

Carbon dioxide exchange and early old-field succession

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[1] Old-field succession is a widespread process active in shaping landscapes in the eastern United States, contributing significantly to the terrestrial sink of atmospheric carbon dioxide, particularly at midlatitudes. However, few studies document ecosystem-scale carbon dioxide exchange during the early years of old-field succession, particularly during the temporal transition from cultivation to abandonment. Rates of carbon dioxide exchange were measured for 20 months over a field in Virginia during the transition from an actively cultivated crop field to an unmanaged old field, including one season of crop growth and two seasons of successional growth. Ecosystem carbon respiration exceeded carbon assimilation during growing seasons and dormant periods, resulting in a net flux of carbon dioxide from the biosphere to the atmosphere of between 1.27 and 1.85 kg C m⁻² for the entire 20-month period (an average loss to the atmosphere of 2.07 to 3.01 g C m⁻² day⁻¹). Crop growth (from 10 January 2001 to 6 June 2001) resulted in a net loss of between 0.22 and 0.32 kg C m⁻² to the atmosphere (an average daily loss of 1.5 to 2.2 g C m⁻²), whereas the two seasons of successional growth combined contributed an additional 1.05 to 1.53 kg C m⁻² to the atmosphere (an average daily loss of 2.2 to 3.3 g C m⁻²). Empirical modeling was used to demonstrate control of ecosystem carbon respiration by soil temperature, soil moisture status, and the status of vegetation growth activity. Tower-based estimates of carbon loss were compared at both short (half hourly) and long (seasonal) timescales to independent, ground-based measurements. Using estimates of carbon exchange from previously published studies, these results are placed in the context of a trajectory of old-field succession.

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1. Introduction

[2] Though reforestation of agricultural land is known to contribute to the northern hemisphere midlatitude terrestrial carbon dioxide sink [Houghton *et al.*, 1999; Caspersen *et al.*, 2000; Schimel *et al.*, 2001], temporal dynamics of the land-atmosphere exchange of carbon dioxide remain largely unstudied across the transition between cultivation and unmanaged old-field succession. Theory of secondary succession [Gorham *et al.*, 1979] predicts a substantial negative pulse in net ecosystem production (NEP) of carbon immediately following a destructive disturbance. In the context of the transition from agriculture to old-field succession, cultivation may be considered a state of perpetual disturbance characterized, for example, by repetitive cycles of planting, harvesting and tilling. Depending on cultivation practices a negative annual NEP may characterize such

ecosystems [Curtin *et al.*, 2000; Brye *et al.*, 2002]. And because NEP is sensitive to land-use practices, it may be possible for a negative annual NEP to persist or even increase during early succession owing to the residual effects of cultivation in combination with lagging plant carbon storage during the land-use change from cultivation to abandonment [Gorham *et al.*, 1979]. Managed old-field succession (including practices such as burning, sowing seed and mowing) introduces additional variability into an already complex natural process. Therefore, to examine transitional NEP in its simplest terms, we limit the scope of this paper to the transition from crop cultivation to unmanaged old-field succession.

[3] Previous studies addressing NEP in the context of reforestation and old-field succession included primarily biometric methods to identify eventual biomass accumulation over the course of years to decades following abandonment [e.g., Bazzaz, 1996; Van der Putten *et al.*, 2000; Liski *et al.*, 2001; Elliott *et al.*, 2002]; however, such studies lack temporal resolution fine enough or do not include all data necessary to distinguish the sharp decrease in NEP that may characterize the transition between cultivation and abandonment. Furthermore, interpolation of biometric estimates of carbon dioxide exchange to timescales shorter than full reforestation may yield large uncertainties that mask

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short term dynamics of these ecosystems [Houghton *et al.*, 1999; Wang *et al.*, 1999; Barford *et al.*, 2001]. An accurate estimate of carbon sequestration by old-field succession at midlatitudes should consider the environmental controls on carbon dioxide exchange during the early stages of reforestation, and particularly during the transition from the disturbed state of cultivation to early old-field succession.

[4] Of the constituent fluxes of NEP, P_G (gross photosynthetic uptake) and R_E (ecosystem respiration), R_E is responsible for much of the temporal and spatial variability in rates of carbon sequestration observed among ecosystems at regional and seasonal scales [Raich and Schlesinger, 1992; Valentini *et al.*, 2000; Epstein *et al.*, 2002; Reichstein *et al.*, 2002]. R_E is comprised of plant (autotrophic) respiration as well as decomposition (heterotrophic respiration). Temperature has been shown to control partially rates of both plant respiration [Ryan, 1991; Griffin *et al.*, 2002] and decomposition of soil organic matter [Lloyd and Taylor, 1994; Winkler *et al.*, 1996]. Consequently, R_E is often modeled as a direct function of soil temperature [e.g., Wofsy *et al.*, 1993; Goulden *et al.*, 1996; Barford *et al.*, 2001]. In addition to soil temperature, both autotrophic and heterotrophic respiration are correlated with, and partially controlled by, soil moisture status [e.g., Bunnell *et al.*, 1977; Baldocchi *et al.*, 1985; Skopp *et al.*, 1990; Ryan, 1991; Lomander *et al.*, 1998; Steduto and Hsiao, 1998; Fang and Moncrieff, 1999].

[5] Because ecosystem respiration often supersedes photosynthetic uptake and is therefore the dominant component of NEP during early succession [Gorham *et al.*, 1979], identifying the functional dependence of respiration on environmental state variables is crucial for understanding the dynamics of terrestrial carbon sequestration. Furthermore, understanding the dynamics of carbon sequestration throughout early succession is necessary for accurate assessment of the impact of such ecosystems on the global budget of carbon dioxide.

[6] Eddy covariance methodologies can provide semi-continuous, high-frequency measurements of the vertical carbon dioxide flux between a land surface and the atmosphere [Baldocchi *et al.*, 1996], and these measurements may be used to estimate NEP for periods as brief as tens of minutes. The eddy covariance carbon dioxide flux is the net sum of the landward and skyward fluxes of carbon dioxide (P_G , and R_E , respectively), and a small net flux (NEP) is actually the balance between these relatively large component fluxes [Moncrieff *et al.*, 1996]. Because P_G and R_E partially cancel one another, they potentially mask the full responses of the component fluxes to the environment. Modeling may be used to reconstruct the constituent fluxes of carbon dioxide [e.g., Wofsy *et al.*, 1993; Aubinet *et al.*, 2000; Suyker and Verma, 2001], but it requires knowledge of the functional relationships between fluxes and environmental state variables.

[7] To determine rates of carbon dioxide exchange during early ecosystem succession, field measurements of eddy covariance fluxes and environmental state variables were made during the temporal transition from cultivation to early old-field succession. These measurements represent the commencement of an effort to monitor long-term interactions between a successional land surface and the atmosphere, an effort whose ultimate aims are aligned with the broader goals of the global flux network community: to

quantify the rates of carbon dioxide exchange over various timescales, and to understand the mechanisms influencing carbon dioxide exchange between the atmosphere and a successional ecosystem [Baldocchi *et al.*, 1996].

[8] Many studies of old-field succession employ a chronosequence approach, in which multiple plots representing various successional ages are juxtaposed to explore certain temporal dynamics of succession [e.g., Knops and Tilman, 2000; Law *et al.*, 2001]. However, differences in land-use histories prior to agricultural abandonment, management strategies during succession, and variability in the natural environment from plot to plot may contribute additional error to these reconstructions. This is not to say that a single-field approach to studying old-field succession is not without its faults; foremost may be the risk of extrapolating results from a single field site to old-field succession in general. Even so, this study provides new insight into the nature of NEP and its controls at high resolution during an important ecological transition. Additionally, observing successional processes and dynamics in real time may be a daunting task for research questions that require long timescales, but for the purpose of studying controls on NEP across the relatively short transition between cultivation and old-field succession (perhaps 1 to 2 years) a single-field approach employing eddy covariance is well suited.

[9] The objectives of this paper are threefold: (1) to provide high temporal resolution quantification of carbon dioxide exchange during the transition between cultivation and old-field succession in an eastern U.S. ecosystem; (2) to explore the major dynamics of carbon dioxide exchange through analysis of factors affecting ecosystem respiration; and (3) to evaluate how carbon dioxide exchanges observed at this site fit into the larger context of a generalized successional trajectory for temperate midlatitudes. We emphasize the importance of ecosystem respiration to the early stages of old-field succession as well as its potential effect on estimates of total carbon sequestered by successional ecosystems over half hourly and seasonal timescales.

2. Methods

[10] This study was carried out at Blandy Experimental Farm (BEF) in Virginia, USA (39.06°N, 78.07°W, elevation 183 m) in a 10 ha old field (successional field) between 10 January 2001 and 15 September 2002. The region has a modern agricultural history dating back over 200 years, and much of BEF has been under cultivation since the mid-1800s [Nelson and Byrd, 2000] due in part to the well-drained silt-loam soils that underlie the area [Soil Conservation Service, 1982]. The successional field is the youngest in a chronosequence of three adjacent old-field plots; the two neighboring fields were also cultivated prior to abandonment in 1920 and 1986. The field abandoned in 1920 is now a secondary forest while the field abandoned in 1986 contains a mixture of grasses, forbs and trees [Riedel and Epstein, 2005]. The successional field has a mixed agricultural land-use history typical of the region [Nelson and Byrd, 2000] and included several decades of livestock grazing followed by conventional row crop cultivation (including corn, barley, and rye) for 10 to 15 years prior to abandonment in 2001. Row crop cultivation utilized a no-till approach in the last several years preceding abandonment, and no land management

strategies (e.g., plowing, herbicide, seeding) have been applied since the final harvest of rye from the successional field on 6 June 2001. Despite no-till cultivation in later years, the successional field displays a “plow zone” of homogeneous soil to a depth of 15 cm. Furthermore, the successional field is depleted in soil organic carbon (SOC) relative to the nearby secondary forest. In 2000, SOC concentrations in the successional field were less than 2% (compared to approximately 3.5% SOC in the secondary forest) [Riedel and Epstein, 2005], further testament to a long history of agricultural land use at this site [Knops and Tilman, 2000].

[11] Measurements were initiated during the final season of crop growth (January through June 2001) and continued through the early stages of old-field succession (June 2001 through September 2002). Bare soil conditions lasted approximately two weeks following harvest of the rye crop, and then successional vegetation began to grow. By late summer 2001 the successional field was dominated by the C₄ grass *Setaria glauca*; however, by spring 2002 *Conyza canadensis*, *Solidago spp.* and *Carduus spp.* (all C₃ forbs) had replaced *Setaria* as the dominant vegetation.

2.1. Environmental Conditions

[12] Measurements were collected using an instrument tower as well as an array of ground-based instruments installed at the center of the successional field. Half-hourly fluxes of momentum (U_* , m s⁻¹), sensible heat (H , W m⁻²), latent heat (LE , W m⁻²), and carbon dioxide (F_c) were measured using an eddy covariance system consisting of a triaxial sonic anemometer (CSAT3, Campbell Scientific, Logan, Utah) and an open-path CO₂/H₂O infrared gas analyzer (7500, LI-COR, Lincoln, Nebraska) installed 3.5 m above the ground and sampling at 10 Hz. We adopted the standard micrometeorological sign convention for F_c of positive fluxes from the land to the atmosphere. Standard tilt correction, spike filtering, sonic anemometer virtual temperature correction, and Webb correction were performed on half-hourly flux data [Webb et al., 1980; Schotanus et al., 1983; Kaimal and Finnegan, 1994; Paw U et al., 2000].

[13] Fluxes measured during periods of low nighttime turbulence were filtered from the results using a U_* threshold [Baldocchi et al., 1996; Goulden et al., 1996]. Where appropriate (i.e., during periods assumed to have no photosynthetic uptake), filtered or missing F_c measurements were substituted with synchronous values of R_E , modeled using methods described in the following section. Daily averages of energy fluxes were used to calculate energy balance closure using linear regression of $H + LE$ versus $R_N + G$. Additionally, flux measurements were used to perform a footprint analysis [Hsieh et al., 2000]. The composite flux footprint was integrated into a geospatial model of the successional field using a procedure similar to that of Amiro [1998], allowing quantification of the uncertainty associated with contributions from neighboring land surfaces to the measured flux. The flux footprint and energy balance analyses were incorporated into a full uncertainty analysis for the carbon budget of the successional field based on the methods of Goulden et al. [1996] and Moncrieff et al. [1996].

[14] Complementary measurements included above-ground radiometer (CNR1, Kipp and Zonen, Delft, Nether-

lands) measurements of longwave and shortwave net radiation (R_N , W m⁻²) at 2.75 m above the ground surface and soil heat flux (G , W m⁻²) measured using an array of heat flux plates (HFT3, Campbell Scientific, Logan, Utah) buried 5 cm below the soil surface and approximately 5 m away from the tower base. Precipitation was measured using a tipping bucket (TE525, Texas Electronics, Dallas, Texas) and volumetric water content (θ , m³ m⁻³) was measured using a reflectometer probe (CS615, Campbell Scientific, Logan, Utah) installed vertically to measure moisture in the upper 30 cm of soil. A second reflectometer probe was installed horizontally in the vicinity of the heat flux plates to measure soil moisture at a depth of 5 cm. Soil temperature (T_S), measured using a pair of thermocouples (Omega Engineering, Stamford, Connecticut) placed at 2.5 cm and 7.5 cm depth (surrounding each heat flux plate) and soil moisture at 5 cm were used to correct G for changes in heat storage within the top 5 cm of the soil [Artya, 2001].

[15] In addition to tower-based measurements, soil respiration, (R_S , $\mu\text{moles m}^{-2} \text{s}^{-1}$), was measured at various points within the successional field during the 2002 growing season using a closed path CO₂ infrared gas analyzer (6200, LI-COR, Lincoln, Nebraska) with a soil chamber attachment. Soil respiration measurements were made by placing the soil chamber over one of 24 PVC collars permanently installed within the successional field. Similar measurement techniques are described by Law et al. [1999] and Curtis et al. [2002]. Simultaneous measurements of soil temperature and volumetric soil moisture were obtained using a hand-held thermometer and portable reflectometer probe (HydroSense, Campbell Scientific, Logan, Utah).

[16] Additionally, aboveground biomass from three 1-m² plots was harvested, dried and weighed to estimate above-ground net primary production (ANPP) and leaf to stem ratio following the peak of the 2002 growing season in late August 2002. Concurrent with ANPP biomass harvesting, seven additional, individual plants representing the three dominant species (three of *Conyza canadensis* and two each of *Solidago altissima* and *Carduus acanthoides*) were excavated, along with several liters of surrounding soil to a depth of 30 cm, preserving as much of the root structure as possible. Each plant was divided into belowground and aboveground portions, dried, and weighed to determine the ratio of belowground to aboveground biomass (root/shoot ratio). This ratio was used to estimate belowground net primary production (BNPP) at the peak of the 2002 growing season. Although excavation methods frequently underestimate BNPP by failure to collect considerable portions of the fine root structure [Niklas and Enquist, 2002], we utilize this method nonetheless to obtain a coarse estimate of BNPP for the successional field. Samples of leaves, stems and roots were combusted in an elemental analyzer (CE Elantech, Lakewood, New Jersey) to determine carbon concentration by mass, allowing ANPP and BNPP to be expressed in units of kg C m⁻².

2.2. Modeling Ecosystem Respiration

[17] The empirical model seeks to define ecosystem respiration as dependent upon soil temperature, soil moisture and vegetation growth status (i.e., whether vegetation is growing or absent/dormant). Modeling ecosystem respiration in the successional field serves two purposes: first it

facilitates gap-filling of eddy covariance measurements, and second it facilitates corroboration of eddy covariance-derived R_E by independent, ground-based measurements of respiration. Crucial to the development of an empirical model for R_E was the selection of data for which $F_c \approx R_E$. Substitution of F_c during periods of no photosynthesis (i.e., dormant periods or nighttime, and bare soil periods during the growing season) as a measure of R_E is a common practice in the evaluation of carbon dioxide exchange [e.g., Lavigne *et al.*, 1997; Law *et al.*, 1999; Barford *et al.*, 2001; Pilegaard *et al.*, 2001]. For modeling purposes, F_c is assumed equivalent to R_E during nighttime periods, and daytime periods when vegetation is absent or dormant. For this study, two blocks of half-hourly data points were selected from each of two possible conditions: nongrowth and growth. Dates for representative growth and nongrowth periods were established from a synthesis of historical agricultural data [*Soil Conservation Service*, 1982] and field observations. Within these periods, data were further subdivided into regimes having θ greater than or less than the mean volumetric soil moisture for the study period (θ_M), $0.30 \text{ m}^3 \text{ m}^{-3}$: nongrowth/dry, nongrowth/wet, growth/dry, and growth/wet.

[18] After classification by growth and moisture status, data were filtered to accept only those half-hour periods for which U_* and F_c exceeded threshold values. The minimum U_* requirement ($U_{*Min} = 0.20 \text{ m s}^{-1}$) eliminates half-hourly periods with insufficient turbulence for reliable eddy covariance calculations, and the minimum flux requirement ($F_c \geq 0$) is based on the assumption that $F_c \approx R_E$ (i.e., no photosynthesis).

[19] Filtered T_S and R_E data were compared within each regime using the *Lloyd and Taylor* [1994] adaptation of the Arrhenius relationship for respiration,

$$R_E(T_S) = R_{10} \exp \left[E_0 \left(\frac{1}{56} - \frac{1}{T_S - 227.13} \right) \right], \quad (1)$$

where R_E is ecosystem respiration ($\mu\text{moles m}^{-2} \text{ s}^{-1}$), and T_S is soil temperature (in units K for this equation only). Half of the available T_S and R_E measurements were selected randomly from each regime (the other half being reserved for model validation), and least-squares regression was used to determine the best fit for R_{10} (respiration at 10°C , $\mu\text{moles m}^{-2} \text{ s}^{-1}$) and E_0 (exponential slope derived from activation energy having units K), both of which are determined from the regression analysis. Having conditioned R_{10} and E_0 on moisture and vegetation status, R_E was modeled for each half-hourly period using equation (1). Similar methods have been used to examine the relationship between eddy covariance derived R_E , T_S and θ for other ecosystems [e.g., Suyker and Verma, 2001; Reichstein *et al.*, 2002; Novick *et al.*, 2004], but generally without exploring the impact of vegetation growth status. Analysis of covariance was used to assess the response of R_E among the different moisture and vegetation regimes.

2.3. Comparing Tower-Based and Ground-Based Carbon Flux

[20] To ensure the credibility of our carbon dioxide exchange measurements, tower-based measurements of carbon dioxide exchange were corroborated with ground-based

measurements at both short (half-hourly) and long (seasonal) timescales. Because F_c was not reconstructed fully from ground-based measurements, validation of F_c was considered dependent upon successful closure of carbon budgets at half-hourly and seasonal timescales using both tower and ground-based measurements. To validate half-hourly measurements, R_E was estimated for ground-based point measurements of T_S and θ (collected alongside chamber-based R_S) using values for E_0 and R_{10} determined through least squares regression of the tower-based data. R_S , the sum of heterotrophic and root respiration, and the modeled point values of R_E were contrasted to determine the difference, which was attributed to R_A by way of the relationship

$$R_E = R_S + R_A, \quad (2)$$

where R_A was aboveground plant respiration, which was estimated from the literature and scaled using ANPP measurements from the successional field. In this case, closure was considered to be agreement between $R_E - R_S$ and literature-based values of R_A , as scaled using ANPP measurements from the successional field.

[21] For periods of time longer than one half hour, F_c was integrated and converted to NEP with units of kg C m^{-2} and a positive sign representing sequestration by the biosphere. An independent estimate of NEP can be derived, provided we have measurements of NPP (i.e., ANPP + BNPP) and heterotrophic respiration, using the relationship

$$\text{NEP} + R_H = \text{NPP} = \text{ANPP} + \text{BNPP}, \quad (3)$$

where R_H is total heterotrophic soil respiration for a season. R_H was modeled as a continuous time series function of T_S and θ using the modeling strategy described earlier, but parameterized using only F_c from time periods with no growing vegetation (nongrowth periods). R_H was integrated through time to obtain seasonal totals of heterotrophic respiration which were combined in equation (3) with ground-based estimates of NPP to balance tower-based estimates of NEP. Finally, annual estimates of NEP for 2001 and 2002 (through 15 September) were compared to estimates of NEP from similar ecosystems in later stages of reforestation. Previously published estimates of annual NEP were plotted as a function of the reported age of the reforested ecosystem. The relationship between NEP and successional age was used to evaluate the validity of the hypotheses concerning the pattern of succession described by *Gorham et al.* [1979].

3. Results and Discussion

3.1. Environmental Conditions

[22] For the study period (10 January 2001 through 15 September 2002), average monthly air temperature and cumulative monthly precipitation measured at the successional field (Figure 1) were compared to long term air temperature and precipitation records from National Weather Service (NWS) stations. Whereas temperatures during the study (mean temperatures for January and July were 0.9°C and 21.9°C , respectively) were similar to long-term averages (mean temperatures for January and July are -1.02°C and 23.5°C , respectively [*National Climate Data Center*

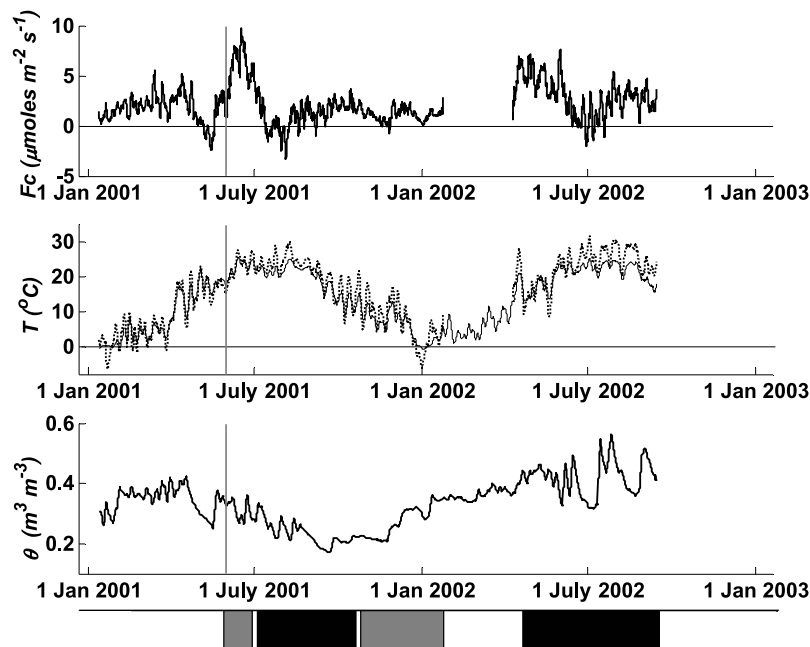


Figure 1. Time series of successional field micrometeorology including carbon dioxide flux (F_c), temperature (T , soil: dotted line, air: solid line), and volumetric soil moisture (θ). For this figure only, data have been smoothed using a moving average. Measurements commenced on 10 January 2001, harvest occurred on 6 June 2001, old-field succession began on 7 June 2001 and measurements ceased on 15 September, 2002. Timeline shows periods of no growing vegetation (gray) and growing vegetation (black) from which points were selected for modeling R_E . The vertical gray line in each pane indicates harvest.

(NCDC, 2003a, 2003b)), the period from January 2001 to August 2002 (20 months) was noticeably drier than normal, having total precipitation of 1161 mm compared to an expected 20-month total of 1605 mm based on 56 years of NWS records [NCDC, 2003a, 2003b] and was noted as a time of drought in Virginia [NCDC, 2001, 2002]. Because on-site precipitation measurements did not commence until 12 October 2001, precipitation measurements from a nearby NWS station (approximately 40 km distant) were substituted for missing data. For months where data were available for comparison, monthly precipitation totals were well correlated between the successional field and the NWS station ($R^2 = 0.81$).

[23] Precipitation for 2001 (675 mm) totaled only 71% of the long-term annual average (951 mm), and precipitation between January and August 2002 (486 mm) totaled only 74% of the long-term average for the same months (654 mm). Furthermore, precipitation during both the 2001 and 2002 growing seasons (April through September) totaled less than 80% of the long-term growing season average (530 mm). Soil moisture, θ , varied notably between the 2001 and 2002 growing seasons with a significantly drier growing season in 2001 ($\bar{\theta} = 0.29 \text{ m}^3 \text{ m}^{-3}$) than 2002 ($\bar{\theta} = 0.42 \text{ m}^3 \text{ m}^{-3}$) (Figure 1). Because 2001 and 2002 were years of drought, we presumed soil moisture to exert influence over F_c and its component fluxes.

[24] Maximum rates of carbon dioxide loss to the atmosphere (positive F_c) occurred during the warm, dry summers of 2001 and 2002, with the greatest losses occurring within two weeks following the final crop harvest on 6 June 2001 (Figure 1). These high rates of loss may be explained

by enhanced microbial decomposition associated with warm, summer temperatures [Lloyd and Taylor, 1994] combined with the residual effects of disturbance by cultivation [e.g., Knops and Tilman, 2000]. For the entire study period, half-hourly F_c had a median value of $1.60 \mu\text{moles CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ with 50% of all measurements falling between $-0.03 \mu\text{moles CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and $4.31 \mu\text{moles CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Ninety-nine percent of all half-hourly F_c measurements fell between $-20.63 \mu\text{moles m}^{-2} \text{ s}^{-1}$ and $26.56 \mu\text{moles m}^{-2} \text{ s}^{-1}$.

[25] From the micrometeorological record, subsets were selected to represent either growing seasons, or periods of bare soil or dormancy (Figure 1). Comparison of these subsets revealed that whereas growing season median F_c ($1.88 \mu\text{moles CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) exceeded median F_c for periods of bare soil or dormancy ($0.94 \mu\text{moles CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), when temperature was accounted for CO_2 loss rates were much greater during the bare soil period than during the growing season (Figure 2). Variability in half-hourly F_c was greater during growing seasons (interquartile range, IQR = $5.67 \mu\text{moles m}^{-2} \text{ s}^{-1}$) than during bare soil or dormant periods (IQR = $2.15 \mu\text{moles m}^{-2} \text{ s}^{-1}$), which may have resulted from increased activity of microbiota and vegetation alike with higher temperatures during the growing season, or differences in soil moisture variability between the periods. That all subsets of the F_c time series have positive median values confirms, even before gap filling, that R_E was the dominant component of F_c during these early successional stages.

[26] Approximately 22% of all half-hourly flux measurements (6,390 measurements) were lost owing to instrument problems. In comparison, flux tower networks have

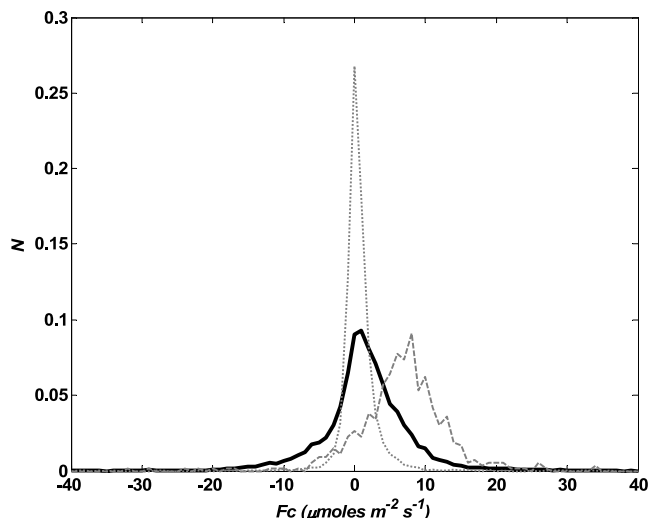


Figure 2. Histogram of F_c for selected growing season measurements (solid black line), warm bare soil measurements following harvest (dashed gray line), and cool dormant period measurements (dotted gray line). Median F_c for growing season was $1.88 \mu\text{moles m}^{-2} \text{s}^{-1}$ ($N = 10,595$), median F_c for warm bare soil was $7.43 \mu\text{moles m}^{-2} \text{s}^{-1}$ ($N = 470$), and median F_c for cool dormant periods was $0.80 \mu\text{moles m}^{-2} \text{s}^{-1}$ ($N = 3955$). Median F_c for combined bare soil/dormant periods (not shown) was $0.94 \mu\text{moles m}^{-2} \text{s}^{-1}$ ($N = 4425$). Growing season F_c was significantly higher than combined bare soil/dormant F_c ($P < 0.001$) and cool dormant F_c ($P < 0.001$), but significantly lower than warm bare soil F_c ($P < 0.001$).

reported instrumentation-based loss rates ranging from 13% (EUROFLUX) [Aubinet *et al.*, 2000] to 35% (FLUXNET) [Falge *et al.*, 2001]. Sixty percent of our instrument losses (3,814 measurements) occurred in a continuous block between 22 January 2002 and 12 April 2002 owing to instrument availability issues. An additional 19% of all flux measurements (5,664 measurements) were discarded owing to low nighttime turbulence ($U_* < 0.20 \text{ m s}^{-1}$). Of the 12,054 total missing or discarded F_c measurements, 90% (10,850 measurements) occurred during periods of no photosynthesis (i.e., nighttime, periods of bare soil or periods of dormancy). For these half hours, we directly substituted modeled R_E for missing F_c , using the modeling strategy for R_E presented in section 2. Because the time series of environmental state variables (T_S and θ) used to model R_E was more than 99.5% complete, there were only seven half hours for which this substitution could not be made.

[27] Random and systematic uncertainty estimates were computed for gap-filled F_c using flux footprint and energy balance closure analyses. The flux footprint analysis was performed using half-hourly measurements for which eddy covariance data were available (23,270 measurements, or approximately 79% of all half hours). Ninety percent of the measured flux (90% flux footprint) originated wholly within the successional field during only 30% (6866) of these half hours. However, the 70% flux footprint was wholly contained within the successional field over 85% of the time (19,858 half hours). Adjacent land surfaces contribut-

ing to the flux footprint were normally the two adjacent chronosequence plots (abandoned in 1920 and 1986) described in the Methods. Other research has shown these two plots and the successional field to have similar growing season soil CO₂ effluxes [Browne, 2002] and nearly identical land-use histories prior to abandonment [Nelson and Byrd, 2000; Riedel and Epstein, 2005]. However, the vegetation of these fields differed in composition, structure, and presumably carbon assimilation and was therefore considered a source of uncertainty in measured F_c . As stated by Moncrieff *et al.* [1996], and particularly applicable to this study, the varying extent of the flux footprint is a major contributor to random uncertainty in the measurement of F_c .

[28] The slope of the linear regression between daily averaged values of $H + LE$ and $R_N - G_S$ was 0.69 (Figure 3). Lack of energy balance closure is a recognized challenge among eddy covariance deployments [Twine *et al.*, 2000; Wilson *et al.*, 2002], and it indicates a selective undersampling of true ecosystem fluxes by as much as 25% during the day and 50% at night [Goulden *et al.*, 1996; Moncrieff *et al.*, 1996]. Our undersampling rate of 31% falls within the typical range. To account for undersampling of F_c , estimates of NEP are reported as ranges whose upper limit is calculated from this uniform systematic uncertainty [Moncrieff *et al.*, 1996; Twine *et al.*, 2000].

3.2. Environmental Controls on Ecosystem Respiration

[29] Throughout the study period, R_E was typically positively correlated with T_S and θ ; respiration increased as conditions grew warmer and wetter. For each regime of vegetation and moisture defined in section 2, the relationship between T_S and R_E was determined using least-squares regression (Figure 4). Considerable variability in R_E remained unexplained by T_S when conditioned upon θ and vegetative state. Across all soil moisture and vegetation conditions the model explains 56% of the variability in half-hourly respiration measurements used for model fitting.

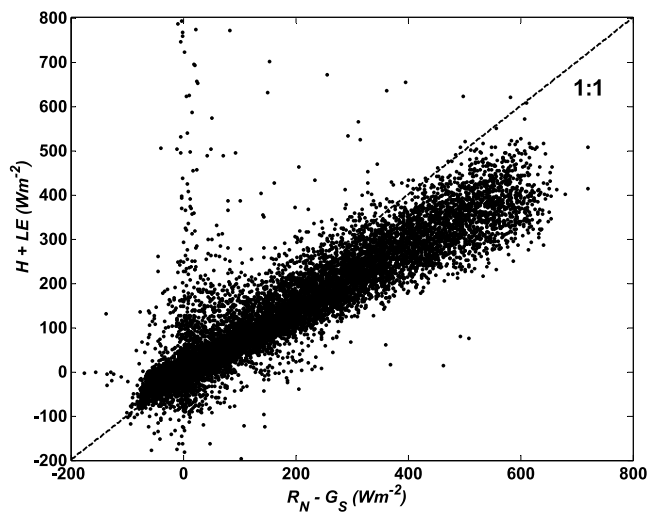


Figure 3. Energy balance closure for daily averages of the components H , LE , R_N , and G_S ; 1:1 line shown to illustrate complete closure. Slope of least-squares regression line is 0.69 ($R^2 = 0.84$).

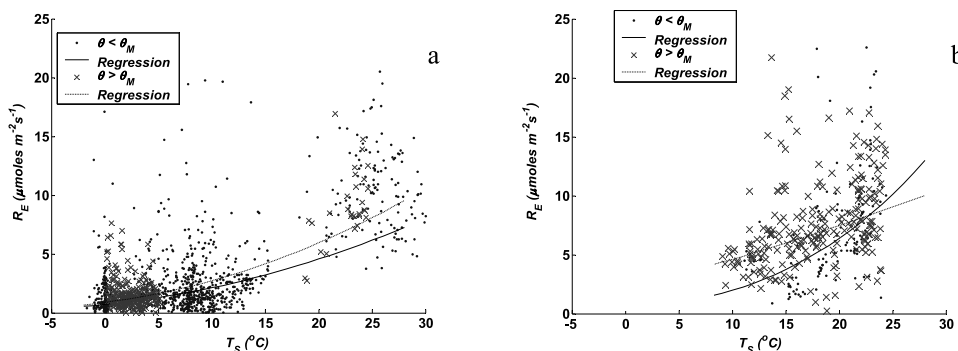


Figure 4. Scatterplot of soil temperature (T_S) versus ecosystem respiration (R_E) for (a) nongrowth periods and (b) growth periods. Least squares regression of equation (3) is shown for dry periods (solid line through closed circles) and wet periods (dotted line through crosses). For nongrowth periods, dry $R_{10} = 2.56 \mu\text{moles CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, dry $E_0 = 263 \text{ K}$ ($R^2 = 0.51$), wet $R_{10} = 2.86 \mu\text{moles CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, and wet $E_0 = 330 \text{ K}$ ($R^2 = 0.39$). For growth periods, dry $R_{10} = 1.95 \mu\text{moles CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, dry $E_0 = 413 \text{ K}$ ($R^2 = 0.21$), wet $R_{10} = 4.60 \mu\text{moles CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, and wet $E_0 = 192 \text{ K}$ ($R^2 = 0.17$).

Furthermore, as temperature increased, the model systematically underestimated R_E .

[30] Analysis of covariance (performed simultaneously on all four regimes) confirmed that despite having a range of 192 K to 413 K, none of the E_0 values differed significantly, meaning that the response of ecosystem respiration to changes in temperature was uniform among all regimes of moisture and vegetation. Because the exponential slopes were found to be statistically indistinguishable, any response of R_E to vegetation or moisture would be expected to manifest itself in the regression intercept, R_{10} .

[31] R_{10} is defined by *Lloyd and Taylor* [1994] as the respiration rate at 10°C. Whereas all four regimes have homogeneous exponential slopes (E_0), significant differences exist among the R_{10} values, suggesting that differences in R_{10} among regimes may reflect the relative response of ecosystem respiration to different vegetation or moisture regimes not only at 10°C, but across a wide range of temperatures. Respiration during wet periods ($\theta > \theta_M$) had a significantly higher R_{10} (by $1.7 \mu\text{moles m}^{-2} \text{ s}^{-1}$) when vegetation was actively growing compared to when vegetation was absent or dormant. This observation suggests that during wetter periods autotrophic respiration may be responsible for increased R_E , or that there is an interaction between soil moisture and vegetation activity on heterotrophic soil respiration. Furthermore, R_{10} for growth/wet and nongrowth/dry are significantly different, with growth/wet R_{10} exceeding nongrowth/dry R_{10} by $2.0 \mu\text{moles m}^{-2} \text{ s}^{-1}$ (Figure 4). Thus the combined effect of absent or dormant vegetation and dry soil ($\theta < \theta_M$) is a reduction in R_E compared to wet soil ($\theta > \theta_M$) and actively growing vegetation.

[32] Analysis of covariance reveals that during periods when vegetation was growing, the response of R_E to soil temperature was controlled, in part, by whether the soil was wetter or drier than θ_M . In general, R_E was enhanced for wet soil conditions ($\theta > \theta_M$) over dry soil conditions ($\theta < \theta_M$). However, the limited variance explained by T_S in our model suggests that either (1) R_E responds to changes in soil moisture at a conditional resolution finer than the “wet or dry” criterion used by this analysis or (2) additional processes besides soil moisture and soil temperature signif-

icantly influence R_E during periods when vegetation was growing. Regarding the former explanation, a linear multiple regression of R_E on θ and T_S from among all four regimes explained nearly the same variance ($R^2 = 0.52$) as the conditional regime modeling technique ($R^2 = 0.56$). Because a model with much greater resolution of soil moisture status could make no better prediction of R_E , “wet or dry” status of the vegetation and soil moisture regimes is believed to be sufficient for assessing the R_E response to soil moisture.

[33] Although moisture has no significant effect on the response of R_E to soil temperature during nongrowth

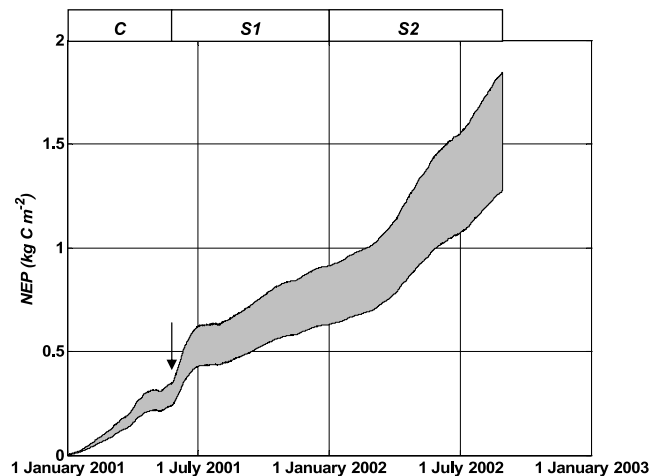


Figure 5. Cumulative, gap-filled NEP error bounds for the entire study period, 10 January 2001 through 15 September 2002. Crop harvest occurred on 6 June 2001 (indicated by arrow). For 2001, we estimated NEP of between -0.63 and $-0.91 \text{ kg C m}^{-2}$ (net source to the atmosphere). The crop season (C, 10 January 2001 through 6 June 2001) had NEP of -0.22 to $-0.32 \text{ kg C m}^{-2}$, and the first successional season (S1, 7 June through 31 December 2001) had NEP of -0.41 to $-0.59 \text{ kg C m}^{-2}$. From 1 January to 15 September 2002 (S2), we estimated NEP of between -0.64 and $-0.94 \text{ kg C m}^{-2}$.

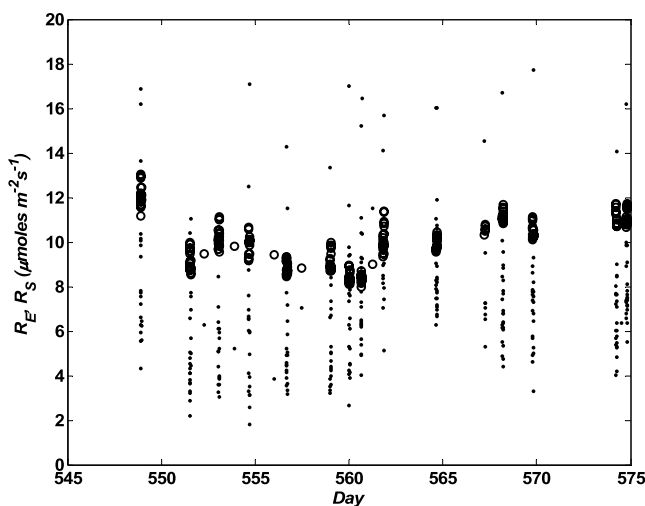


Figure 6. Paired measurements of chamber-based R_S (points), and R_E modeled from ground-based soil temperature and moisture (open circles). R_E exceeds R_S by between 2.5 and 3.2 $\mu\text{moles m}^{-2} \text{s}^{-1}$ ($\alpha = 0.05$, $P < 0.001$).

periods, the model explains more variance in R_E during nongrowth periods ($R^2 = 0.51$ for nongrowth/wet and $R^2 = 0.39$ for nongrowth/dry) than during growth periods ($R^2 = 0.21$ for growth/wet and $R^2 = 0.17$ for growth/dry). This observation simply reaffirms the well-established correlation between heterotrophic soil respiration and T_S as well as between root respiration and T_S .

3.3. Comparing Tower-Based and Ground-Based Carbon Flux

[34] As an independent assessment of the reliability of tower-based flux measurements, NEP (computed from gap-filled F_c) was compared to ground-based measurements of carbon flux components. Modeled R_E was used to fill the 80-day gap in F_c between 22 January 2002 and 12 April 2002. By substituting R_E for F_c we assume that no photosynthesis occurred before 12 April 2002. The agricultural growing season begins historically between 19 April and 3 May [Soil Conservation Service, 1982; National Agricultural Statistics Service, 2002] and the minimum daily air temperature (measured in the absence of sonic anemometer temperature as the body temperature of the net radiometer) averaged -1.44°C during the gap period. Remaining gaps in the data, periods of inadequate fetch, and a general lack of energy balance closure were all recognized as potential contributors to the overall uncertainty of F_c and NEP measurements. The ranges reported for NEP refer to the differences between F_c measured and F_c rescaled by the deficit in energy balance closure (i.e., systematic error rate). For the entire

20-month study period, the ecosystem was a net source to the atmosphere of between 1.27 and 1.85 kg C m^{-2} (Figure 5).

[35] We corroborated these carbon exchange measurements by comparing tower-based estimates to ground-based measurements at two timescales. To obtain independent estimates of short-term (half-hourly) canopy-scale carbon dioxide exchange (i.e., F_c), we conducted 345 chamber-based measurements of soil respiration in the successional field during the summer of 2002. For each measurement, R_E was modeled using ground-based measurements of T_S and θ , along with parameters E_0 and R_{10} previously determined through regression. Measured values of R_S and modeled R_E were plotted (Figure 6), and a paired T-test was used to compare R_E and R_S for each of the 345 pairs. This comparison revealed the mean of R_E to be significantly greater than the mean of R_S by 2.5 to 3.1 $\mu\text{moles CO}_2 \text{m}^{-2} \text{s}^{-1}$. Represented as a fraction of mean R_E , this difference would be approximately 25% to 31% of R_E for each half hour.

[36] On the basis of equation (2), any true difference between R_E and R_S should be wholly accounted for by R_A in the absence of measurement or model errors. Shoot respiration was not measured directly for these species, so previously published estimates of R_A for C₃ crop ecosystems are presented for comparison in Table 1. Because calculated R_A correlated poorly with ground-based T_S ($R^2 = 0.05$), we did not consider temperature to have a meaningful impact on this comparison. Nevertheless, our estimates of R_A for the summer of 2002 (2.5 to 3.1 $\mu\text{moles CO}_2 \text{m}^{-2} \text{s}^{-1}$) fall clearly within the range of R_A for crops reported in Table 1. Furthermore, the fraction of R_E that was assigned to R_A (25% to 31%) was reasonable compared to other studies. Specifically, R_A has been estimated at 18% of R_E for a southern U.S. pine forest [Lai et al., 2002] and 23% of R_E for a Pacific Northwest pine forest [Law et al., 2002]. The latter two estimates are derived from annual measurements that include periods of reduced plant carbon dioxide assimilation and continued heterotrophic respiration, whereas we estimate R_A only for the peak of the growing season. In a general sense, this comparison highlights the expected trend of increased contribution of R_A to R_E during the growing season (when compared to a annualized estimate of the R_A fraction of R_E). Despite increased contribution of R_A during the growing season, R_S measurements indicate that soil respiration is the main contributor to R_E during this period.

[37] To assess the validity of NEP estimated for an entire season, three 1-m² plots plus seven individual plants were harvested and analyzed for total carbon content following the 2002 growing season. Biomass harvesting and elemental analysis were used to determine ANPP (Table 2). Equation (1) was parameterized anew for E_0 and R_{10} using ground-based

Table 1. Aboveground (Shoot) Respiration Rates (R_A) and Measurement Temperature Ranges for C₃ Crops, Converted From Published Units of $\text{mg CO}_2 \text{m}^{-2} \text{hr}^{-1}$ to Units of $\mu\text{moles CO}_2 \text{m}^{-2} \text{s}^{-1}$

| Description | R_A , $\text{mg CO}_2 \text{m}^{-2} \text{hr}^{-1}$ | R_A , $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ | Temperature, $^\circ\text{C}$ | Source |
|-----------------------|---|--|-------------------------------|------------------------|
| Alfalfa | 187 | 1.18 | 18.8 to 24.6 | Da Costa et al. [1986] |
| Barley (early season) | 800 | 5.05 | 20.0 | Mogensen [1977] |
| Barley (late season) | 400 | 2.53 | 20.0 | Mogensen [1977] |
| Soybean | 466 | 2.94 | 9.4 to 26.0 | Da Costa et al. [1986] |
| Soybean | 494 | 3.12 | 15.6 to 25.2 | Da Costa et al. [1986] |

Table 2. Biometric Measurements From Three Harvested Plots and Seven Additional Individual Plants Used to Calculate NPP^a

| Site | Aboveground Biomass, kg m ⁻² | Leaf Biomass, kg m ⁻² | Stem Biomass, kg m ⁻² | ANPP, kg C m ⁻² | Root Biomass, kg m ⁻² | BNPP, kg C m ⁻² | NPP, kg C m ⁻² |
|------|--|-------------------------------------|-------------------------------------|-------------------------------|-------------------------------------|-------------------------------|------------------------------|
| 1 | 2.30 | 0.727 | 1.57 | 1.03 | ... | ... | 1.15 |
| 2 | 1.59 | 0.501 | 1.08 | 0.708 | ... | ... | 0.836 |
| 3 | 1.22 | 0.386 | 0.834 | 0.545 | ... | ... | 0.673 |
| Mean | 1.70 | 0.538 | 1.16 | 0.888 | 0.304 | 0.128 | 1.02 |

^aMeasurements were made on successional vegetation. Ratio of root to shoot biomass was 0.18. Mass concentrations of carbon used to convert kg biomass to kg C were 44% (leaves), 45% (stems), and 42% (roots).

measurements of T_S , θ , and R_H . The new parameter estimates were used to develop a complete time series of R_H from tower-based measurements of T_S and θ . By integrating R_H through time, carbon loss by heterotrophic soil respiration was determined for the crop season and the two seasons of successional growth. Integrated seasonal values of R_H and NEP were used to estimate NPP for each season (Table 3), and NPP estimates from eddy covariance-based and ground-based measurements were compared.

[38] For 2002, the eddy covariance-based estimate of NPP ranges from 0.71 to 1.01 kg C m⁻². The 2002 ground-based estimates of NPP range from 0.67 to 1.15 kg C m⁻². The median of the eddy covariance-based range of NPP (0.86 kg C m⁻²) is almost identical to the median ground-based NPP estimate (0.84 kg C m⁻²). Even though values for ground-based NPP are likely underestimated owing to undersampling of the fine root component of BNPP, we consider this degree of closure adequate validation of eddy covariance measurements at the seasonal scale. Because instruments and measurement techniques did not change during the study period, we assume that the agreement between ground-based and flux-based NPP for 2002 indicates that eddy covariance-based NEP estimates are reliable and consistent with ground-based measurements of carbon fluxes.

[39] NEP estimates from the successional field for 2001 and 2002 (through 15 September) were compared to published ranges of NEP for other ecosystems in Table 4, developing a trajectory of succession ranging from disturbed (cultivated) sites to century-old deciduous forests (Figure 7). At the near end of the trajectory lie agricultural and recently abandoned sites. These agricultural systems may be either sources or sinks for carbon; however, none of the agricultural carbon sources shown in Table 4 is nearly as great as the carbon source from our successional field during the transition year or the first full year of succession. Fourteen- and 17-year-old pine forests and a 30-year-old deciduous forest represent intermediate stages of succession, and all are carbon sinks, ranging from very small NEP (0.028 kg C m⁻² yr⁻¹ [Law et al., 2002]) to a strong carbon sink (0.605 kg C m⁻² yr⁻¹ [Lai et al., 2002]). The late

stages of the successional trajectory include mature deciduous, coniferous and mixed deciduous and coniferous forests. Nearly all of these forests are sinks of carbon ranging from very small NEP (0.005 kg C m⁻² yr⁻¹ [Valentini et al., 2000]) to a strong carbon sink (0.629 kg C m⁻² yr⁻¹ [Wilson and Baldocchi, 2001]).

[40] This trajectory of successional ecosystems represented here by NEP as a function of age since abandonment or disturbance is highly generalized and certainly does not consider the effects of different climates, interannual climate variability, species composition, or land-use history. The unifying factor among all of these sites is that each one exists in the wake of anthropogenic or natural disturbance, or in the case of cultivated ecosystems, still in a disturbed state. When examined collectively, NEP estimates from these ecosystems reveal a sharp decline in NEP in the immediate aftermath of disturbance followed by a recovery of NEP, as hypothesized by Gorham et al. [1979].

[41] The results of this study support the claim that the transition from an agricultural ecosystem to an abandoned successional ecosystem may be accompanied by a net release of significant amounts of carbon dioxide to the atmosphere. Although the long-term duration of this particular carbon source remains undetermined, we have shown that the magnitude of the annual net carbon source from our successional field may be equal to or even greater than the annual net carbon sinks of latter-stage successional ecosystems.

[42] Our results indicate that across the transition from cultivation to unmanaged old-field succession, ecosystem respiration clearly dominates photosynthesis, and our subsequent estimates of NEP represent some portion of the negative pulse in NEP predicted by Gorham et al. [1979]. On the basis of growing season data, soil respiration is the dominant component of ecosystem respiration in the successional field (Figure 6), and we demonstrate enhancement of ecosystem respiration under warm and wet conditions. It is possible (though not determined by these results) that in addition to contributing directly to NEP through CO₂ assimilation, early successional vegetation may indirectly offset NEP by reducing soil temperature (shading) and soil

Table 3. Measured Net Ecosystem Production of Carbon (NEP), Modeled Heterotrophic Soil Respiration (R_H), and Net Primary Production of Carbon (NPP_{Flux}) Calculated as NEP + R_H Integrated Over Each Season^a

| Season | NEP, kg C m ⁻² | R_H , kg C m ⁻² | NPP_{Flux} , kg C m ⁻² | NPP_{Ground} , kg C m ⁻² | NEP_{Ground} , kg C m ⁻² |
|-----------------|---------------------------|------------------------------|-------------------------------------|---------------------------------------|---------------------------------------|
| 2001 Crop | -0.22 to -0.32 | 0.62 | 0.30 to 0.40 | ... | ... |
| 2001 Succession | -0.41 to -0.59 | 1.44 | 0.85 to 1.03 | ... | ... |
| 2002 Succession | -0.64 to -0.94 | 1.65 | 0.71 to 1.01 | 0.67 to 1.15 | -0.50 to -0.98 |
| Total | -1.27 to -1.85 | 3.71 | 1.86 to 2.44 | ... | ... |

^a NPP_{Ground} is the range of NPP estimated from measurements in Table 2. NEP_{Ground} is calculated as $NPP_{Ground} - R_H$.

Table 4. Location, Description, Age, and Net Ecosystem Production of Carbon (NEP) and Measurement Period for 22 Ecosystems Representing Various Stages of Secondary Succession Plotted in Figure 7^a

| Location | Ecosystem Description | Age, Years | NEP, kg C m ⁻² yr ⁻¹ | Period of Measurement | Source |
|----------------------|--|------------|--|-----------------------|---|
| Wisconsin, USA | C3 and C4 crops | 0 | -0.24 to 0.06 ^b | 1995–1999 | <i>Brye et al.</i> [2002] |
| Oklahoma, USA | crop field | 0 | 0.155 ^b | 1997 | <i>Law et al.</i> [2002] |
| Denmark | C3 and C4 crops | 0 | 0.031 ^b | 1998–1999 | <i>Soegaard et al.</i> [2003] |
| Pan-European | crop field | 0 | -0.084 ^b | 2008–2012 | <i>Vleeshouwers and Verhagen</i> [2002] |
| Virginia, USA | crop field, abandoned crop field | 0 | -0.63 to -0.91 | 2001 | this study |
| Virginia, USA | abandoned crop field | 1 | -0.64 to -0.94 | 2002 (Jan–Sep) | this study |
| Oregon, USA | Ponderosa pine forest | 14 | 0.028 | 1999–2000 | <i>Law et al.</i> [2002] |
| North Carolina, USA | pine forest | 17 | 0.605 | 1999 | <i>Lai et al.</i> [2002] |
| France | broad-leaved deciduous (natural) | 30 | 0.22 to 0.26 | 1996–1997 | <i>Valentini et al.</i> [2000] |
| Massachusetts, USA | deciduous forest | 60 | 0.165 to 0.200 | 1990–2002 | <i>Curtis et al.</i> [2002] |
| Tennessee, USA | deciduous forest | 60–120 | 0.470 to 0.629 | 1995–1999 | <i>Wilson and Baldocchi</i> [2001] |
| Wisconsin, USA | mixed hardwood forest | 66 | 0.220 to 0.106 | 1998–2002 | <i>Curtis et al.</i> [2002] |
| Belgium | mixed broad-leaved and coniferous forest (planted) | 70 | 0.157 | 1997 | <i>Valentini et al.</i> [2000] |
| Belgium | mixed coniferous and broad-leaved forest (planted) | 75 | 0.43 | 1996–1997 | <i>Valentini et al.</i> [2000] |
| Indiana, USA | deciduous forest | 80 | 0.236 to 0.354 | 1997–2002 | <i>Curtis et al.</i> [2002] |
| United Kingdom | mixed coniferous forest (planted) | 80 | -0.09 to 0.005 | 1998 | <i>Valentini et al.</i> [2000] |
| Denmark | broad-leaved deciduous (natural) | 80 | 0.09 to 0.17 | 1996–1998 | <i>Valentini et al.</i> [2000] |
| Ontario, Canada | mixed temperate forest | 90 | 0.06 to 0.24 | 1996–1998 | <i>Barr et al.</i> [2002] |
| Michigan, USA | mixed hardwood and boreal transition | 90 | 0.073 to 0.212 | 1998–2002 | <i>Curtis et al.</i> [2002] |
| Massachusetts, USA | deciduous forest | 90 | 0.195 | 1992 | <i>Law et al.</i> [2002] |
| Italy | broad-leaved deciduous (planted) | 100 | 0.47 | 1993–1994 | <i>Valentini et al.</i> [2000] |
| Italy | broad-leaved deciduous (natural) | 105 | 0.66 | 1996–1997 | <i>Valentini et al.</i> [2000] |

^aCurrently disturbed (cultivated) sites are assigned an age of 0 years for this analysis. All forest sites were assumed to be cultivated or similarly disturbed prior to regrowth.

^bNEP represents perpetually disturbed state, i.e., crop growth.

moisture (interception and transpiration). Other research at BEF indicates that soil temperature decreases along a transect through the chronosequence plots abandoned in 2001, 1986, and 1920 (J. Wang and H. Epstein, unpublished

data, 2005), suggesting interplay between vegetation and controls on ecosystem respiration.

[43] This study fills an important gap in the record of NEP during old-field succession. Rates of carbon exchange

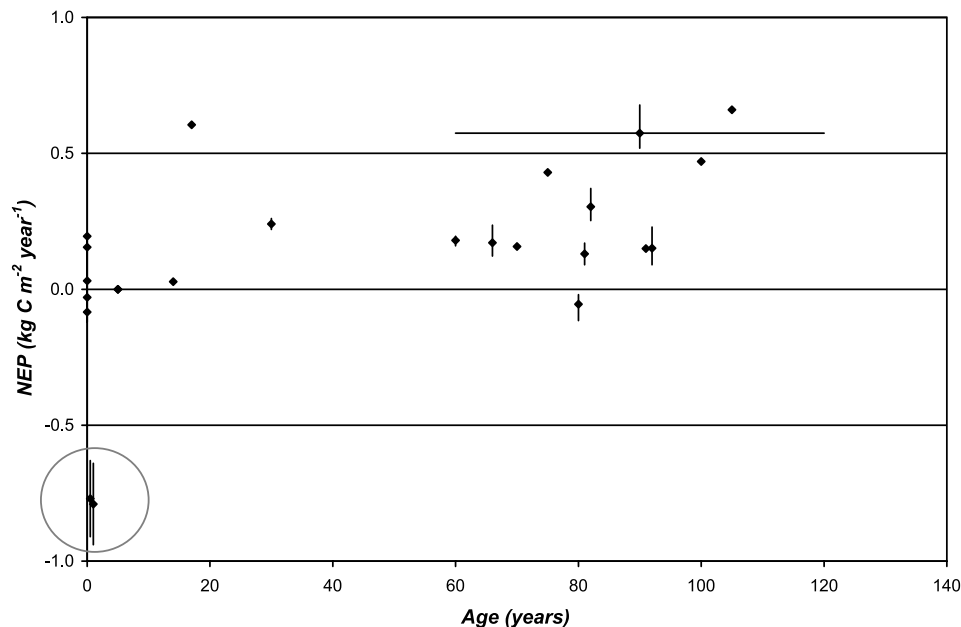


Figure 7. NEP for ecosystems identified in Table 4 arranged to form a hypothetical trajectory of succession ranging from disturbed (cultivated) sites to mature secondary forests. NEP for the present study is circled in gray.

and NEP have previously been determined for cultivated ecosystems as well as forest ecosystems at various stages of old-field succession, but the transition period between cultivation and succession has rarely been studied in terms of NEP. This study has shown carbon exchange during early old-field succession to be dominated by ecosystem respiration, which is influenced by temperature, moisture and vegetative state. Even when early successional vegetation growth was at its peak, ecosystem respiration was largely comprised of heterotrophic respiration.

[44] Although the successional field was a strong source of carbon to the atmosphere throughout the study period, both theory and other field studies indicate the eventual conversion of these ecosystems from carbon sources to carbon sinks. Additional study in this field is necessary to determine the point at which a successional ecosystem converts from a net annual source of carbon dioxide to a net annual sink, and how interannual variability of environmental state variables such as temperature and moisture affect the timing of this conversion. Further study may also reveal whether the temporal transition of successional ecosystems from carbon sources to carbon sinks is initiated by a reduction in the components of R_E (both R_H and R_A), a relative increase in photosynthesis, or a combination of these factors.

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