

Changes in temperature-moisture covariance could increase soil carbon loss

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Soils store about 1.5×10^{16} g of carbon (C), about as much as terrestrial vegetation and atmosphere combined ¹. The complex interplay between factors that regulate C release from soil through respiration is not completely understood, but could potentially exert strong influence on global radiation balance and climate change². Respiration exerts strong effect on the spatial heterogeneity of terrestrial C cycle³ and its temporal variation remains more poorly understood compared to gross ecosystem production (GEP)⁴. This variation can analytically be attributed to changes in environmental factors, but forecasting individual deviations remains a challenge⁴. Here we propose that deviations of the typical covariance pattern of primary environmental drivers (temperature, T, and moisture, presented in this study as volumetric water content, VWC) may affect the deviations of respiratory C loss. Typically, T and VWC are inversely related, with warm periods being generally drier and *vice versa*, and therefore the stimulating effect of one factor is counterbalanced by unfavorable levels of the other⁵. However, should the driving variables be positively related, respiratory carbon release can increase significantly (Supplementary Fig. 1a). This hypothesis is supported by two consecutive years of ecosystem-level and soil carbon exchange data that differed in

rain fall periodicity and T-VWC-covariance. With changing climate patterns, including the intensity and frequency of rainfall events, there is the possibility that the covariance patterns of T and VWC may change, and more frequent periods of positive T-VWC covariance may lead to greater loss of soil carbon, and contribute to greater radiative forcing on Earth's energy budget.

The susceptibility of soil C stores to changing climate ⁶ is of great concern as the regulation of soil and ecosystem respiration remains a major source of uncertainty in estimating regional and global carbon balance ^{2,7}. The uncertainty is greatest about rich organic soils where even small changes in growing season length and environmental conditions could trigger the release of large amounts of C. For example, in UK the loss of soil C has been the largest in C-rich soils, reaching as high as 3% yr⁻¹ over 25 years ⁸. The universal trend of declining soil C stocks was attributed to the combined effect of climate and land use change ^{8,9}, but the exact mechanism remains a matter of debate ^{10, 11}.

Modeling and scaling up respiration measurements remains a challenge because the effects of temperature, moisture and substrate availability usually co-vary ¹² and their effects are difficult to conclusively separate. Although in essence the upscaling models are straightforward and been in use pretty much unchanged since Arrhenius ^{13, 14}, the implicit assumptions made in the process of selecting a particular version of upscaling model ^{12, 15} do affect the time-integrated flux estimates. In fact, model choice has been found to have greater effect on annual ecosystem respiration (ER) estimates than the uncertainties in the measurement of driving variables (Hagen et al., 2006; Kruijt et al., 2004). Therefore, there is a need for more sophisticated mechanistic respiration models that could help explain and forecast the variability in land surface C exchange.

In current study, we traced contrasting annual SR at a loblolly pine (*Pinus taeda* L.) plantation, growing on the lower coastal plain of North Carolina, USA, to different precipitation frequency and T-VWC-covariance during two otherwise climatically similar years. The entire ecosystem gained 474 ± 119 g less C per m^2 per year during a year with fewer and more intense rain events (i.e. 2005) than during a year with smaller and more frequent rain events (2006). This difference was largely due to the 269 ± 18 g C $\text{m}^{-2} \text{yr}^{-1}$ (30%) difference in SR, whereas the interannual differences in ER and GEP were smaller than the uncertainty due to gapfilling (Table 1). Furthermore, the biometric estimates of net ecosystem productivity (NEP_B) were nearly identical between the two years. However, biometric relationships are not well suited for identifying variations in belowground allocation, and root growth and turnover, which at least in principle could have contributed to the contrasting NEE. It is conceivable that the deeper aerated soil layer, and increased nutrients released from soil organic matter decomposition due to increased SR could stimulate root growth. However, the slight difference in belowground NEP_B (Table 1) was opposite to what one would expect if the lower NEE in 2005 was caused by greater belowground allocation.

Compared to Duke Forest, a similar-aged loblolly pine plantation in similar climate but on upland soils, both GEP and ER were 20-23% higher at current site¹⁶. The difference in respiration most likely derives primarily from much larger soil carbon stores at our site, whereas the greater productivity could be due to both better moisture availability and nitrogen released in the decomposition of soil organic matter¹¹. While carbon balance studies from ecosystems with C-rich soils are rare, Hirano et al.¹⁷ reported comparable differences between a drained tropical peatland forest in Indonesia and upland forests in Amazon, which are also exposed to similar climatic conditions. They observed about 22-31% higher annual ER at the peatland site than reported for the Amazonian forests^{18, 19}.

In current study, the interannual difference in SR was not directly attributable to contrasting weather patterns. The mean monthly temperatures were very similar during the two years and slightly lower than the 30-year normal at the nearby weather station (Supplementary Fig. 2). Likewise, the annual precipitation was similar to the long-term normal. Even the monthly sums were not too dissimilar between the two years during the first half of the growing season. However, the individual rain events were about twice as frequent and twice smaller in 2006 than 2005 (Supplementary Fig. 3). The contrast between years was largest from May through September, when 51% of total rainfall (732 mm) came in events greater than 50 mm d⁻¹ in 2005, whereas in 2006 only 25% (of total of 744 mm) fell in such large events. A detectable increase in soil volumetric water content (VWC; >1% in the top 30 cm) required about 10-15 mm of rain over 3 days, and such events were separated by an average of 9.1 days in 2005 and 6.7 days in 2006 (May-September).

Between rain events, SR decreased in parallel with decreasing VWC (Fig. 1), and increased by variable amount following the rain events. There was no correlation between the extent of SR stimulation and the magnitude of the triggering rain event (data not shown). Rather, the extent of stimulation depended on whether the increase in VWC coincided with a positive change in temperature. We observed a general seasonal pattern in the correlation between T and VWC, showing a predominantly negative correlation in spring and summer, and a positive correlation in fall and winter (Fig. 2a). Similar pattern described the correlation of the rate changes in daily T and VWC (dT (°C d⁻¹), and dVWC (% d⁻¹), Fig. 2b), which showed stronger relationship than T and VWC *per se*. Rain events triggered deviations in this relationship, which in turn were reflected in SR. Large rain episodes (>50 mm week⁻¹) always decreased soil temperature and caused negative deviations in the T-VWC-covariance (data not shown), but smaller rain events were as often associated with positive deviations as with negative ones. However, the response of SR to these changes was not symmetrical.

Positive deviations in dT-dVWC relationship were associated with greater SR, whereas negative deviations did not significantly reduce SR (Fig. 3). The biggest contrast between the years derives from unequal representation of positive and negative deviations from the seasonal norm during the period of peak plant activity (weeks 16-35, late April through early Sept.), but the response of SR to the deviations was also more pronounced during the high-SR year of 2005.

The SR-VWC covariation apparent in Fig. 1 was confirmed with spectral analysis, which showed spectral peaks at about weekly and biweekly intervals (Supplementary Fig. 4). However, the exact extent of VWC effect on SR remains uncertain as some of the observed patterns suggest that VWC effect may have been secondary. For example, the co-spectral amplitude of SR and VWC had weekly and biweekly maxima during both years, albeit of different magnitudes. The cospectral amplitude of SR and GEP also had maxima at the same frequencies, and the greater amplitude at 5-7 days in 2005 suggests that the VWC effect on SR may have been secondary, possibly mediated through GEP and carbohydrate availability²⁰. If VWC were the primary driver of the cyclic behavior of SR, one would have expected that SR would be more responsive to improved moisture conditions in 2005, when the intervals between rain events were longer, and the mean VWC slightly lower ($P < 0.0001$ in May and June, in July and August the pattern reversed). This, however, was not observed. In fact, SR peaked at intermediate VWC (Supplementary Fig. 1b, c), suggesting that in 2006 with higher mean GWT and VWC, the moisture conditions may have been supra-optimal for SR, and that VWC may not have been limiting. Because of this reversal of the SR-VWC relationship, and variation in T-VWC covariance (Fig. 2b), SR may exhibit contrasting VWC response during different seasons¹⁷.

While separating the direct and indirect effects of VWC will remain difficult, the more frequent low GWT in 2005 may have stimulated SR by exposing deeper soil

layers to aerobic conditions. It is possible that soil CO₂ emission may have increased after rain events due to the water displacing the CO₂-rich soil air. Based on the observed time-lag between major rain events and the consequent increase in GWT, we estimated that with 10 cm increase in GWT over 10 hours (e.g. DOY 125, Supplementary Fig. 3), soil porosity of 40%, and soil air CO₂ concentration of 2000 μmol mol⁻¹, sustained increase in SR throughout such an event could have been on the order of 0.1 μmol m⁻² s⁻¹. However, this borders on the measurement error of SR, and it also would not explain the sustained SR once GWT began to decrease. Therefore, it is unlikely that such “outwashing” contributed significantly to higher SR following rain events.

Our results suggest that variations in rainfall distribution and intensity, and its covariance with temperature may affect the decomposition of soil carbon in coastal areas with high water table and C-rich soils. As the projected changes in precipitation patterns²¹ are expected to affect annual moisture dynamics more towards the patterns observed in 2005, the coastal wetlands, both drained and undrained, are expected to have more of their soil C reserves exposed to aerobic conditions. The greater fluctuations in GWT and VWC may prove more favorable for aerobic decomposition and root growth. The annual precipitation patterns in both 2005 and 2006 showed significantly greater rainfall in summer and lower in winter than the 30-year mean monthly sums (Supplementary Fig. 2), but it is not clear if this would represent a trend.

Our findings corroborate those of others^{6,8} pointing to the vulnerability of C-rich soils to decomposition due to the combined effects of climate and land use change. It is likely that our study system exhibited greater sensitivity to these environmental triggers than ecosystems on drier and poorer substrate. However, given that the world's wetlands stock about 529×10¹⁵ g C²² and recent evidence pointing to its sensitivity to climate change-related decomposition, these processes represent a potentially important

positive feedback mechanism between the climate-biosphere interaction², and a novel link between ecosystem C and water cycles.

Methods summary

The study site is a Loblolly pine (*Pinus taeda* L.) plantation, located at 35°48'N 76°40'W, on the lower coastal plain in North Carolina, USA. The area is flat, <5 m above sea level, on deep Belhaven series histosol (loamy mixed dysic thermic terric Haplosaprists). The canopy height was 13 m, and growing season leaf area index (LAI) was 3.0 m² m⁻² during both years. In winter LAI decreased to 2.6.

The standing biomass was estimated in 13 7 m diameter Tier-3-type vegetation survey plots²³ using standard allometric relationships²⁴⁻²⁶ with details given in the Supplementary Methods. Ecosystem-level fluxes were measured with open-path eddy covariance system at the height of 19 m and the fluxes were calculated following standard protocols²⁷. Data quality control, screening criteria and gapfilling protocols were the similar to Noormets et al.²⁸, and are explained in further detail in Supplementary Methods. Soil respiration (SR) was measured bi-weekly in 5 out of the 13 vegetation plots using portable infrared gas analyzers (LI-8100 (Licor, Lincoln, Nebraska, USA) with 8100-102 survey chamber, and EGM-4 (PP Systems, Hertfordshire, United Kingdom) with SRC-1 chamber) and permanently installed 10-cm diameter soil respiration collars. Soil temperature at 10 cm was measured at the time of SR measurements. Starting May, 2005, SR was measured continuously near the base of the eddy covariance instrument tower with LI-8100 and an 8100-101 long-term chamber. The relationship between biweekly survey SR chamber measurements and soil temperature throughout the stand was used to interpolate between measurements. The automated chamber measurements were used to evaluate temporal covariance with

temperature, moisture and ecosystem gross productivity during the growing season, using finite Fourier transform in the SPECTRA procedure in SAS (v9.1).

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Table 1 | Annual carbon fluxes (g C m⁻² yr⁻¹)

	Year	
	2005	2006
NEP _{B-coast} ^{26 *}	800±240 [†]	810±320
NEP _{B-piedmont} ²⁵	860±270	870±330
NEP _{B-loblolly} ²⁴	760±270	700±490
NEP _{EC} = (-NEE)	361±242	835±123
ER	2121±280	2074±193
GEP	2482±522	2911±316
SR	959±78	690±60
Aboveground NEP _{B-coast} ²⁶	650±200	640±250
Belowground NEP _{B-coast} ²⁶	150±40	170±80
Belowground NEP _B :	0.19	0.21
Total NEP _B		

* NEP_{B-coast} – net ecosystem productivity using allometric relationships for loblolly pine plantations in the lower coastal plain in North Carolina; NEP_{B-piedmont} – net ecosystem productivity using allometric relationships for loblolly pine in the North Carolina upland or piedmont area; NEP_{B-loblolly} – net ecosystem productivity using allometric relationships for loblolly pine data throughout its range.

[†] The error terms for biometric NEP (NEP_B) are the standard deviations of the 13 subplot estimates (n=13), and the gapfilling uncertainty for eddy covariance-based net ecosystem productivity (NEP_{EC}), ecosystem respiration (ER), gross ecosystem productivity (GEP) and soil respiration (SR).

Figure legends

Figure 1 | Seasonal dynamics of precipitation (P), soil volumetric water content (VWC) and soil respiration (SR). **a, b,** Daily P in 2005 and 2006; **c, d,** Daily VWC (line) and automatic SR (gray circles) in 2005 and 2006. Only periods when simultaneous SR and VWC coverage was available are shown. The frequency of and magnitude of rain events is reflected in VWC, and differed by nearly two-fold between the years. All respiration data were measured with an automated, continuously operating system. No modeled data are shown.

Figure 2 | Coefficients of determination (R^2) of weekly correlations between soil temperature (Ts) and soil volumetric water content (VWC) and the rate changes in Ts and VWC. **a,** R^2 of correlation between Ts and VWC; **b,** R^2 of the daily rate change in Ts and VWC (dT and dVWC, respectively). The small symbols refer to weekly correlations, and the large symbols to monthly correlations in 2005 (filled) and 2006 (open). The third-degree polynomials are fitted to the weekly Pearson correlation coefficients, with the R^2 of the polynomial fits shown on the Figure.

Figure 3 | The dependence of soil respiration (SR) on the deviation in the weekly correlation between the rate change in soil temperature (dT_s) and soil volumetric water content (dVWC) compared to the seasonal mean as estimated on Figure 2. Data are weekly means of automated (squares) and portable survey chamber (circles) measurements in 2005 (filled) and 2006 (open). Although stronger than in 2006, the trend in 2005 was only marginally significant ($p=0.096$, $R^2=0.73$ for survey measurements; $p=0.259$, $R^2=0.32$ for

automatic measurements). Only weeks 16 through 35 (late April through early September) are shown. During this period the years differed in the frequency and magnitude of rainfall events, which regulated the temporal dynamics of SR.

Figure 1

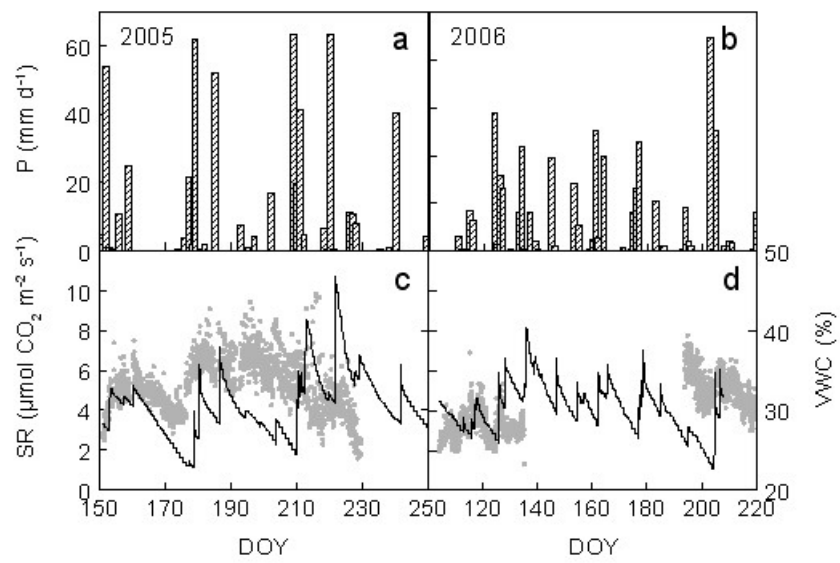


Figure 2

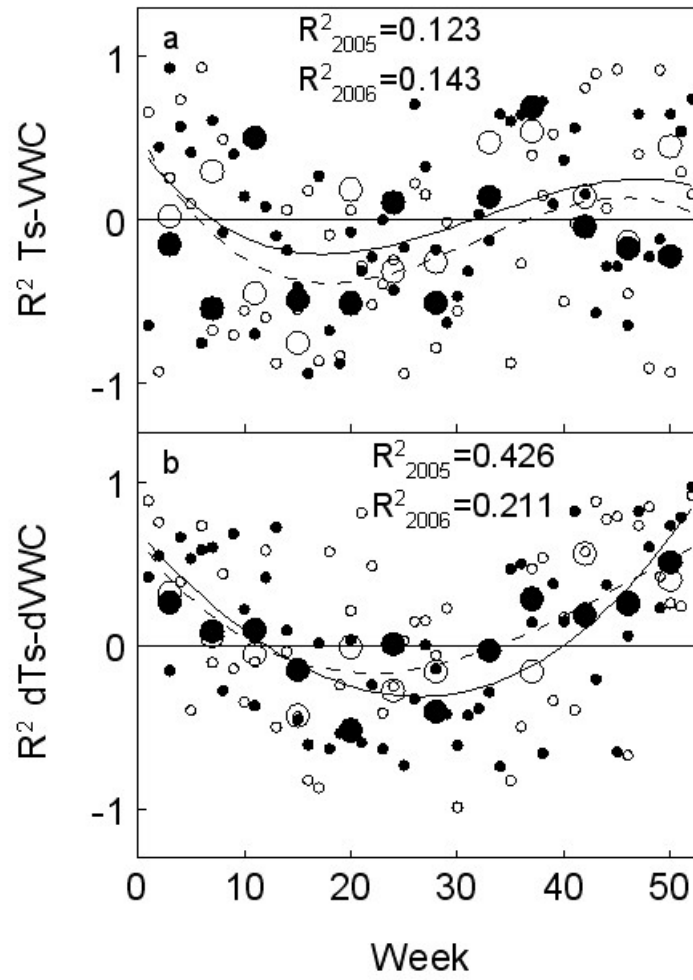
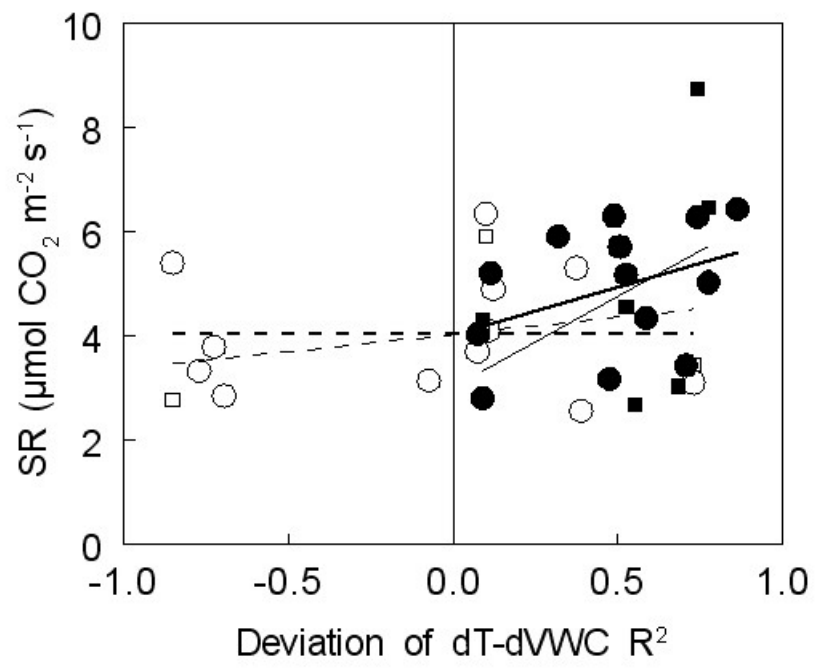


Figure 3



Supplementary Methods

Biometric estimation of net ecosystem productivity. The biomass (B) of loblolly pine was estimated with three sets of allometric models²⁴⁻²⁶. The models were based on tree height and diameter at breast height (1.5 m), measured in the 13 Tier 3-type vegetation survey plots (7 m in diameter²³), located throughout the 1 square mile study area. NEP was calculated as the annual change in biomass estimates at any given plot, and the estimates in Table 1 represent the mean and standard deviation of the 13 plots. As the models differed in their geographical specificity, the biomass estimates differed by up to 40% (the generic model for loblolly pine²⁴ was consistently higher than the site-specific models^{25,26}, data not shown). However, NEP estimates were within 15-25% of each other, and the standard errors of the mean NEP estimates from different methods overlapped (Table 1).

Micrometeorological parameters. Micrometeorological parameters were measured at the central eddy covariance tower every 20 seconds and recorded as 30-minute means. Air temperature and humidity were measured above and throughout the canopy with HMP45AC probes (Vaisala, Finland). Soil temperature was measured with CS107 probe (Campbell Scientific (CSI), Logan, Utah, USA), soil volumetric water content with CS616 time domain reflectometer (CSI), net radiation with Q7.1 (Radiation and Energy Balance Systems, Seattle, Washington, USA), photosynthetically active radiation with LI-190SB quantum sensor (Licor, Lincoln, Nebraska, USA), ground water table with pressure water level data logger (Infinites Inc., Port orange, Florida, USA) and precipitation with TE525 tipping bucket rain gauge (Texas Electronics, Dallas, Texas, USA).

Eddy flux measurements and fetch. The turbulent exchange of CO₂ between the forest canopy and atmosphere was measured from throughout 2005 and 2006 using the eddy-

covariance method. The 25 m instrument tower was located in the middle of the 1 square mile stand. The minimum fetch was 500 m (26× measurement height of 19 m). However, in most directions, including west, the predominant wind direction, uniform canopy of the same type covered the nearest 1300 m (nearly 70× measurement height). The turbulent flux showed no directional variability, suggesting that the fetch was sufficient for periods when other quality control criteria were met (below). The tower was instrumented with an LI-7500 open-path infrared gas analyzer (Li-Cor Inc., Lincoln, Nebraska, USA), a CSAT3 3-dimensional sonic anemometer (Campbell Scientific (CSI), Logan, Utah, USA) and a CR5000 data logger (CSI). The equipment was powered by four 120 A·h deep-cycle marine batteries, recharged by solar panels (4×100W). The 30-minute mean fluxes of CO₂ were computed as the covariance of vertical wind speed and the concentration of CO₂, using a custom software package (EC_Processor, <http://research.eescience.utoledo.edu/lees/ECP/ECP.html>) designed for processing open-path eddy covariance data. The algorithm uses the formulation of Leuning²⁷ in the planar fit coordinate system²⁹, which was defined from the entire season's mean wind data. The turbulent fluxes were adjusted for fluctuations in air density³⁰. Sonic temperatures were corrected for changes in humidity and pressure³¹. The 30-minute fluxes were corrected for the warming of IRGA according to³². Net ecosystem exchange of CO₂ (NEE) was calculated as the sum of turbulent flux and change in CO₂ storage in the canopy air space. CO₂ concentration was measured at four heights (about 0.05×, 0.2×, 0.6× and 0.9× of canopy height) in the canopy air column, and the storage flux was estimated as the mean rate change during an averaging period.

Quality control and gapfilling of eddy covariance data. Data quality was judged by atmospheric stability and flux stationarity³³ during well-developed turbulence³⁴. Overall data coverage was 42% (2005) and 47% (2006), with gaps caused primarily by periods of dew and precipitation, and poorly developed turbulence ($u^* < 0.20$). The latter often co-occurred with very stable or very unstable atmospheric conditions. The extent

of data coverage observed in this study has been found to be adequate for unbiased gapfilling

However, it has been demonstrated with artificially generated gaps that if the gaps are randomly distributed between all functional states (diurnally and seasonally) reliable gapfilling model can be built on as little as 25% of total data³⁵. We used a dynamic parameter model, where the respiration model was parameterized first using only the nighttime data, and once daytime respiration estimates were available, gaps in daytime NEE were filled. The performance of the gapfilling model was typical network-wide standards. A recent comprehensive comparison of commonly used gapfilling methods³⁶, of which our method was a part of, showed that throughout different methods, at 30-minute level there remains about 3-5% random error, which is probably more related to the uncertainty and sampling error of the turbulent exchange than to model properties. Uncertainty due to gapfilling was estimated as the sum of mean model residuals, integrated over all gapfilled periods, and are shown in Table 1.

Spectral analysis. The co-spectral density of continuously measured SR (using the automated chamber) and soil volumetric water content (VWC) from May through September was calculated using finite Fourier transform (PROC SPECTRA in SAS v9.1). The data were centered, but not detrended because of the reversal of the trend in mid-season. Gaps in the SR data were padded with zeros to obtain a season-long record despite gaps in the data, but this does not affect the spectral densities. The use of automated chamber data allows the evaluation temporal covariance with VWC, without confounding the covariance spectrum with the assumptions of the gapfilling model.

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Supplementary Figure Legends

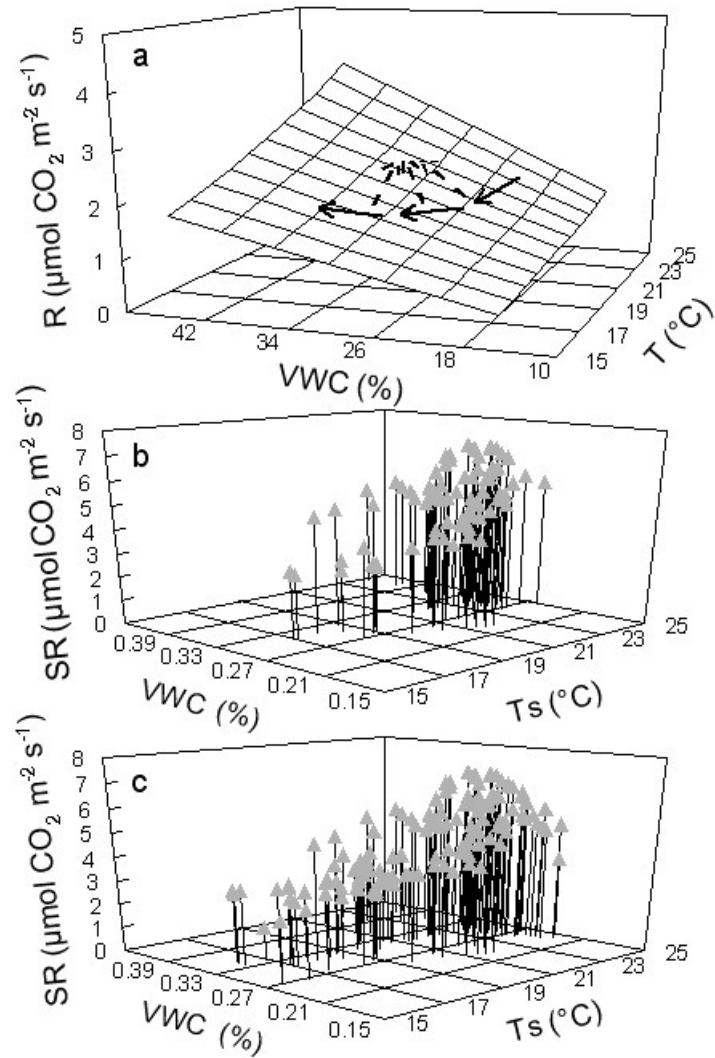
Supplementary Figure 1 Dependence of respiration on temperature and moisture. **a**, Stylized response surface of respiration (R) to soil temperature (T) and volumetric water content (VWC). The solid arrows on the surface indicate that typically T and VWC are inversely related, i.e. increased moisture decreases T and *vice versa*, which leads to little net change in R. The dashed arrows illustrate that simultaneous increase in both T and VWC would lead to much greater stimulation of R than would an increase in either condition alone. Growing season (weeks 16 through 39, late April through early October) soil respiration (SR) in 2005 (**b**) and 2006 (**c**) as a function of soil temperature (Ts) and soil volumetric water content (VWC).

Supplementary Figure 2 Monthly air temperature and precipitation in comparison with 30-year normals. **a**, Monthly mean air temperature (Ta), and **b**, cumulative precipitation (P) during the two study years. The long-term means were obtained from NOAA National Climatic Data Center (<http://www.ncdc.noaa.gov/oa/ncdc.html>).

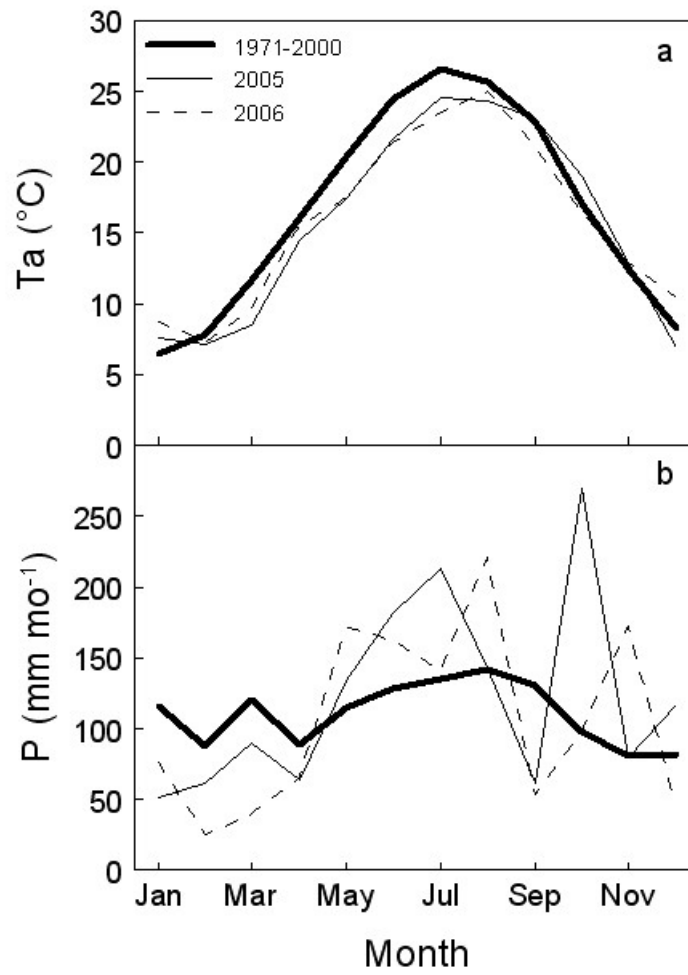
Supplementary Figure 3 Seasonal dynamics of microclimatic variables. **a**, Daily mean soil temperature (Ts), **b**, soil volumetric water content (VWC), **c**, daily total precipitation (P), and **d**, daily mean ground water depth (GWT) at a *Pinus taeda* plantation in the lower coastal plain in North Carolina, USA.

Supplementary Figure 4 Co-spectral amplitude (CSA) of soil respiration (SR) and soil volumetric water content (VWC; a), and of SR and gross ecosystem productivity (GEP; b) during the two study years. The spectral peaks do correspond to the frequency of rain events, which occurred at about biweekly interval in 2005, and at a weekly interval in 2006. The CSA, however, is not proportional to the predominant rain event frequency, suggesting significant interactive effects between moisture, GEP and potentially other drivers. The increasing amplitude at lower frequencies (longer period) is due to seasonal variation in all variables, and is not of interest in current analysis.

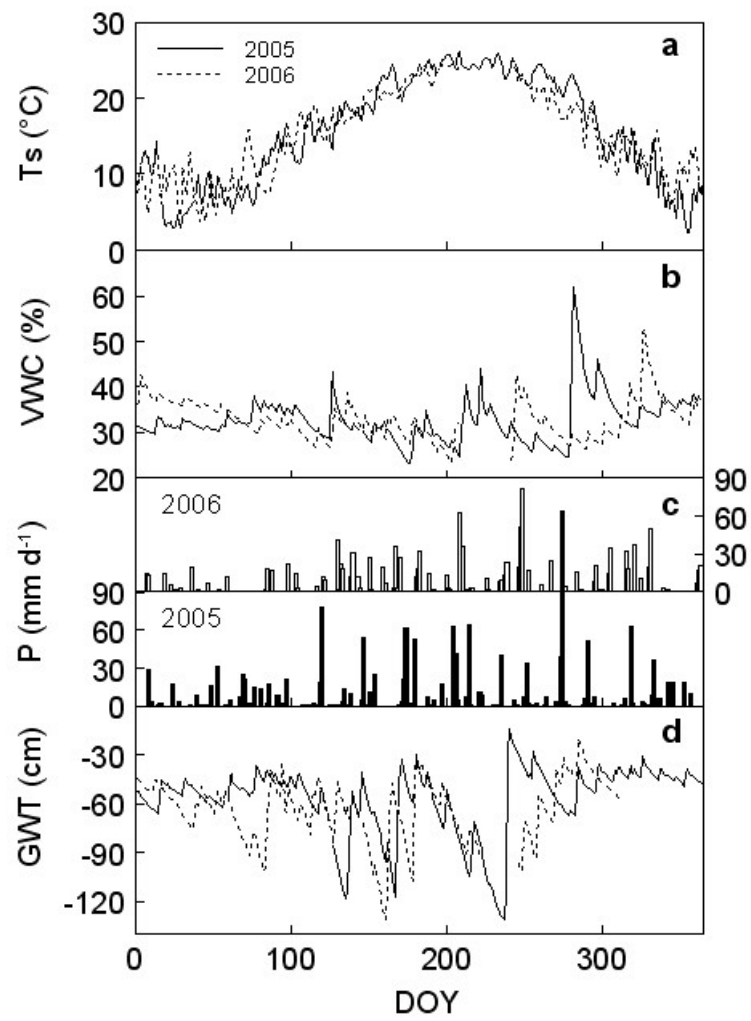
Supplementary Figure 1



Supplementary Figure 2



Supplementary Figure 3



Supplementary Figure 4

