG, Thomas RB, DeLucia EH (2001) Direct and indirect effects of elevated $CO_2$ on leaf respiration in a forest ecosystem. *Plant, Cell, and Environment*, **24**, 975–982.

Hanson PJ, Edwards NT, Garten CT *et al.* (2000) Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogechemistry*, **48**, 115–146.

Hanson PJ, Wullschleger SD, Bohlman SA *et al.* (1993) Seasonal and topographic patterns of forest floor $CO_2$ efflux from an upland oak forest. *Tree Physiology*, **15**, 317–325.

Hogberg P, Nordgren A, Buchmann N *et al.* (2001) Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature*, **411**, 789–792.

Janssens IA, Landkreijer H, Matteucci G *et al.* (2001) Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biology*, **7**, 269–278.

Janssens IA, Pilaaegaard K (2003) Large seasonal changes in $Q_{10}$ of soil respiration in a beech forest. *Global Change Biology*, **9**, 911–918.

Kang S, Doh S, Lee D *et al.* (2003) Topographic and climatic controls on soil respiration in six temperate mixed-hardwood forest slopes, Korea. *Global Change Biology*, **9**, 1427–1437.

Katul GG, Lai C, Schäfer KVR *et al.* (2001) Multiscale analysis of vegetation surface fluxes: from seconds to years. *Advances in Water Resources*, **24**, 1119–1132.

King JS, Hanson PJ, Bernhardt E *et al.* (2004) A multi-year synthesis of soil respiration responses to elevated atmospheric $CO_2$ from four forest FACE experiments. *Global Change Biology*, **10**, 1027–1042.

Lee K-H, Jose S (2003) Soil respiration fine root production, and microbial biomass in cottonwood and loblolly pine plantations along nitrogen fertilization gradient. *Forest Ecology and Management*, **185**, 263–273.

Lee M-S, Nakane K, Nakatsubo T *et al.* (2002) Effects of rainfall events on soil $CO_2$ flux in a cool temperate deciduous broad-leaved forest. *Ecological Research*, **17**, 401–409.

Lichter J, Baron S, Finzi AC *et al.* Soil carbon sequestration and turnover in a pine forest after six years of atmospheric $CO_2$ enrichment. *Ecology*, in press.

Liski J, Erhard M, Taskinen O *et al.* (2003) Climatic effects of litter decomposition from arctic tundra to tropical rainforest. *Global Change Biology*, **4**, 575–584.

Liu X, Wan S, Su B *et al.* (2002) Response of soil $CO_2$ efflux to water manipulation in a tallgrass prairie ecosystem. *Plant and Soil*, **240**, 213–223.

Lloyd J, Taylor JA (1994) On the temperature dependence of soil respiration. *Functional Ecology*, **8**, 315–323.

Maier CA, Kress LW (2000) Soil $CO_2$ evolution and root respiration in 11 year-old loblolly pine (*Pinus taeda*) plantations as affected by moisture and nutrient availability. *Canadian Journal of Forest Research*, **30**, 347–359.

Mielnick PC, Dugas WA (2000) Soil $CO_2$ efflux in a tallgrass prairie. *Soil Biology and Biochemistry*, **32**, 221–228.

Moncrieff JB, Fang C (1999) A model for soil $CO_2$ production and transport 2. Application to Florida *Pinus elliotte* plantation. *Agricultural and Forest Meteorology*, **95**, 237–256.

Naidu SL, DeLucia EH, Thomas RB (1998) Contrasting patterns of biomass allocation in dominant and suppressed loblolly pine. *Canadian Journal of Forest Research*, **28**, 1116–1124.

Nobel PS (1999) *Physicochemical and Environmental Plant Physiology*, 2nd edn. Elsevier, Amsterdam.

Norby RJ, Hanson PJ, O'Neill EG *et al.* (2002) Net primary productivity of a $CO_2$-enriched deciduous forest and the implications for carbon storage. *Ecological Applications*, **12**, 1261–1266.

Oren R, Ewers BE, Todd P (1998) Water balance delineates the soil layer in which soil moisture affects canopy conductance. *Ecological Applications*, **9**, 990–1002.

Pataki DE, Oren R (2003) Species difference in stomatal control of water loss at the canopy scale in a bottomland deciduous forest. *Advances in Water Resources*, **26**, 1267–1278.

Paul KI, Polglase PJ, Smethurst PJ *et al.* (2004) Soil temperature under forests: a simple model for predicting soil temperature under a range of forest types. *Agricultural and Forest Meteorology*, **121**, 167–182.

Pumpanen J, Ilvesniemi H, Hari P (2003) A process-based model for prediction soil carbon dioxide efflux and concentration. *Soil Science Society of America Journal*, **67**, 402–414.

Qi Y, Xu M, Wu J (2002) Temperature sensitivity of soil respiration and its effects on ecosystem carbon budget: nonlinearity begets surprises. *Ecological modeling*, **153**, 131–142.

Raich JW, Nadelhoffer KJ (1989) Belowground carbon allocation in forest ecosystems: global trends. *Ecology*, **70**, 1346–1354.

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, Tufekcioglu A (2000) Vegetation and soil respiration: correlations and controls. *Biogechemistry*, **48**, 71–90.

Ramsey F, Schafer D (1997) *The Statistical Sleuth: A Course in Methods of Data Analysis*. Duxbury Press, Belmont, CA, USA.

Reichstein M, Rey A, Freibauer A *et al.* (2003) Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices. *Global Biochemical Cycles 1*, **17**, art no. 1104.

Reichstein M, Tenhunen JD, Roupsard O *et al.* (2002a) Ecosystem respiration in two Mediterranean evergreen Holm Oak forests: drought effects and decomposition dynamics. *Functional Ecology*, **16**, 27–39.

Reichstein M, Tenhunen JD, Roupsard O *et al.* (2002b) Severe drought effects on ecosystem $CO_2$ and $H_2O$ fluxes at three Mediterranean evergreen sites: revision of current hypotheses? *Global Change Biology*, **8**, 999–1017.

Rey A, Pegoraro E, Tedeschi V *et al.* (2002) Annual variation in soil respiration and its components in a coppice oak forest in Central Italy. *Global Change Biology*, **8**, 851–866.

Schäfer KVR, Oren R, Ellsworth DE *et al.* (2003) Exposure to an $CO_2$ enriched atmosphere alters carbon assimilation and allocation in a pine forest ecosystem. *Global Change Biology*, **9**, 849–861.

Schlesinger WH, Lichter J (2001) Limited carbon storage in soil and litter of experimental forest plots under elevated atmospheric $CO_2$. *Nature*, **411**, 466–469.

Singh JS, Gupta SR (1977) Plant decomposition and soil respiration in terrestrial ecosystems. *Botanical Reviews*, **43**, 449–528.

Tjoelker MG, Oleksyn J, Reich PB (2001) Modelling respiration of vegetation: evidence for a general temperature-dependent $Q_{10}$. *Global Change Biology*, **7**, 223–230.

Wear DN (2002) Land use. In: *Southern Forests Resource assessment. General Technical Reports SRS-53* (eds Wear DN, Greis JG), pp. 153–173. US Department of Agriculture, Forest Service, Asheville, NC.

Yim MH, Joo SJ, Shutou K *et al.* (2003) Spatial variability of soil respiration in a larch plantation: estimation of the number of sampling points required. *Forest Ecology and Management*, **175**, 585–588.

## 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 $\Psi$ 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, $\gamma$. 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.

## 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 $\theta$ and $T_{soil}$) 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

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

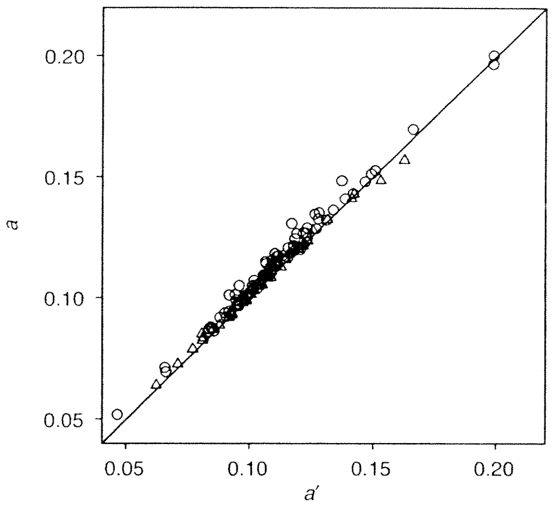

**Fig. 7** Relationship (in Appendix A) between the values of $a$ obtained from the curve fitting (data from Fig. 3b) and those calculated using Eqn (A.6) ($a'$). Triangles stand for the pine plantation (PP) and circles the hardwood forest (HW).

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 $\Psi$ is any of the five variables ($\theta$, $T_{soil}$, $R_b$, $a$, $b$, and $c$) the relative change is given by

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

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