

Using CO₂ efflux rates to indicate below-ground growing seasons by land-use treatment

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Abstract

CO₂ efflux rates are affected by vegetation type, temperature, and soil surface conditions, and serve as an indicator of the length of the below-ground biological and microbial growing season. This study determined the effect of three land-use treatments on CO₂ efflux and growing season lengths in Southeast Virginia on two forested mineral soil wetlands. CO₂ efflux, soil temperature, and soil moisture were measured 24 times in 18 months at plots representing forest, early successional field, and bare ground land-use treatments. CO₂ efflux differed ($p < 0.05$) by treatment in the order forest > field > bare ground. CO₂ efflux was higher in hardwood- than conifer-dominated forest and higher in bare ground plots that were not inundated. Appreciable CO₂ efflux took place even once leaves had fallen off deciduous trees, and most of the CO₂ efflux appeared to be from vegetation rather than microbial sources during that period. Variability in CO₂ efflux was best described by the interaction between soil temperature and soil moisture ($R^2 = 0.32$) ($p < 0.05$). The below-ground growing season indicated by appreciable CO₂ efflux was similar to that indicated by soil temperatures above 5°C measured at 50 cm, the regulatory reference depth. The CO₂ efflux growing season was 365 days in the forest but was 9–16 days shorter in the field and 21–78 days shorter in the bare ground land-use treatment plots. These data can be used to modify the regulatory growing season definition in forested thermic wetlands and to reflect the environmental variation caused by different land uses.

Introduction

Studies on global climate change due to increasing atmospheric CO₂ levels have tried to estimate the response in CO₂ efflux rates from the soil. Wetlands, because of their high carbon and nitrogen content (Inubushi et al. 2003), adequate soil moisture, and fine root growth potential, may be one of the largest contributors of CO₂ emitted

from the soil. Soil CO₂ emissions increase as available labile carbon and nitrogen leached from freshly fallen tree leaves and nitrogen compounds and carbohydrates exuded from fine root exudates boost microbial growth and respiration and organic compound decomposition (Griffin et al. 1996; Pendall et al. 2004). Respiration can range from 30 to 60% of the total CO₂ efflux in forests (Schlesinger 1977; Hanson et al. 2000; Raich and

Tufekcioglu 2000). About 70% of soil respiration may come from microbial activity during the above-ground growing season (Domanski et al. 2001).

Plant community type and land-use management affect soil CO₂ efflux rates through their control of fine root production, labile C inputs as root exudates, surface organic horizon formation and leaf litter inputs, hydrology, and soil moisture and temperature properties. Inubushi et al. (2003) found that changing land use from secondary forest to field in Indonesian peatlands tended to decrease CO₂ emissions. They reported that soil moisture is one of the most important controlling factors for biological reactions in soil. Wagai et al. (1998) found that soil CO₂ efflux in Wisconsin differed between bare ground, prairie, and corn-field land use types. Several researchers have reported a strong positive correlation between soil temperature, soil moisture, and CO₂ efflux rates in non-hydric soils (Wildung et al. 1975; Wagai et al. 1998; Pangle and Seiler 2002). Laporte et al. (2002) used rain shelters to irrigate a grassland ecosystem in northern Ontario, Canada and reported that seasonal soil moisture correlated positively with soil surface CO₂ efflux ($R^2 = 0.756$, $p < 0.001$) and above ground plant biomass ($R^2 = 0.447$, $p = 0.029$). As irrigation frequency decreased, the soil surface CO₂ efflux decreased by 80% ($p < 0.001$), while soil moisture content decreased by 42%, $p < 0.001$. Prior et al. (2000) reported that CO₂ efflux from soils is increased by tillage and increased destruction of surface residue. In wetland soils, drying due to drainage or increased surface evaporation rates may increase aerobic respiration and decomposition by increasing soil temperature and lowering water tables (Pendall et al. 2004). Soil moisture is one of the most important controlling factors for biological reactions in soil (Inubushi et al. 2003). Soil water content and soil temperature dynamics explained 67% of the variation of soil CO₂ emission in a Northeast Germany field and 95% in a climate chamber (Reth et al. 2003). The CO₂ efflux ranged from 1 to 5.5 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in a farmland soil and from 1 to 12.6 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in a meadow soil, indicating CO₂ efflux variability caused by differing land use. Even though the effect has not been reported directly for mineral soil wetlands in the US, the affect of changing land-use should affect the rate of CO₂ efflux from wetland soils.

The growing season concept is defined in federal regulations governing hydric soil and wetland identification and delineation as the period when soil temperature at 50 cm is above 5°C (USDA-SCS 1985; Environmental Laboratory 1987). Wetlands must have water within 30 cm of the surface during atleast 5% of the growing season in poorly drained or wetter soils and for 12.5% in somewhat poorly drained soils. The US Army Corps of Engineers (ACOE) approximates the soil temperature by the number of frost-free days from long-term weather records a frequency of 5 out of 10 years because it is impractical to measure soil temperature at every wetland identification site (Williams 1992). However, soil microbes are well insulated from short-term freezing air temperatures (Day and Megonigal 1993). In effect, the frost-free days approximates the above-ground growing season but may miss periods of biological activity in the soil, indicated by soil CO₂ emissions above a background level.

Pickering and Veneman (1984) measured soil temperatures along a forested toposequence in Central Massachusetts and reported that poorly drained soils supported microbial activity even during winter months, while microbial activity in the better drained soils was undetectable. Soil temperatures at 50 cm stayed above 5°C in the better drained soils from April to mid-November, outside of the frost-free days growing season. Groffman et al. (1992) found that microbial populations were still actively mineralizing nitrogen and carbon sources months when vegetation was dormant. Megonigal et al. (1996) reported a 12-month microbial growing season in South Carolina, Mississippi, and Louisiana for bottomland hardwood forests based on soil temperatures and continuous O₂ consumption. In the Coastal Plain of Texas, a period of high potential for Fe³⁺ reduction was identified outside of the frost-free days growing season (Griffin et al. 1996). These researchers indicated that the growing season inferred from soil temperature regimes and from the regulatory air temperature thresholds had no correlation with soil microbial activity. Instead, potential reduction, respiration, and decomposition were correlated to the availability of labile carbon, specific moisture and soil temperature conditions.

This paper will discuss the use of CO₂ efflux as an indicator of the period of biological and

microbial activity in wetlands under different land uses. We hypothesized that: (1) average frost-free days is not an accurate indicator of soil temperature at 50 cm or activity of plants and microorganisms in wet flats of Southeast Virginia, (2) CO₂ efflux is a reasonable indicator of microbial and plant activity, but it will vary by vegetation type and land-use treatment, and (3) the below-ground growing season based on CO₂ efflux will be longer than the frost-free days growing season. The objectives of this study were to (i) determine the effect of three land-use treatments on CO₂ efflux rates, and (ii) to compare the growing seasons of the different land uses indicated by appreciable CO₂ efflux rates and other indicators with measured soil temperatures above 5 °C at 50 cm in two wet flats study areas in Southeast Virginia. Wet flats are mineral soil wetlands on broad, flat interstream divides with water-tolerant forests (Brinson 1993).

Methods

Study areas

The two study areas are located approximately 24 km apart in Major Land Resource Area 153B, the Tidewater Area of the lower Coastal Plain of southeastern Virginia (USDA-SCS 1981), within the historic reaches of the Great Dismal Swamp ecosystem (Lichtler and Walker 1979; Lane 1998). The thermic temperature regime GS is 273 days from February 1 to the end of October (Soil Survey Staff 1999). The 30-year average annual precipitation for the region is 125 cm, the mean annual winter air temperature is 6.71 °C, the mean annual summer air temperature is 23.32 °C, and the mean annual air temperature is 15.17 °C (NOAA-NCDC 2003). Soils in the area developed in Holocene-aged marine deposits of mixed mineralogy. In general, the soils consisted of poorly drained, moderately permeable soils with sandy loam surfaces, sandy clay loam to clay subsoils, and sandy substratum. The region has been logged, cleared, and dissected by a series of drainage ditches over the past century and is currently primarily a mixture of agricultural, silvicultural, and urban land-use.

The Bruff study area (Bruff) is in the City of Suffolk County, Virginia at an elevation of 15 m

and centered at 36°37'02" N, 76°33'28" W, based on the USGS digital topographic map. Bruff was drained to 0.5 m and managed as an agronomic field and a loblolly pine (*Pinus taeda* L.) forest until 1999. Local ditches were plugged to restore hydrology in March 2000. The field is in an early successional stage of wetland reforestation. The non-woody vegetation is predominantly herbaceous perennials and grass species such as Chinese lespedeza (*Lespedeza cuneata*, Dum. Cours.), panicled ticktrefoil (*Desmodium paniculatum* Lam.), trumpet creeper (*Campsis radicans* L.), and tall fescue (*Festuca arundinacea* Schreb.) that make up 50% of the herbaceous cover. The forest was logged several times and was planted to *P. taeda* in the early 1970s. Predominant vegetation in the forested area consisted of *P. taeda* and red maple (*Acer rubrum* L.) that made up 90% of the overstory cover.

The Hall study area (Hall) is in the City of Chesapeake, Virginia at an elevation of 10 m and centered at 36°37'57" N, 76°18'50" W, based on the USGS digital topographic map. Hall had land-use history similar to Bruff, although the forest was not managed for *P. taeda*. The non-woody vegetation is predominantly ragweed (*Solidago canadensis* L.) and broomsedge bluestem (*Andropogon virginicus* L.) that make up 40% of the herbaceous cover. The forest was logged several times and a section of the forest was clear-cut as recently as 1986. Predominant vegetation in the forested area consists of sweetgum (*Liquidambar styraciflua* L.), *Acer rubrum*, swamp chestnut oak (*Q. michauxii* Nutt.), and sourwood (*Oxydendrum arboreum* L.) that made up 80% of the overstory cover. Complete vegetation descriptions occur in Burdt (2003).

Soil CO₂ efflux

The study was conducted as a complete block design with two study areas with three treatments (forest, field, bare ground) per study area. The soils were surveyed and described to be sure they had hydric morphology. Four 100 m² plots were randomly located across each land-use treatment to represent the observed range of soils and hydrology. Vegetation was not disturbed in the forest or field plots. Beginning in April 2001, the inner 25 m² of the bare ground plots were tilled

four times a year to simulate active cropland. CO₂ was not measured in the week following tillage. Herbaceous seedlings were carefully pulled or clipped from a 3 m² area around the soil temperature sensors bi-monthly throughout the study.

Soil CO₂ efflux was monitored as an index of microbial and root activity in the near surface soil environment over an 18 month sampling period from February 2001 to June 2002. Soil CO₂ efflux was measured monthly during the ACOE air temperature growing season (frost-free days -2.2°C) and bi-monthly during the rest of the year. Measurements began at 1000 h and continued until all plots were sampled on each sampling date. A complete set of treatment combinations were measured followed by another until all 4-block combinations were sampled. Blocking by subsample served to minimize external influences on CO₂ efflux rates that were not easily attributed to soil temperature or moisture (Pangle and Seiler 2002). Soil CO₂ efflux was measured using a LI-COR[®] 6400 infrared gas analyzer (LI-COR, Inc., Lincoln, NE) fitted with a PVC end cap that was placed on the soil surface with direct pressure. The end cap had an internal volume of 4150 cm³ and was fitted with a foam sealing gasket and gas sampling and return ports, creating a closed chamber system with the soil surface. Soil CO₂ efflux rates in $\mu\text{moles m}^{-2} \text{s}^{-1}$ were measured over 30-s sampling periods and calculated to the nearest 0.01 $\mu\text{moles m}^{-2} \text{s}^{-1}$. Soil CO₂ efflux measurements were initiated at internal chamber CO₂ concentrations equivalent to ambient conditions at the soil surface. The LI-COR[®] system minimizes the influence of leaks on flux rates (Pangle and Seiler 2002). Total respiration was measured in triplicate in each plot and the mean was reported. Field water content of the upper 15 cm was measured by gravimetric methods using the soil survey laboratory methods procedure 3B1 (Soil Survey Staff 1996).

The beginning and end of the microbial activity season (*sensu* Megonigal et al. 1996) were defined by the dates when the CO₂ efflux rates were considered negligible (measurable but nearly zero) because they crossed below the baseline CO₂ efflux of 0.30 $\mu\text{moles m}^{-2} \text{s}^{-1}$. The baseline was defined by the mean of 54 sample date mean CO₂ efflux recorded when the soil temperature at 15 cm was below 5 °C, in order to correlate the results with the regulatory growing season limits.

Air and soil temperature

Air and soil temperatures were measured using Stowaway Tidbit[®] soil temperature thermistors (Onset Computer Corporation, Pocasset, MA). Air temperature was measured hourly with thermistors installed approximately 1-m west of each well on 1-m tall plastic poles with shade covers. Soil temperature was measured hourly at the 15-cm depth approximately 1-m north of each well and every 4 h at 50-cm depths approximately 1-m east of each well. The growing season measured by the 50-cm soil temperature was determined by identifying the last date that soil temperature went below 5 °C in the spring and the first date air temperature went below 5 °C at 50 cm in the fall for each treatment type at each study area, and then selecting the mean value by treatment at each study area.

Below-ground growing season

Soil temperature at 50 cm is the standard datum (control) because it is a direct measurement of soil temperatures above biological zero (5 °C) and is the basis of the regulatory growing season definition, whereas other growing season indicators are surrogates. The vegetative growing season was assessed by the earliest date when a dominant hardwood overstory species began to show visual signs of bud break. The frost-free days above -2.2°C are published in the City of Suffolk soil survey (Reber et al. 1981) and through the NCDC (NOAA-NCDC 2003). The growing season defined by soil temperature above 5 °C at 50 cm was compared and contrasted to growing seasons estimated by vegetation indicators, frost-free days above -2.2°C , and biological activity as indicated by CO₂ efflux rates.

Statistical analysis

The natural logarithms of the CO₂ efflux rates were used to determine regression equations rather than the measured values because the readings varied by more than 4 orders of magnitude over the course of the study and provided a more linear curve to regress against other variables. The relationships between the natural log of the soil

CO₂ efflux rates and measured soil temperature and moisture at 15 cm were analyzed using multiple regression analysis (Neter et al. 1996) using SASTM software (Statistical Analysis Systems, Cary, NC). Significant variables that were included in individual regression models were initially selected using the SAS stepwise procedure and PROC GLM to develop models with high R^2 and optimal Mallows Cp statistic (Mallows 1973) while eliminating collinear variables and controlling for variance inflation of parameters.

Differences in CO₂ efflux rates between study areas and between treatments at each study area by sampling date were assessed using a one-way analysis of variance (ANOVA) ($\alpha = 0.05$) using Fisher's LSD in the Minitab statistical software (Version 13) (Minitab, Inc., State College, PA 16801-3008) (Snedecor and Cochran 1989). Descriptive statistics were then used to compare variability within tested populations.

Results

Soil CO₂ efflux

Soil temperature and moisture influenced soil CO₂ efflux in this study. As an example, the mean CO₂ efflux rates from the forest treatment plots at Hall were plotted along with the mean soil temperature and moisture (Figure 1) for each sampling period. The four highest mean CO₂ efflux rates occurred when soil temperatures at 15 cm were above 20 °C, within the range of growth of most soil microbes (15–35 °C) and during times of increased vegetation growth and rates of biological processes (Paul and Clark 1989). Mean CO₂ efflux rates $> 2 \mu\text{mol m}^{-2} \text{s}^{-1}$ were measured when mean soil temperatures were at 14 °C or above except when mean soil moisture content was below 18%. Mean CO₂ efflux rates were clearly limited by mean soil moisture content of 20% and below in August 2001 and June 2002. Low soil moisture

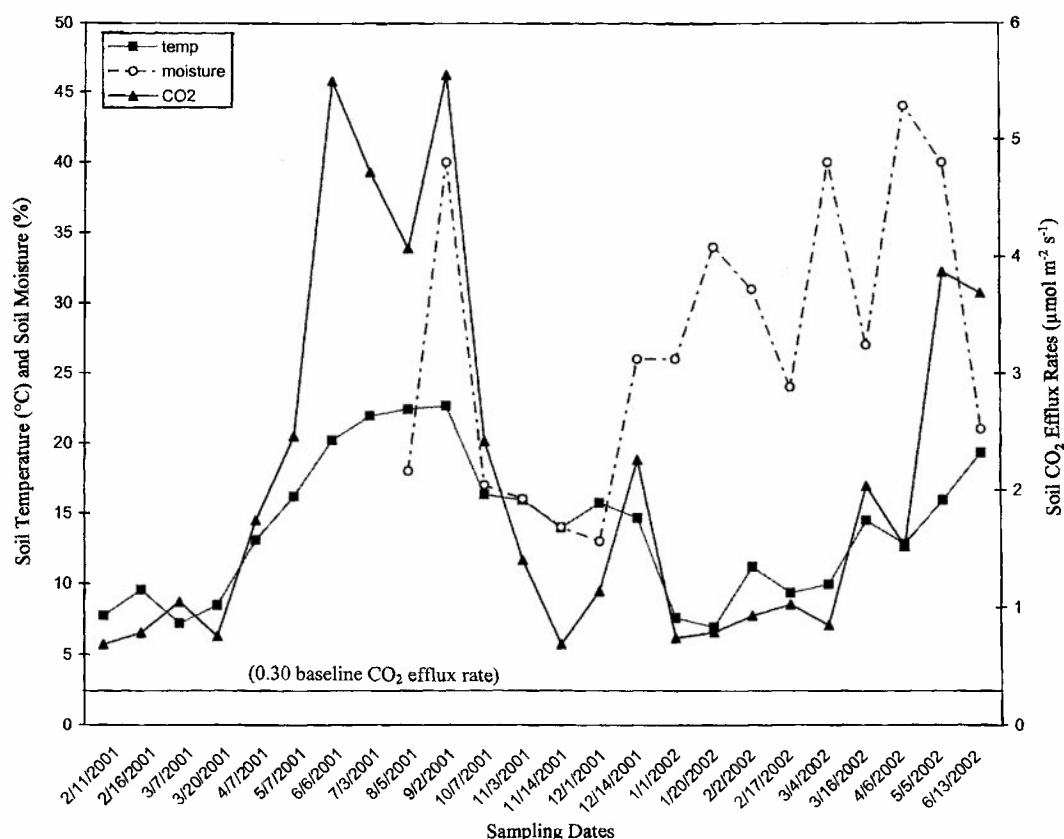


Figure 1. Mean monthly soil CO₂ efflux rates, soil temperature, and soil moisture during monthly sampling dates in a representative forest treatment plot (10) at the Hall property.

was more limiting to CO₂ efflux when temperatures were high. High temperatures did not limit soil respiration or plant growth on constantly moist sites (Kirshbaum 2002; Pangle and Seiler 2002). Soil temperature and CO₂ efflux tracked each other in January through March of both years, regardless of soil moisture content.

There were differences in soil properties by land use. The loblolly forest plots at Bruff had between 4 and 7 cm of surface Oi (fibric), Oe (hemic), and Oa (sapric) horizons. Hardwood forest plots at Hall had continuous Oi and Oe horizons 1–2 cm thick but most did not have Oa horizons. The field plots had discontinuous Oi and Oe horizons 1–2 cm thick and lacked Oa horizons altogether. A representative Bruff forest plot had about three times as much organic carbon (carbon) in the A horizon as a representative field plot A horizon and a higher C/N ratio (Table 1). The soils at Hall had similar C/N values but the A horizon in the Hall forest had about 14 times as much carbon as the A horizon in the field. The A horizon carbon at Hall was higher than at Bruff because at Bruff more carbon was tied up in the Oa loblolly leaf litter above the mineral soil but at Hall it was incorporated into the A horizon. Repeated plowing and farming depleted the carbon in the field A horizons.

The CO₂ efflux data from both study areas were combined into one dataset because there was no difference ($p > 0.05$) in mean efflux rates between the Bruff and Hall study areas (1.610 vs. 1.611 $\mu\text{mol m}^{-2} \text{s}^{-1}$, $n = 285$, $\text{SD} = 1.494$ and 1.571). The combined interaction of soil temperature and moisture at 15 cm on CO₂ efflux was found to be stronger than that of the individual effect of soil temperature or soil moisture at 15 cm alone. The regression of the interaction of soil temperature and moisture at 15 cm on CO₂ efflux

rates revealed significant differences ($p < 0.001$) between treatments (Forest: $R^2 = 0.52$, Field: $R^2 = 0.38$, and Bare ground: $R^2 = 0.30$). However, since the soil moisture dataset was incomplete, only soil temperature was regressed against natural log-transformed CO₂ efflux rates. The differences between treatments (Forest: $y = 0.0288x^{1.5637}$ $R^2 = 0.71$; Field: $y = 0.0538x^{1.1815}$ $R^2 = 0.65$; and Bare ground: $y = 0.0628x^{1.011}$ $R^2 = 0.49$) were significant ($p < 0.001$), indicating that land use and vegetation type have a strong influence on the CO₂ efflux (Figure 2). Differences in CO₂ efflux between treatments increased at soil temperatures above 8–10 °C. These results partially agree with Wildung et al. (1975) who reported that CO₂ efflux had a strong positive correlation with soil temperature when soil moisture was greater than 10% ($R^2 = 0.93$, $p < 0.01$). However, the Wildung study was conducted on non-hydric soils and dealt with non-saturated soil conditions. These results may be useful to modelers who predict global climate change because they allow estimates of CO₂ efflux rates from various land-use scenarios using predicted soil temperatures. The forest and field CO₂ efflux rates were higher than in the bare ground because of the contribution of root and rhizosphere respiration. The forest plots had much higher live root densities than the field plots.

There were differences in mean CO₂ efflux rates between treatments on many sampling dates during the study (Tables 2 and 3). The CO₂ efflux rates were higher ($p < 0.05$) in the forest than bare ground plots on most sampling dates after April 2001 when root and rhizosphere respiration were at their peak (Raich and Tufekcioglu 2000). There were no differences ($p = 0.05$) between forest and other treatments in January to March of 2001 because of observed extremely dry soil conditions. However, the forest plots had higher CO₂ efflux rates than the other plots on winter 2001–2002 sampling dates when soil temperature and soil moisture at 15 cm were comparable between treatments and soil moisture was higher. The higher January to March forest plot CO₂ efflux rates may have been due to higher biological and microbial activity resulting from higher soil temperatures and soil carbon content (Burdett 2003). The forest soils were warmed from below and insulated from cold air by surface litter, allowing the trees to begin vigorous growth before the

Table 1. Organic carbon, total nitrogen, and C/N ratios of representative soils in forest and early-successional field (field) land uses.

Study area (treatment)	Organic carbon (g kg ⁻¹)	Total nitrogen (g kg ⁻¹)	Carbon/ nitrogen ratio
Bruff (forest)	44.18	2.17	20.40
Bruff (field)	16.11	1.13	14.21
Hall (forest)	98.86	5.01	19.73
Hall (field)	7.41	0.65	11.41

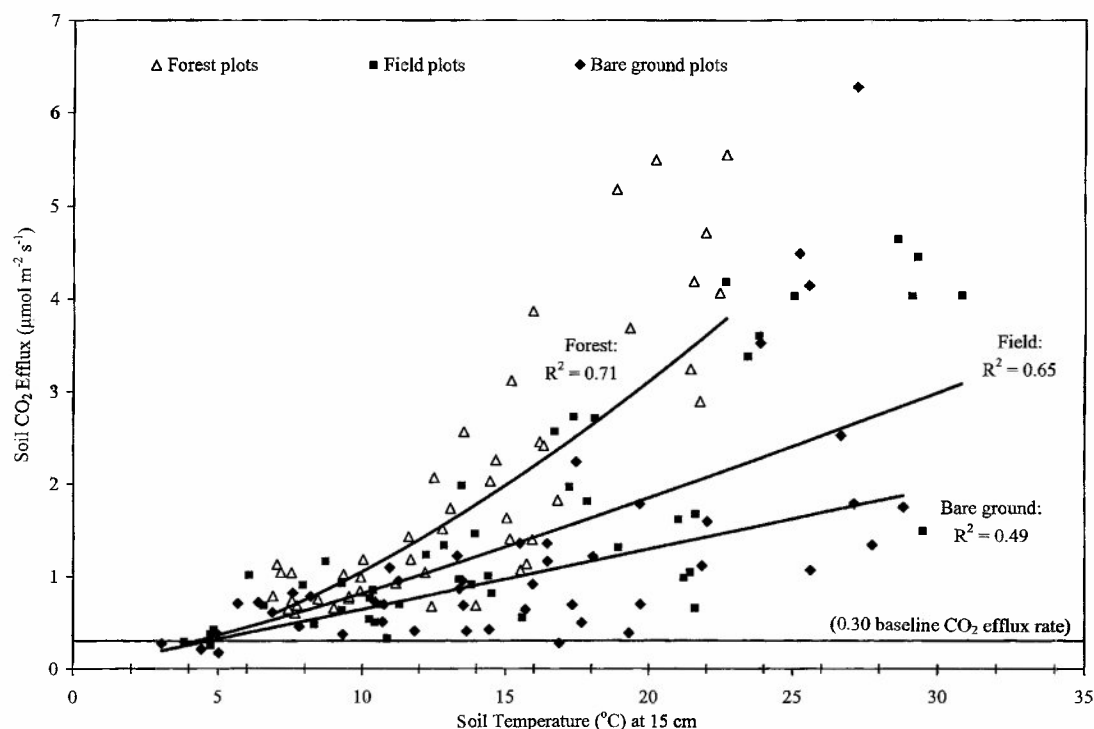


Figure 2. Correlation coefficients (R^2) of the significantly different ($p < 0.001$) exponential relationships between soil CO_2 efflux and soil temperature at 15 cm by land-use treatment.

field plot vegetation. Available labile carbon and nitrogen leached from freshly fallen tree leaves and nitrogen compounds and carbohydrates exuded from vigorous fine root growth just before bud-break in mid-January to mid-February may have boosted microbial growth and respiration (Griffin et al. 1996; Pendall et al. 2004). The CO_2 efflux rates in the forest and field were very similar to each other and higher than in the bare ground plots. The CO_2 efflux rates were higher in the Bruff field plots than in the forest and bare ground plots in May 2001 because they were warmer than the shaded forest. The herbaceous field plot vegetation produced a flush of leaf and fine root growth during May and the increased levels of CO_2 efflux may have been driven by fast turnover of current photosynthate derived from the rapidly growing vegetation (Pendall et al. 2004). The bare ground plot CO_2 efflux rates at Bruff were the highest in August 2001 because of the high soil temperature. Between December and March, the bare ground plots had the highest albedo during the day and highest redradiation heat loss at night, and the coldest soil temperatures. Between April and

November, the bare ground plots were tilled, reducing the albedo and increasing the total surface soil warming. The low CO_2 efflux rates in the bare ground during mid-March to June have been caused by a combination of ponding, an absence of vegetation, and lower labile carbon inputs. The rainfall did not infiltrate the surface of the bare ground plots easily because they were compacted by tillage and lacked soil structure. The compaction and ponding may have created anaerobic conditions and shifted production of CO_2 to methane (CH_4) by methanogenic bacteria, as reported by Inubushi et al. (2003). High evaporation rates from the bare surface and slow percolation rates resulted in relatively drier surface conditions in 2001 that could have depressed soil CO_2 efflux rates during warm periods (Kirshbaum 2002; Pangle and Seiler 2002). The bare ground CO_2 efflux rates climbed above those in field plots in April 2002 when soil temperatures in the bare ground plots began to exceed those of the other treatments.

Low soil CO_2 efflux rates in the ponded bare ground plots at Hall in mid-March and April of 2002 were surprising, as surface ponding has been

Table 2. 2001 Soil CO₂ efflux rates compared by treatment and sample date at each study area.

Bruff					Hall				
Date	Treatment	N	μ	SD	Date	Treatment	N	μ	SD
2/10/01	Forest	12	1.1826a	0.371	2/11/01	Forest	12	0.6826a	0.424
	Field	12	0.8504a	0.332		Field	12	0.9042a	0.713
	Bare ground	12	1.2227a	0.437		Bare ground	12	0.6079a	0.235
2/19/01	Forest	12	1.1257a	0.315	2/16/01	Forest	12	0.7798a	0.485
	Field	12	1.0125a	0.485		Field	12	0.9684a	0.717
	Bare ground	12	0.7059a	0.448		Bare ground	12	0.6966a	0.481
3/7/01	Forest	12	0.6439a	0.251	3/7/01	Forest	12	1.0410a	0.868
	Field	12	0.6808a	0.382		Field	12	0.6369a	0.492
	Bare ground	12	0.7172a	0.584		Bare ground	12	0.8168a	1.182
3/19/01	Forest	12	0.7562a	0.498	3/20/01	Forest	12	0.7502a	0.473
	Field	12	0.5026a	0.371		Field	12	0.5369a	0.478
	Bare ground	12	0.6854a	0.5607		Bare ground	12	0.4535a	0.407
4/7/01	Forest	12	1.0427a	0.598	4/7/01	Forest	12	1.7368a	0.779
	Field	12	0.9096a	0.433		Field	12	1.6768a	1.086
	Bare ground	12	1.1618a	0.878		Bare ground	12	1.3545a	0.460
5/8/01	Forest	12	1.6299b	0.762	5/7/01	Forest	12	2.4590a	1.479
	Field	12	2.7133a	0.967		Field	12	0.9870b	0.622
	Bare ground	12	1.5966b	0.832		Bare ground	12	1.0250b	0.917
6/5/01	Forest	12	5.1746a	1.751	6/6/01	Forest	12	5.4970a	1.320
	Field	12	4.1887a	1.068		Field	12	4.4530a	2.190
	Bare ground	12	4.1451a	1.795		Bare ground	12	4.4910a	1.930
7/2/01	Forest	12	2.8956a	1.678	7/3/01	Forest	12	4.7180a	1.301
	Field	12	4.0309a	1.420		Field	12	4.0280a	1.754
	Bare ground	12	1.0685b	0.832		Bare ground	12	1.7890b	1.432
8/7/01	Forest	12	3.2448b	1.067	8/5/01	Forest	12	4.0650a	1.585
	Field	12	3.3828b	1.283		Field	12	4.0420a	1.260
	Bare ground	12	6.2741a	3.138		Bare ground	12	1.3430b	1.405
9/2/01	Forest	12	4.1903a	0.885	9/2/01	Forest	12	5.5470a	1.132
	Field	12	3.6043ab	0.939		Field	12	4.6450a	2.424
	Bare ground	12	2.5288b	0.933		Bare ground	12	3.5250a	1.896
10/7/01	Forest	12	1.8244a	0.683	10/7/01	Forest	12	2.4161a	1.095
	Field	12	1.9669a	0.731		Field	12	1.8142ab	0.613
	Bare ground	12	1.7867a	0.894		Bare ground	12	1.3579b	0.918
11/3/01	Forest	12	1.4056a	0.688	11/3/01	Forest	12	1.3992a	0.468
	Field	12	1.0022ab	1.035		field	12	1.0473ab	0.360
	Bare ground	12	0.4982b	0.276		Bare ground	12	0.6926b	0.418
11/17/01	Forest	12	0.6772a	0.364	11/14/01	Forest	12	0.6843a	0.340
	Field	12	0.3266a	0.190		Field	12	0.8140a	0.593
	Bare ground	12	0.4072a	0.529		Bare ground	12	0.4037a	0.298
12/1/01	Forest	12	1.0656a	0.744	12/1/01	Forest	12	1.1341a	0.286
	Field	12	0.5513b	0.216		Field	12	0.6607b	0.358
	Bare ground	12	0.3864b	0.164		Bare ground	12	0.2756c	0.175
12/13/01	Forest	12	2.5678a	0.611	12/14/01	Forest	12	2.2583a	0.590
	Field	12	1.3352b	0.410		Field	12	1.3139b	0.629
	Bare ground	12	0.9530b	0.510		Bare ground	12	0.6397c	0.446

For each sampling date, means followed by different lowercase letters are significantly different at the 0.05 probability level.

reported to cause overestimate soil CO₂ efflux rates made by the infrared gas analyzer by up to 17% (Widen and Lindroth 2003). However, the anaerobic conditions caused by ponding probably reduced CO₂ and favored CH₄ production, and there were no higher plants present to generate

CO₂. A laboratory study by Moore and Dalva (1997) on core samples taken from wetlands shows that CH₄ emission had a negative logarithmic correlation with the depth of the groundwater level. CO₂ emission exhibited a positive linear correlation with water table depth. Therefore, the

Table 3. 2002 Soil CO₂ efflux rates compared by treatment and sample date at each study area.

Bruff					Hall				
Date	Treatment	<i>n</i>	μ	SD	Date	Treatment	<i>n</i>	μ	SD
1/2/02	Forest	12	0.6017a	0.195	1/1/02	Forest	12	0.7369a	0.334
	Field	12	0.2933b	0.145		Field	12	0.2526b	0.121
	Bare ground	12	0.2713b	0.187		Bare ground	12	0.1705b	0.135
1/20/02	Forest	6	0.9118a	0.507	1/20/02	Forest	9	0.7841a	0.208
	Field	6	0.4075b	0.174		Field	6	0.3718b	0.179
	Bare ground	6	0.3733b	0.278		Bare ground	6	0.2117b	0.223
2/2/02	Forest	12	1.1838a	0.406	2/2/02	Forest	12	0.9244a	0.387
	Field	12	0.6976b	0.345		Field	12	0.7653a	0.297
	Bare ground	12	0.9499ab	0.420		Bare ground	12	1.0942a	0.505
2/17/02	Forest	12	0.6573a	0.330	2/17/02	Forest	12	1.021a	0.934
	Field	12	0.4800a	0.428		Field	12	0.6976a	0.555
	Bare ground	12	0.3683a	0.231		Bare ground	12	0.7821a	0.559
3/4/02	Forest	12	0.9919a	0.300	3/4/02	Forest	12	0.8429ab	0.312
	Field	12	0.9245a	0.302		Field	12	1.1614a	0.629
	Bare ground	12	0.7237a	0.457		Bare ground	12	0.5084b	0.302
3/16/02	Forest	12	2.0708a	0.569	3/16/02	Forest	12	2.032a	1.280
	Field	12	1.9841a	0.476		Field	12	1.6190ab	1.051
	Bare ground	12	0.9144b	0.647		Bare ground	12	0.7b	0.536
4/6/02	Forest	12	1.4287a	0.468	4/6/02	Forest	12	1.5147a	0.706
	Field	12	1.2318ab	0.551		Field	12	1.4611a	0.900
	Bare ground	12	0.8667b	0.461		Bare ground	12	0.4204b	0.493
5/5/02	Forest	12	3.1178a	1.013	5/5/02	Forest	12	3.868a	1.029
	Field	12	2.5710a	1.205		Field	12	2.728a	1.432
	Bare ground	12	2.2430a	1.669		Bare ground	12	1.216b	0.799
6/13/02	Forest	12	3.2440a	1.153	6/13/02	Forest	12	3.6847a	0.994
	Field	12	2.0029b	1.131		Field	12	1.4903b	0.725
	Bare ground	12	1.7860b	0.941		Bare ground	12	1.7517b	0.981

For each sampling date, means followed by different lowercase letters are significantly different at the 0.05 probability level.

low soil CO₂ efflux rates in the bare ground plots at Hall were probably caused both by anaerobic soil conditions and low soil temperatures during the winter and spring and by low soil moisture at high temperatures (Ino and Monsi 1969; Howard and Howard 1993). These results agree with those of Inubushi et al. (2003) who reported that soil moisture is one of the most important controlling factors for biological reactions in soil, including microorganisms and plant roots, which produce CO₂. These results also partially agree with Wildung et al. (1975) who reported that CO₂ efflux had a strong positive correlation with soil temperature when soil moisture was greater than 10% ($R^2 = 0.93$, $p < 0.01$), rather than when soil moisture was above 22% as in this study. The research by Wildung et al. (1975), Wagai et al. (1998), and Pangle and Seiler (2002) were conducted on non-hydric soils and the saturated conditions experienced during this study may explain the difference in results.

Growing season measurements and indicators

The study was implemented in mid-January, limiting the 2001 growing season to a maximum duration of 344 days, and it concluded on June 14, a period of 167 days in 2002 (Figures 3 and 4). The growing season measured by soil temperature above 5 °C at 50 cm is presented for comparison to growing seasons estimated by frost-free days above -2.2 °C, vegetation indicators, and biological activity as indicated by CO₂ efflux rates.

At both Bruff and Hall, the growing season measured by soil temperature above 5 °C at 50 cm was continuous throughout the study in the forest, and was continuous in the bare ground plots except for four days between January 5 and 10, 2002. The 50-cm temperature growing season was continuous in the field plots at Bruff, and was continuous except between for four days between January 25 and 30, 2001 at Hall (Burdett 2003).

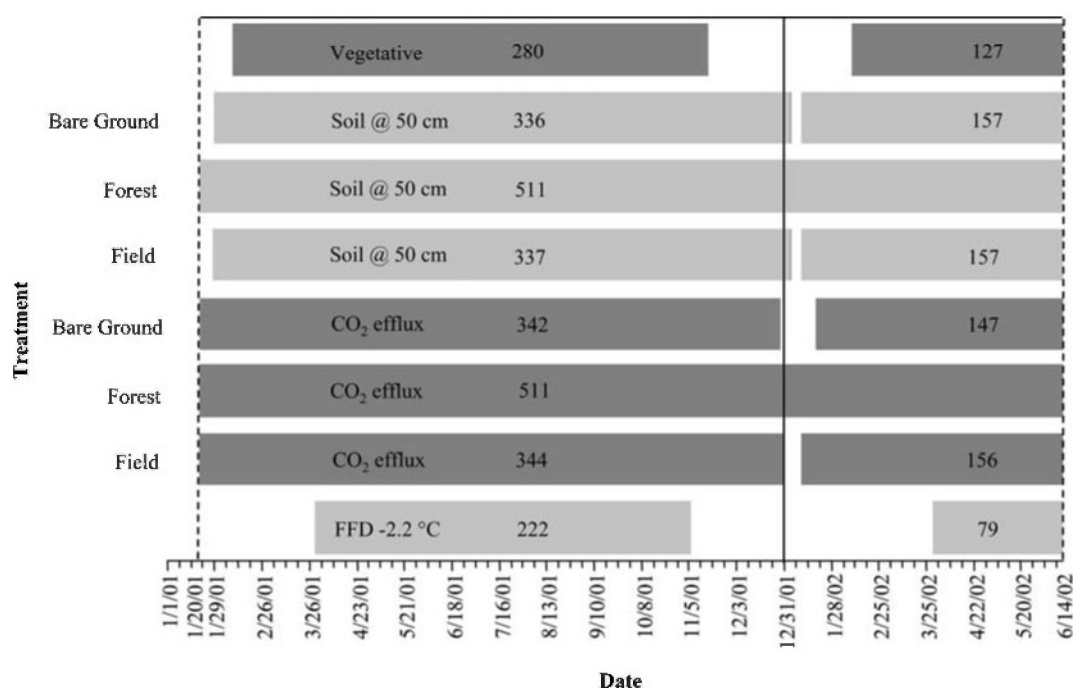


Figure 3. Extent of vegetative, soil temperature at 50 cm (Soil at 50 cm), CO₂ efflux, and frost-free days at –2.2 °C (FFD –2.2 °C) growing seasons at the Bruff study area with treatment and length in days indicated. Dashed vertical lines mark the beginning and end of the study, and the solid vertical line marks January 1, 2002.

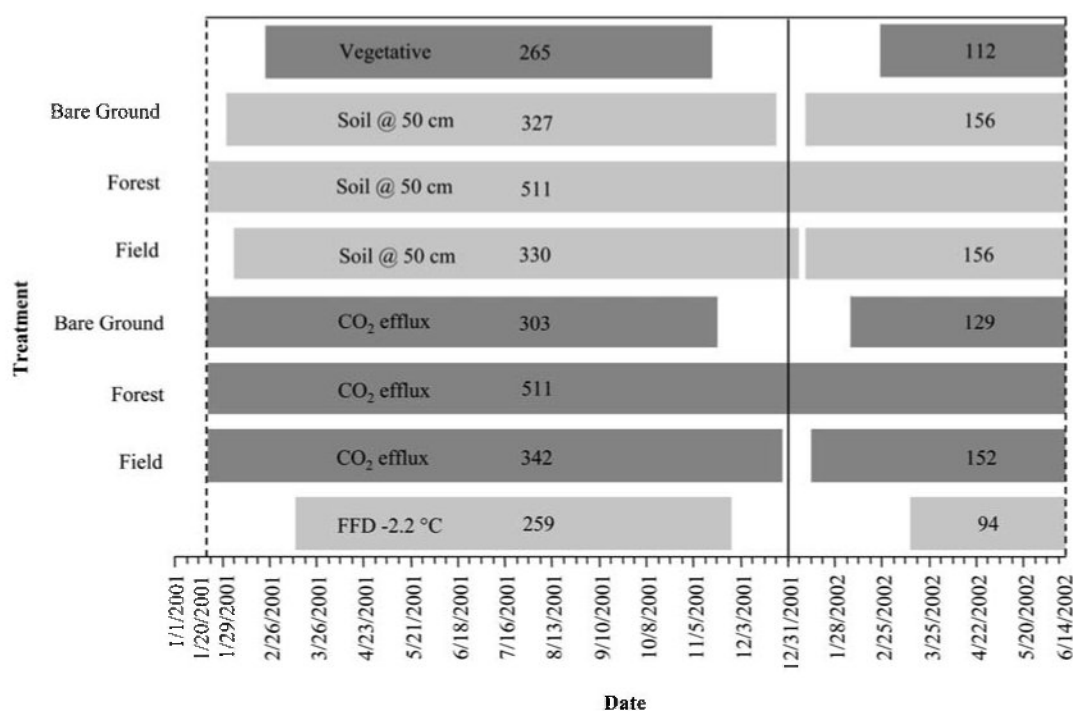


Figure 4. Extent of vegetative, soil temperature at 50 cm (Soil at 50 cm), CO₂ efflux, and frost-free days at –2.2 °C (FFD –2.2 °C) growing seasons at the Hall study area with treatment and length in days indicated. Dashed vertical lines mark the beginning and end of the study, and the solid vertical line marks January 1, 2002.

The vegetative growing season was assessed by the earliest date when a dominant hardwood overstory species began to show visual signs of bud break. In the Bruff study area, bud break of *Acer rubrum* was observed as early as the first week of February of 2001. At Hall, bud break was not observed in *Acer rubrum* or *L. styraciflua* until the middle of February in 2001. In the middle of November 2001 the overstory species began to senesce and lose their leaves, terminating the vegetative growing season. Bud break was initiated at Bruff by the middle of January and by the end of January at Hall in 2002 (Burdett 2003).

There was little agreement between the length of the growing season based on listed frost-free days or the vegetative indicators and the CO₂ efflux data. However, the CO₂ efflux data agreed with the soil temperature at 50 cm (control) measurements and appears to be an accurate indicator of biological or microbial growing seasons. Microbial and biological activity were assumed to be significant when the CO₂ efflux rates were above the baseline level of $0.30 \mu\text{moles m}^{-2} \text{s}^{-1}$ calculated from the CO₂ efflux data for periods when soil temperature was $< 5^\circ\text{C}$ at 15 cm.

At Bruff, the CO₂ efflux rates in the forest plots were above the baseline throughout the study. The CO₂ efflux in the field plots were above the baseline except for 9 days between December 31, 2001 and January 10, 2002. The CO₂ efflux rates in the bare ground plots (first tilled in April 2001), were above the baseline except for 21 days between December 29, 2001 and January 20, 2002.

At Hall, the CO₂ efflux rates in the forest plots were above the baseline throughout the study. The CO₂ efflux in the field plots were above the baseline except for 16 days between December 29, 2001 and January 15, 2002. The CO₂ efflux rates in the bare ground plots (first tilled in April 2001), were above the baseline except for 78 days between November 20, 2001 and February 7, 2002.

The CO₂ efflux rates were appreciable in the forest treatment during the period that more closely matched the 50-cm soil temperature growing season than the vegetative indicator growing season, indicating that root and microbial respiration continued in the forest even when leaves are not on the trees and shrubs. CO₂ efflux rates fell below the baseline level in the bare ground plots earlier than soil temperatures at 50 cm fell below 5°C . This indicates that soil temperatures at 15 cm cooled

enough to inhibit microbial activity even though the temperatures at 50 cm were still warm and that the temperatures at 15 cm were not representative of those at 50 cm. CO₂ efflux continued in the field treatment plots longer than indicated by hardwood leaf presence and longer than in the bare ground plots due to the presence of herbaceous vegetation that stayed green almost year-round. These results indicate that higher plant activity produces more CO₂ efflux in wet flats soils in January to March than microbial activity. This effect was more pronounced at Hall than at Bruff because the Bruff plots were drier and received almost no measurable rainfall in November 2001, resulting in lower total plant metabolic activity in the plots (Burdett 2003). The bare ground plots were not insulated against the cold January and February air temperatures that affected the soil temperature at 15 cm in the open fields.

Biological and microbial activity was very minimal for up to 2 and 11 weeks during January to March in the field and bare ground plots. There were many consecutive days with soil temperatures at 15 cm below 5°C when appreciable CO₂ efflux was measured and when water was within 30 cm of the surface (Burdett 2003). These results indicate that even though low soil temperatures may inhibit biological and microbial activity, the redox depletions and concentrations found in wet flats soils may form or have formed during January to March saturation and reduction events, as reported by Pickering and Veneman (1984), Groffman et al. (1992), and Megonigal et al. (1996).

Discussion

Differences in land use affected the duration and the timing of measured soil CO₂ efflux rates directly by presence and type of vegetation and surface organic horizons and indirectly through its effect on soil temperature and moisture in the upper 15 cm. Peak CO₂ efflux corresponded to periods of adequate but not excessive moisture, combined with high soil temperatures and a flush of available labile carbon from fallen tree leaves or vigorous fine root growth. The forest land use had higher CO₂ efflux than the field and the field had higher CO₂ efflux than the bare ground. This implies that forests soils may evolve more CO₂ than other land uses that are in apparent carbon pool

equilibrium and have not been recently cleared of forests. It is clear that land use and its associated soil properties should be considered in modeling of CO₂ emissions from wetland systems as part of greenhouse gas studies.

As expected from upland soil respiration studies, soil temperature regulated CO₂ efflux when soil moisture was not limiting, whereas CO₂ efflux was low during very dry conditions, even if temperatures were high (Inubushi et al. 2003; Pendall et al. 2004). Increases in soil temperature and availability of labile carbon and nitrogen should be the driving forces in wetlands except during times when they have limited soil moisture and high water potentials. The wetlands most likely to be limited are those that are intermittently saturated, such as the wet flats studied in this paper. On the other hand, excess soil moisture (inundation) in wetlands produces anaerobic conditions and probably production of CO₂ to that of CH₄. Few previous studies have reported detailed changes in soil respiration in wetland forests, and none have been reported in wet flats.

CO₂ efflux rates are important indicators of the below-ground growing season for wetland ecosystems. Based on this study of CO₂ efflux, early successional fields following cropping in wet flats have a shorter biological growing season than forested wet flats, while currently tilled wet flats have the shortest biological growing season. CO₂ efflux also appears to be a reliable and accurate indicator of the growing season defined by current federal regulations as periods when soil temperatures at 50 cm stay above 5 °C. Researchers need to make many measurements to get a good time-integrated value and a more accurate idea of the overall CO₂ efflux and biological and microbial functioning of the ecosystem than would be provided by individual measurements. Both soil temperature measurements and CO₂ efflux rates indicate that the biological growing season of forested thermic wet flats is continuous and much longer than originally assumed by the regulated frost-free days -2.2 °C threshold used by the ACOE.

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