Methane emissions from floodplain swamps of the Ogeechee River: long-term patterns and effects of climate change

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Abstract. Patterns and rates of wetland methane emissions and their sensitivity to potential climate change are critical components of the global methane cycle. In this study, we use empirical simulation models to investigate these processes in floodplain swamps of the Ogeechee River in Georgia, U.S.A. We developed statistical models that relate methane emissions to monthly climate and river flow based on field observations of methane emissions from this system made during 1987—1989. Models were then applied to observed climate and hydrograph for 1937—1989 and to simulated altered climates. Altered climates were generated from the present-day climate by changing monthly temperatures by a constant amount and/or changing monthly precipitation by a constant proportion, thus altering long-term averages and preserving year-to-year variation.

Under the present-day climate regime, simulated methane emissions were variable between years and responded very strongly to changes in river discharge. The long-term average was 27 g C m⁻² yr⁻¹, with no significant linear trend over the model period. In the altered climate simulations, methane emissions were very sensitive to changes in precipitation amounts, with a 20% decrease in rainfall resulting in 30–43% declines in methane emissions. Predicted effects of temperature changes on methane emissions were less consistent, and were strongly dependent on assumptions made about the response of evapotranspiration to elevated temperatures. In general, hydrologic impacts of changes in evapotranspiration rates (such as may occur in response to temperature shifts) were more important than direct temperature effects on methane production.

Introduction

Freshwater wetlands are considered to be a major source of atmospheric methane (Cicerone and Oremland 1988). However, the actual magnitude of global methane emissions from wetlands remains somewhat uncertain. Past estimates have been as low as 11-57 Tg/yr (Seiler 1984) and as high as 190-300 Tg/yr (Ehhalt and Schmidt 1978). Recently, a value of 110-115 Tg/yr (Matthews and Fung 1987, Cierone and Oremland 1988) has been widely accepted. There are two major factors that have contributed to this uncertainty in the wetland CH_4 source term. First, the extent of wetlands on a global scale has been poorly known until recently, with

estimates ranging from 2.0×10^6 km² (Lieth 1975; Whittaker and Likens 1975) to 6.7×10^6 km² (Rodin et al. 1975). Matthews and Fung's (1987) compilation of data from various sources has substantially improved this situation, leading to an estimate of 5.3×10^6 km².

Equally important in determining the global wetland CH_4 flux are rates of methane emissions from these systems, which are also incompletely known. The estimate of 111 Tg/yr by Matthews and Fung (1987) is based on methane flux measurements from only four other studies. It is difficult to characterize methane emissions from a given system in a short time period because of their high intrinsic spatial and temporal variability. Much recent work has been directed at improving resolution of spatial variability in methane source areas (e.g. Bartlett et al. 1988). Temporal variability has received far less attention. Studies in which CH_4 emissions have been determined over long periods have found rates that range over several orders of magnitude between sample dates (e.g. Harriss et al. 1982; Wilson et al. 1989).

A major impetus for research on wetland CH₄ emissions is their potential to provide a feedback on global climate change and atmospheric chemistry; thus, the question of temporal variability is key. Observed temporal variability in wetland CH₄ emissions has been strongly tied to temperature and hydrology, both of which are under climatic control. A variety of climate models have predicted that increasing tropospheric concentrations of CO₂, CH₄, and other gases will lead to global temperature increases of 0.5 to 4.2 C and shifts in global precipitation patterns (Schlesinger and Mitchell 1987; Mitchell et al. 1989; Meehl and Washington 1990). Hansen et al. (1988) project that global warming from CO₂, methane, and other atmospheric trace gases will be clearly identifiable within the present decade. In their model, eastern North America was one of the earliest regions affected. Temperature and hydrologic regimes of many wetlands will be altered by climate shifts associated with this "greenhouse warming". Projections of how wetlands will be affected as global methane sources are difficult to make without adequate knowledge of patterns and rates of wetland methane emissions under current conditions. To date, those studies that have examined the potential impact of greenhouse warming on wetland CH₄ emissions have investigated only direct temperature effects (Hameed and Cess 1983; Lashof 1989; Harriss and Frolking 1992). Hydrologic processes have not been addressed.

In this study, we address these questions of temporal variability and long-term change by examining the dynamics of CH₄ emissions from a temperate wetland system using empirical simulation models. The study system is the forested floodplain of the Ogeechee River in Georgia, U.S.A. The Ogeechee is a blackwater coastal plain river that has been the subject

of extensive previous work on carbon dynamics and river-floodplain interactions (e.g. Edwards and Meyer 1987; Wallace et al. 1987; Benke and Meyer 1988; Cuffney 1988; Meyer 1990). It is representative of the extensive riparian swamps of the southeastern United States, and is a member of the broad global assemblage of forested wetlands which are thought to contribute over half of global wetland CH₄ emissions (Matthews and Fung 1987).

The work we present here is based on extensive field studies of CH₄ emissions from the Ogeechee floodplain conducted from 1987 through 1989, which are fully presented in Pulliam (1991). CH₄ emissions were measured monthly from a variety of floodplain habitats and examined in relation to seasonal shifts in floodplain inundation and soil temperature. Spatial variability in CH₄ emissions (between habitats) was found to be large but was consistent over time, with 33% of floodplain area serving as the source for all of net floodplain CH₄ emissions. As would be expected, the CH₄ source habitats were the most frequently inundated portions of the floodplain, comprising the low gum-cypress swamps of swale and backswamp areas. Higher sites with mixed bottomland hardwood forests did not show significant net CH₄ emissions. The distinction between low, frequently-flooded gum-cypress swamps and high, infrequently flooded bottomland hardwood forests is a fundamental feature of coastal plain floodplains throughout the southeastern U.S., and is tied to many biological and biogeochemical processes in these systems (Wharton 1982; Mitsch and Gosselink 1986). At the Ogeechee, there was also a quantitative difference between CH₄ emission rates from low habitats on the east and west sides of the river, with those of the east floodplain (EFP) showing higher average rates than those of the west floodplain (WFP) on the opposite side of the river.

Temporal variability in CH₄ emissions from the Ogeechee floodplain was also large and was more complex. Annual average methane emissions at the Ogeechee for two separate years of study differed by a factor of three (10–34 g C m⁻² yr⁻¹ from low habitats). CH₄ emissions were controlled largely by the interaction of seasonal temperature shifts and inundation patterns. CH₄ emissions took place only from inundated sites, with no statistically significant net flux (positive or negative) from non-flooded sites at any season. Emission rates from flooded sites (Fig. 1) showed a very strong response to soil temperature. At low temperatures CH₄ fluxes are near zero. As soil temperatures increase above 15 C, CH₄ flux rates rise abruptly. Emission rates remain high at all temperatures above 15 C, and although there is considerable variability they do not show a consistent trend of increase of decrease with higher temperatures on either EFP or WFP. Thus, the temperature response of CH₄ emissions

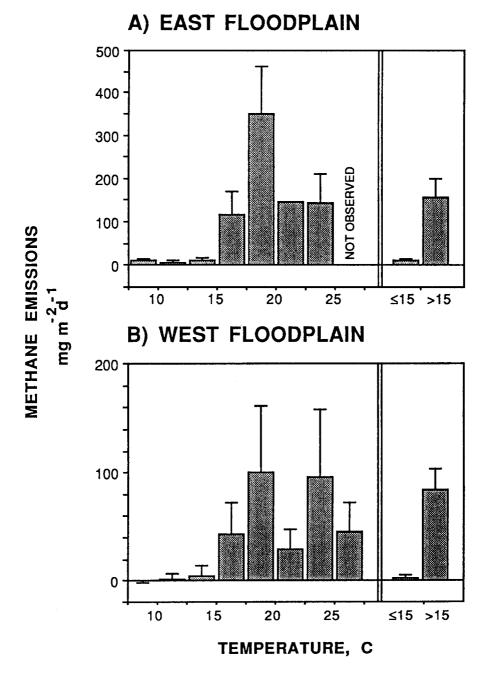


Fig. 1. Observed methane emissions from Ogeechee floodplain low habitat sites versus soil temperatures. Values show average of all individual methane flux measurements made from flooded low habitat sites within the indicated temperature range during 1987—1989. Error bars show ± 1 s.d. Left hand portion of each graph shows data pooled by 2.5 C temperature intervals. Right hand portion shows data pooled by temperature above or below 15 C.

at this site can be approximated as a step function, with small-scale and short-term variability superimposed.

This dramatic temperature response is not unique to the Ogeechee system. Sharply seasonal CH_4 emissions have been widely observed from numerous wetlands (e.g. Harriss et al. 1982, 1985; DeLaune et al. 1983; Wieder et al. 1990), and Wilson et al. (1989) described a step function temperature response for CH_4 emissions from Virginia swamps that is very similar to the Ogeechee pattern.

Overall, we have found that most of the variation in CH₄ emissions from the Ogeechee floodplain can be predicted simply by defining a methane producing habitat within the floodplain (low, frequently flooded gum-cypress swamps) and a methane production condition within this habitat (flooded when soil temperatures are above 15.5 C). A total of 73% of all net floodplain methane emissions took place at sites and times meeting these criteria, although they accounted for only 13% of all floodplain sites and times during the study period. As the two phenomena dictating this pattern (requirement for flooding and sharp seasonal temperature response) are general features of CH₄ emissions from most wetlands studied to date, a similar descriptive model may apply to many temperate wetlands. Of course, the details of temperature thresholds and inundation characteristics will be site-specific.

We used these patterns observed in the field as the basis for extrapolation of our results to longer time periods and alternative climate scenarios by use of empirical simulation models. The objectives of this work were two-fold:

- a) Estimation of average patterns and year-to-year variation of methane emissions from this site in order to better characterize methane emissions under the present-day climate.
- b) Assessment of sensitivity of methane emissions to shifts in temperature and precipitation in order to project the effects of long-term climate change on methane emissions from this system.

The latter objective necessitated the development of scenarios for altered climate and hydrologic regimes. Unfortunately, the potential climatic impacts of greenhouse warming at regional scales are unclear. As it is regional, not global climate dynamics that directly affect wetland hydrology, this uncertainty is a major handicap to projection of future system behavior. Specifically, in the southeastern U.S. three frequently cited general circulation models (GCMs) agree in predicting equilibrium temperature increases of 2–5C in both summer and winter in response to doubling of atmospheric CO₂ or equivalent increases in a combination of radiatively active trace gases (Hansen et al. 1984; Washington and Meehl 1984; Wetherald and Manabe 1986; Schlesinger and Mitchell 1987). However, there is no consensus among these models as to effects on

precipitation patterns in this region. Predicted changes range from near zero to increases or decreases of as much as 30%, depending on the model and time of year. The robustness of climate simulations from GCMs is such that relatively small predicted changes may be of low reliability. For example, Mitchell et al. (1989) altered the manner in which clouds were simulated in a GCM, thereby reducing predicted greenhouse warming for mid-northern latitudes by roughly half. Meehl and Washington (1990) revised a different GCM to incorporate more realistic simulation of formation and melting of snow and sea ice, thereby doubling predicted greenhouse warming for the southeastern U.S. and changing both the magnitude and direction of predicted shifts in soil moisture in this region. Thus, we did not feel it was possible to devise any specific scenario for potential greenhouse warming effects on the climate of our study system. Rather, we investigated the general sensitivity of floodplain methane emissions to changes in temperature and precipitation patterns.

Model structure

The system modeled is a site on the Ogeechee River in the coastal plain of Georgia, U.S.A. (32°08′ N, 81°25′ W). It has been described in detail elsewhere (Benke and Meyer 1988; Cuffney 1988; Meyer 1990; Pulliam 1991). The Ogeechee is a blackwater river with extensive forested floodplains typically 1—2 km wide. In order to incorporate the observed difference in methane emission rates between EFP and WFP, separate simulations were made for each of these floodplains. We simulated only the low floodplain habitats that were significant net CH₄ sources. EFP and WFP low habitats account for 18 and 15% of total floodplain area at this site, respectively. By dividing the floodplain both between high and low habitats and between EFP and WFP, the model incorporates much of the observed spatial variability within this system.

Climate and hydrology

The methane emission model was driven by soil temperatures and flood-plain inundation. All calculations were based on monthly time intervals. We selected the period May 1937 through December 1989 for simulation, as complete daily river discharge records for the Ogeechee River at Eden, 8 km above the study site, are available for this time (U.S. Geological Survey 1951—1989). Monthly temperature and precipitation for the entire Ogeechee drainage basin above the study site were represented by the average of data from four reporting stations within the basin that had

the most complete climate records for this period. These stations (Brooklet, Louisville, Millen, and Warrenton) are spaced nearly uniformly along the length of the basin. The 53-year climate record for the drainage basin is summarized in Figure 2. There was no significant trend in temperature, precipitation, or river discharge over this time period, although persistent wet, dry, warm, and cool periods of 5—10 years length were evident.

We approximated weather conditions at the study site using records from the Savannah National Weather Service office 20 km east of the study site (Weather Bureau 1937–1969, National Oceanic and Atmospheric Administration 1970–1989). Intermittent on-site records over 1987–1989 showed that Savannah climate data predict observed study site daily air temperatures with s.d. = ± 1 C and monthly rainfall totals with s.d. = $\pm 10\%$. Savannah weather data have been collected continuously for over 100 years. We predicted soil temperatures at the study site (S) from Savannah air temperatures (A) using the following model:

$$S = M + 0.74 (A - M)$$

Here, M represents mean Savannah air temperature for the previous 12 months. The slope term of 0.74 provided the best fit ($r^2 = 0.97$) to observed monthly soil temperatures at the study site for 1987—1989. We used the mean air temperature for the previous 12 months as the midpoint of the model rather than prescribing a fixed mid-point in order to accommodate gradual shifts in annual mean temperatures as shown in the climate record (Fig. 2).

We estimated floodplain inundation from river discharge, making separate simulations for EFP and WFP. The inundation characteristics of the study site are well known, having been documented in detail from 1982—1989 (Cuffney 1984; Pulliam 1991). For the present study, we predicted monthly mean inundation of EFP and WFP from monthly mean river discharge using the models shown in Fig. 3. These models are derived from observed monthly mean floodplain inundation and river discharge over the period January 1987 through December 1989. WFP inundation is highly predictable in this manner. EFP inundation is predicted adequately, but less precisely. Actual EFP water levels at low river stages are maintained largely by local rainfall and groundwater rather than by river water (Pulliam 1991), thereby somewhat decoupling EFP inundation and river stage. Although individual predicted monthly values for EFP inundation deviated significantly from observations, average seasonal and annual EFP inundation was predicted accurately by this model.

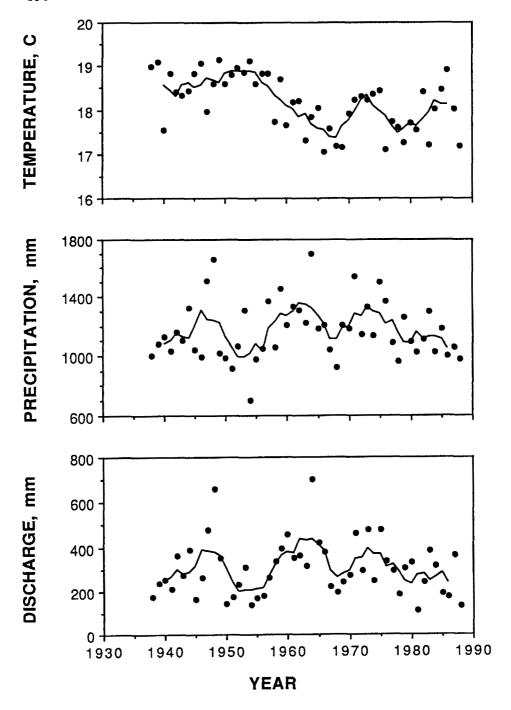


Fig. 2. Observed climate and river discharge for Ogeechee River drainage basin, 1937—1989. Circles show annual averages and lines show 5-year running average. Data are mean of four stations distributed across basin.

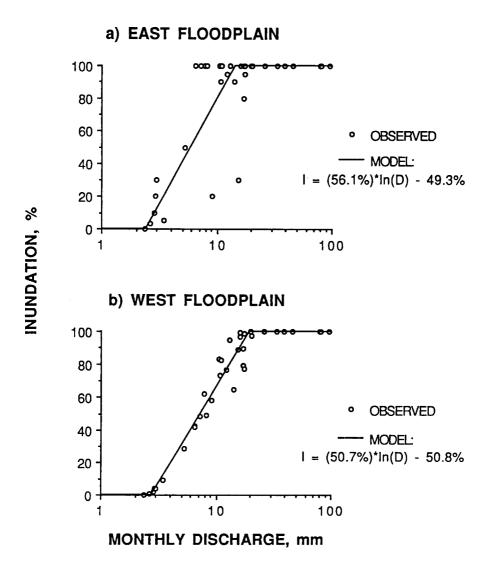


Fig. 3. Relationship between monthly river discharge and monthly average inundation of gum-cypress swamps on Ogeechee River floodplain, 1987—1989. Values are plotted separately for east and west sides of river channel. Line for model shows empirical equations used to predict inundation in simulation models.

Methane emissions

We based our simulation of methane emissions on data summarized above and presented in detail by Pulliam (1991). Monthly average methane emission rates for EFP and WFP were calculated using a step-function response to soil temperature as follows:

If soil T \leq 15.5 C then emissions = O

If soil $T \ge 15.5$ C then emissions = $I \cdot R$

where I is the average portion of floodplain inundated during month and R is methane emission rate for flooded sites. We assigned R the average value of observed emissions from low habitats on each floodplain while inundated during the warm season, equal to 156.9 mg m⁻² d⁻¹ for EFP and 84.0 mg m⁻² d⁻¹ for WFP.

Modeling climate change

We generated altered climates from the actual 53-year climate record by increasing temperatures by a constant amount and/or changing precipitation by a constant proportion. The climate shift was applied individually to each monthly temperature and precipitation value, thus changing average values while preserving seasonal and interannual variation. We simulated temperature increases of 2 and 4 C, precipitation shifts of -20% and +20%, and combinations thereof. Additionally, the seasonality of rainfall was altered in one scenario by increasing warm-season (May—October) precipitation by 20% while simultaneously decreasing cool-season precipitation by the same proportion.

Because river discharge is one of the two parameters driving methane flux simulations, it was essential to develop a model for prediction of discharge patterns under altered climates. A monthly water balance model for the Ogeechee drainage basin was constructed in which runoff was calculated from precipitation and evapotranspiration (ET). The structure of this model is given in the appendix and discussed in detail by Pulliam (1991). The use of water balance models to investigate hydrologic effects of climate change has been discussed and recommended by Gleick (1986, 1987). The prediction of ET is a critical component of these models; however, the direction and magnitude of greenhouse warming effects on ET is yet another area of uncertainty and disagreement. Higher temperatures are predicted to cause increases in ET (Revelle and Waggoner 1983; Gleick 1987), although observed interdecadel temperature shifts have not been found to significantly affect streamflow in North America (Karl and Riebsame 1989). Conversely, direct effects of elevated CO₂ may cause reductions in ET via increases in water-use efficiency of vegetation. Idso and Brazel (1984) predicted that this effect might be large enough in some regions to cause increases in streamflow, even if temperatures rise and precipitation is diminished to the extent predicted by GCMs. Other studies by Wigley and Jones (1985) and Martin et al. (1989) project that

direct CO₂ effects will not be large enough to increase runoff above present-day levels, but may somewhat ameliorate direct temperature effects.

In the present study, these different possible effects of greenhouse warming on ET were addressed by using two separate formulations for estimating ET from temperature and precipitation. Both were fit empirically using observed temperature, precipitation, and river discharge from 1980—1989. Though this 10-year period was on average drier than normal (Fig. 2), it included both the highest and lowest daily river flows for the entire period and spanned a wide range of conditions. The first model developed was a temperature-dependent (TD) model in which ET was calculated from monthly air temperature (T) and precipitation (P) according to the following formula:

$$ET = 9.0 + 2.0 T + 0.15 T \cdot P$$

where P and ET are expressed as mm/month and T as degrees C. This model predicts higher ET with higher temperatures both within and between years. The second model was a temperature-independent (TI) seasonal model in which ET was calculated from precipitation and calendar month alone, with no explicit temperature dependence:

$$ET = I_m + 0.42 P$$

The value of the intercept term; I_m , was determined separately for each calendar month, and ranged from O in midwinter to 65 mm/month in June and July (Table 1). In this model seasonal variation of ET is driven explicitly by I_m rather than implicitly by temperature. More detailed descriptions of this discharge modeling are contained in Pulliam (1991). Both the TD and TI discharge models simulated monthly discharge values well. Correlation coefficients (r^2) between actual and predicted monthly runoff for 1937–1979 (512 months, excluding 1980–1989 data used in model calibration) were 0.767 for TD and 0.763 for TI models. In comparison, Thornthwaite-Mather (1957) algorithms for calculating ET were much poorer predictors of discharge. The best fit was $r^2 = 0.3$ using these formulations.

Results

Model validation

Comparison of predicted and observed methane fluxes. The model predicted methane emissions during the time covered by the field study with

Table 1. Values for the intercept term, I_m , for each calendar month in the temperature-independent ET model (values in mm/month).

Calendar month	I_{m}
1	0
2	0
3	0
4	30
5	60
6	65
7	65
8	60
9	50
10	30
11	15
12	0

reasonable accuracy (Table 2). The model correctly predicted substantially higher methane emissions in the second year than in the first year on both floodplains, though the predicted difference was smaller than that actually observed. Similarly, the model correctly predicted higher methane emissions from EFP than WFP, but again to a smaller extent than was actually measured. Simulated whole-floodplain methane emissions for the entire 2-year field study agree with observed rates to within 4%. However, these comparisons are of limited value in assessing general model validity, as these field data were used to develop and calibrate the model.

Accuracy of this modeling approach can be better assessed by using CH₄ flux data from only one of the two years of the field study to predict methane emissions in the other year, thus deriving predicted gas flux rates that are computationally independent of the corresponding observed values (Table 3). The average (root mean square) error of these predictions was 9.5 g m⁻² yr⁻¹, or 43% of observed average fluxes. There was not a consistent trend for model predictions to over-or underestimate observed fluxes, with errors occurring in both directions.

Together, the comparisons of predicted and observed methane emissions shown in Tables 2 and 3 indicate that the model correctly predicts the direction of differences between sites and between years. However, the absolute magnitudes of the predicted and observed rates compare less favorably. It must be borne in mind that the observed rates are themselves subject to sample variance and are not precise values. The monthly

Table 2. Comparison of Ogeechee floodplain methane emissions (g m^{-2} yr⁻¹) observed in field and predicted by empirical simulation model for two years of field study (EFP = east floodplain, WFP = west floodplain).

Time period	Observed (Pulliam 1991)			Model		
	EFP	WFP	All	EFP	WFP	All
1937—1989	<u> </u>	_	_	33.9	16.6	26.6
August 1987—July 1988	15.4	2.4	9.9	19.7	9.2	15.3
August 1988—July 1989	47.2	15.8	34.0	38.5	18.7	30.2
Both years (Aug 87—Jul 89)	31.3	9.1	22.0	29.1	14.0	22.8

Table 3. Comparison of methane emissions observed and predicted by simulation model, using data from only one year of field study to predict rates for other year.

	Methane emissions, g m ⁻² yr ⁻¹		
	Observed	Model	Error
Year 1 predicted from year 2:			
EFP	15.4	20.6	+5.2
WFP	2.4	11.1	-28.7
All	9.9	16.6	+6.7
Year 2 predicted from year 1:			
EFP	47.2	33.8	-13.4
WFP	15.8	6.8	-9.0
All	34.0	22.5	-11.5

observed averages on which they are based typically show standard errors equal to 50—100% of the mean (Pulliam 1991). In this context, the model errors shown in Tables 2 and 3 are not excessive. The modeling approach of simply tracking the extent of warm, flooded conditions does reflect actual year-to-year variation in CH₄ emissions reasonably well. The fact that the model overpredicted fluxes for both floodplains in year 1 and underpredicted both in year 2 may indicate a real difference between the two years for which the model does not account. Given the simple model structure used, this is certainly a possibility. However, there are only 16 potential combinations of signs of errors for a comparison such as this, two of which (all positive or all negative) are very unlikely given the method of model calibration. Two of the remaining 14 combinations would show consistent overprediction in one year and underprediction in the other. Thus, the statistical significance of this pattern of model errors is low.

Model CH_4 emissions under observed vs. predicted discharge regimes. Under present-day climate, annual methane emissions predicted using the TI discharge model are closer to those generated with the actual discharge regime than are those predicted using the TD model ($r^2 = 0.760$ for TI vs. 0.596 for TD). The TD model tended to exaggerate variance between years when compared to the TI model, with standard deviation between years equal to 31.6% of mean for TD versus 23.4% for TI and 22.2% for actual discharge regimes. The better performance of the TI model is probably a consequence of its direct representation of seasonality of ET, rather than using temperature to indirectly drive seasonal patterns as in the TD model. Both TI and TD discharge predictions tended to underestimate methane emissions by an average of 7–8% relative to predictions based on actual discharge.

Methane emissions under present-day climate

Predicted single-year average methane emissions ranged by a factor of three during the 53-year simulation period (Fig. 4) on both EFP and WFP, with a standard deviation between years equal to 22% of the mean. Even averages across 5 years varied by as much as a factor of 1.6. This emphasizes the difficulty of characterizing rates of methane efflux using data from studies of a few years duration, even before this inherent variability is enhanced by sampling error. Averages for the entire simulation period are given in Table 2. The long-term average was 27 g m⁻² yr⁻¹. Total methane emissions for the two-year period spanned by the field study (Pulliam 1991) were 83–86% of predicted long-term average. The combination of very dry and relatively wet conditions experienced during this time apparently averaged to a fairly representative two-year period. Predicted monthly average methane emissions (Fig. 5) from both EFP and WFP peaked in spring and early summer when the floodplain was most likely to be both warm and wet at the same time.

Effects of greenhouse warming on methane emissions

Simulated methane emissions under four temperature regimes are shown in Figure 6 for both TI and TD discharge models. The two ET formulations led to very different predicted effects of temperature increases. In the TD model (Fig. 6a) average methane emission rates declined while range and variance of annual totals increased sharply with increasing temperature. The increase in variance was great enough that minimum and maximum annual values shifted in opposite directions. This larger variance arose from greater variability in floodplain inundation brought about by

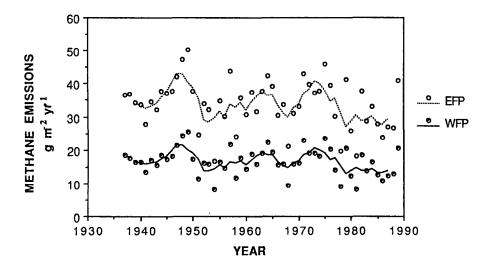


Fig. 4. Methane emissions from Ogeechee floodplain swamps predicted by simulation model, 1937—1989. Circles show averages for single calendar years, lines show 5-year running averages.

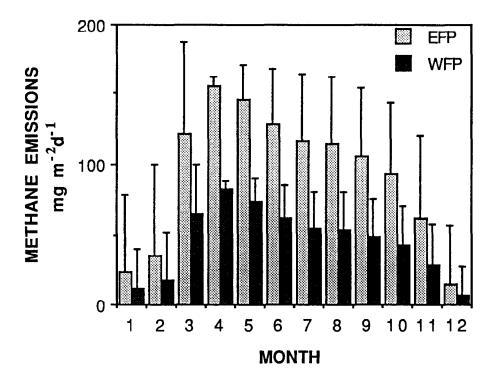


Fig. 5. Average monthly methane emissions from Ogeechee floodplain swamps predicted from simulation model. Error bars indicate ± 1 standard deviation of monthly predicted values for 53-year simulation.

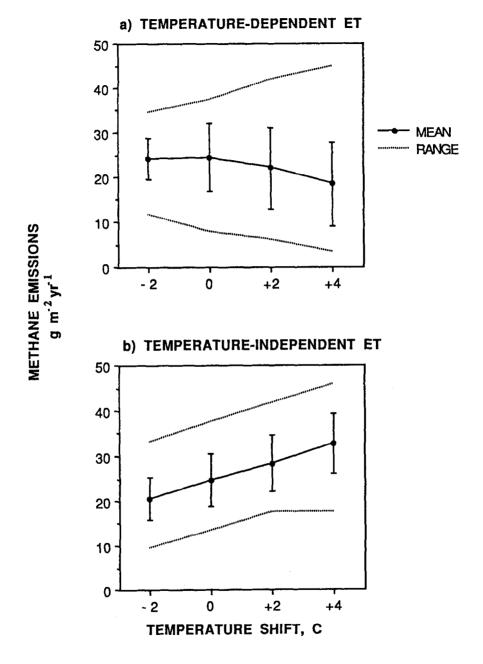


Fig. 6. Predicted effects of temperature shifts on methane emissions from Ogeechee floodplain swamps. Predictions shown separately for models using two methods for estimating evapotranspiration (ET) from temperature, precipitation, and season. Error bars show ± 1 standard deviation between single year averages, range indicates largest and smallest single-year average in 53-year simulation.

the elevated ET at higher temperature predicted by this model. Wet years still showed extensive floodplain inundation under these conditions, but dry years became more frequent and much drier in these simulations.

In contrast, the TI model (Fig. 6b) predicted steadily increasing methane emissions with increasing temperatures, with only slightly larger year-to-year variability. As ET did not change with temperature in this model, discharge and floodplain inundation patterns remained constant. Thus, the only effect of elevated temperatures was lengthening of the warm season and resultant increases in methane emissions. The TD and TI models agreed that methane emissions during the wettest years will be substantially larger under warmer temperatures. They disagree significantly, though, on their predictions for dry years and overall averages.

The TD and TI models both predicted similar effects of precipitation shifts, a result of their similar structures with respect to precipitation inputs. Predictions from the TI model are summarized in Fig. 7. Changes in rainfall were amplified in shifts in methane emission rates, especially in the case of precipitation decreases. A 20% drop in precipitation resulted in a 30% decrease in methane emissions (43% in TD model). Effects of 20% precipitation increases amounted to 22-24% increases in methane emissions. Variability in methane emissions was enhanced by reduced precipitation. With 20% lower precipitation, in the driest years there was virtually no methane production or floodplain inundation (96% reduction), whereas the maximum values for the wettest years were reduced by only 11%. Predicted methane emissions also were affected by shifts in seasonality of precipitation. Increasing warm season precipitation by 20% while simultaneously decreasing cool season precipitation by 20% increased average methane emissions by 8% (TD) and 14% (TI), although with little change in the range of annual averages.

Interactive effects of temperature and precipitation shifts were most evident in the TD model (Fig. 8). The TI model predicted simply that higher temperatures would result in higher methane emissions under all precipitation regimes (data not shown). However, the TD model demonstrated notable synergism between lower precipitation and higher temperatures that reduced methane emissions by nearly 60%. At 20% elevated precipitation, this model predicted little effect of temperature shifts on methane emissions.

Discussion

The CH₄ emission model presented here is quite simple in its ecological structure. It depends on few critical assumptions that are readily apparent

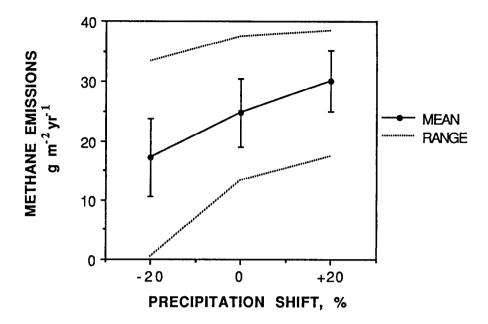


Fig. 7. Predicted effects of changes in precipitation on methane emissions from Ogeechee floodplain swamps using temperature-independent model. Error bars show ± 1 standard deviation between single year averages, range indicates largest and smallest single-year average in 53-year simulation.

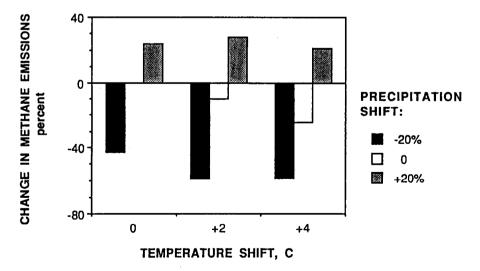


Fig. 8. Effects of combined changes in temperature and precipitation on Ogeechee floodplain methane emissions predicted by model with temperature-dependent estimation of evapotranspiration. Values show change in average emissions (53-year simulation) relative to nominal case driven by present day climate.

and largely supported by field observations. However, this simplicity does not allow the incorporation of a high level of ecological detail. Metabolic processes are not explicitly simulated, and floodplain response to environment is assumed to be constant over time. Thus, when extrapolated beyond the range of observed conditions, this model may be overly constrained in its behavior. For instance, when subjected to actual climate shifts, the real floodplain ecosystem is likely to show changes in primary production, carbon storages, and other properties that may directly or indirectly affect CH₄ emission rates. Although the simple structure of our model is justifiable as one valid approach to the questions investigated here, its limitations must be kept in mind when examining its predictions.

Predicted temperature effects on methane emissions were very sensitive to assumptions made about temperature effects on ET. Given the large discrepancies between predictions of the two models, it appears that net effects of greenhouse warming on methane emissions from forested floodplains are uncertain and cannot be clarified without more detailed accounting of the combined effects of elevated CO₂ and higher temperatures on ET. Reliable predictions of the effects of precipitation changes on methane emissions must also await more detailed regional projections of responses of precipitation patterns to greenhouse warming.

Few other predictions of responses of wetland methane emissions to global warming have been reported. Hameed and Cess (1983), Lashof (1989), and Harriss (1992) all predict that warmer global temperatures will stimulate wetland methane emissions. They base these predictions on the direct effects of higher soil temperatures and longer summers on net methane production, and primarily consider boreal sites. The indirect effects of greenhouse warming on wetland hydrology were not incorporated in their predictions. Results for the Ogeechee floodplain show that in this mid-latitude system, hydrologic factors were more important than direct temperature effects, and were the most difficult of modeled controls on methane emissions to predict. As the processes underlying these behaviors of the Ogeechee system are general features of wetland hydrology and biogeochemistry, there is good reason to think that many other types of wetlands will display similarly complex behavior.

The increased year-to-year variability under many climate change scenarios shown by the models presented here may have broad implications for the ecology of floodplain swamps. This is particularly true of the higher methane emissions predicted for wet years. These results indicated that even if the net effect of greenhouse warming is a decrease in floodplain inundation, during wet years floodplains may actually experience more extensive anaerobic conditions than they do at present. An expansion of the growing season in these systems so that it includes the peak

flood periods of late winter and early spring may have far-reaching consequences for floodplain vegetation and biogeochemistry. Simply expecting that lower river flows will cause floodplains to become more aerobic and more like upland systems may be grossly misleading.

Summary

- 1. Long term methane emissions from the Ogeechee floodplain low habitats average $27 \text{ g m}^{-2} \text{ yr}^{-1}$, and are highly variable between years. Totals for single years range over a factor of three, and even 5-year averages vary by as much as a factor of 1.6.
- 2. Methane emissions are very sensitive to changes in precipitation. At the Ogeechee site, our models predict that a 20% rainfall decreases will cut average methane emissions by roughly one third. Similar responses may be likely for other wetlands.
- 3. Although the direct effect of temperature increases is stimulation of methane emissions, indirect hydrologic effects of temperature shifts are often dominant. Realistic modeling of hydrologic factors, especially evapotranspiration, is critical to realistic projection of effects of global warming on wetland methane emissions.

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Appendix: Structure of water balance model of Ogeechee drainage basin

A. Calculation of runoff

Monthly runoff is predicted from the water balance equation,

$$R = P - ET - \Delta S + I$$

where:

R = monthly runoff

P = monthly precipitation

ET = monthly evapotranspiration

 ΔS = monthly change in soil water storage

I = direct interception of rainfall to generate runoff

Throughout this model hydrologic variables are expressed in mm. Values for P are specified by the precipitation regime being used to force the model. ET and I are calculated from P, T (monthly temperature), and/or seasonal variables as discussed below and in the main text. S (soil moisture) is explicitly modeled with an upper value of O (field capacity). No lower bound for S is specified. The method for calculating R and ΔS from P, ET, and I is described by the following PASCAL algorithm:

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\begin{split} S := S + P - ET - I; & \{ \text{add net water gain or loss for month to } S \} \\ IF S > 0 \text{ THEN} \\ BEGIN \\ R := S + I; & \{ \text{set } R \text{ equal to excess } S \text{ plus } I \} \\ S := O; & \{ \text{reset } S \text{ at field capacity} \} \\ END \\ ELSE R := I; & \{ \text{set } R \text{ equal to interception only} \} \end{split}
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B. Generation of monthly river discharge.

Runoff generated in a given month was divided among discharge totals (D) for that and future months to simulate the observed gradual rise and fall of the river in response to precipitation events. Examination of daily and monthly discharge records for the Ogeechee at Eden resulted in the following method of allocation of runoff to discharge:

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30% of runoff discharged in month 1 30% of runoff discharged in month 2 16% of runoff discharged in month 3 (0.6)^{(i-3)} \cdot 16\% of runoff discharged in month i (i \ge 3)
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C. Calculation of direct interception, I

Discharge patterns of the Ogeechee at low flow indicate that on average 3% of monthly P directly becomes runoff regardless of the soil moisture status of the basin. Thus, in the runoff model direct interception, I, is set as $0.03 \cdot P$ at all seasons. The actual mechanisms generating this runoff are not addressed here. Without this term, the model predicts excessively low discharges in summer when soil moisture is generally below field capacity.

D. Calculation of ET

As discussed in the main text, two formulations are used for predicting ET. Values of parameters within both models were optimized to provide the best fit (least r² criterion) to observed river discharge for 1980—1989, then rounded to one or two significant figures in order to avoid a false impression of precision in these values.

References

Bartlett KB, Crill PM, Sebacher DI, Harriss RC, Wilson JO & Melack JM (1988) Methane flux from the central Amazonian floodplain. J. Geophys. Res. 93: 1571—1582

Benke AC & Meyer JL (1988) Structure and function of a blackwater river in the southeastern U.S.A. Verh. Intenat. Verein. Limnol. 23: 1290-1298

- Cicerone RL & Oremland RS (1988) Biogeochemical aspects of atmospheric methane. Global Biogeochem. Cycles 2: 299—327
- Cuffney TF (1984) Characteristics of riparian flooding and its impact upon the processing of organic matter in coastal plain streams of Georgia. Ph.D. dissertation, University of Georgia, Athens, Georgia
- Cuffney TF (1988) Input, movement, and exchange of organic matter within a subtropical coastal blackwater river-floodplain system. Freshwater Biol. 19: 305—320
- DeLaune RD, Smith CJ & Patrick WH, Jr. (1983) Methane release from gulf coast wetlands. Tellus 35B: 8-13.
- Edwards RT & Meyer JL (1987) Metabolism of a subtropical low gradient blackwater river. Freshwat. Biol. 17: 251–264
- Ehhalt DH & Schmidt U (1978) Sources and sinks of atmospheric methane. Pure Appl. Geophys. 116: 452-464
- Gleick PH (1986) Methods for evaluating the regional hydrologic impacts of global climatic changes. J. Hydrology 88: 97—116
- Gleick \overrightarrow{PH} (1987) Regional hydrologic consequences of increases in atmospheric CO₂ and other trace gases. Clim. Change 10: 137–161
- Hameed S & Cess RD (1983) Impact of global warming on biospheric sources of methane and its climatic consequences. Tellus 35B: 1—7
- Hansen J, Lacis A, Rind D, Russell G, Stone P, Fung I, Ruedy R & Lerner J (1984) Climate sensitivity: Analysis of feedback mechanisms. In: Hansen JE & Takahashi T (Eds) Climate Processes and Climate Sensitivity, Geophysical Monograph Series, vol. 29 (pp 130—163). American Geophysical Union, Washington, DC
- Hansen J, Fung I, Lacis A, Rind D, Lebedeff S, Ruedy R & Russell G (1988) Global Climate changes as forecast by Goddard Institute for Space Studies three-dimensional model. J. Geophys. Res. 93D: 9341—9364
- Harriss RC & Frolking SE (1992) The sensitivity of methane emissions from northern wetlands to global warming. In: Firth P & Fisher SG (Eds) Global climate change and freshwater ecosystems (pp 48-67). Springer-Verlag, New York
- Harriss RC, Gorham E, Sebacher DI, Bartlett KB & Flebbe PA (1985) Methane flux from northern peatlands. Nature 315: 652-654
- Harriss RC, Sebacher DI & Day FP (1982) Methane flux in the Great Dismal Swamp. Nature 297: 673-674
- Idso SB & Brazel AJ (1984) Rising atmospheric carbon dioxide may increase streamflow. Nature 312: 51-53
- Karl TR & Riebsame WE (1989) The impact of decadal fluctuations in mean precipitation and temperature on runoff: A sensitivity study over the United States. Clim. Change 15: 423-447
- Lashof DA (1989) The dynamic greenhouse: Feedback processes that may influence future concentrations of atmospheric trace gases and climatic change. Clim. Change 14: 213—242
- Lieth H (1975) Primary production of the major vegetation units of the world. In: Lieth H & Whittaker RH (Eds) Primary Productivity of the Biosphere, Ecological Studies 14 (pp 203-215). springer-Verlag, New York
- Martin P, Rosenberg NJ & McKenney MS (1989) Sensitivity of evapotranspiration in a wheat field, a forest, and a grassland to changes in climate and direct effects of carbon dioxide. Clim. Change 14: 117—151
- Matthews E & Fung I (1987) Methane emissions from natural wetlands: Global distribution, area, and environmental characteristics of sources. Global Biogeochem. Cycles 1: 61–86
- Meehl GA & Washington WM (1990) CO₂ climate sensitivity and snow-sea-ice albedo

- parameterization in an atmospheric GCM coupled to a mixed-layer ocean model. Clim. Change 16: 283-306
- Meyer JL (1990) A blackwater perspective on riverine ecosystems. Bioscience 40: 643-651
- Mitchell JFB, Senior CA & Ingram WJ (1989) CO₂ and climate: A missing feedback? Nature 341: 132-134
- Mitsch WM & Gosselink JG (1986) Wetlands. Van Nostrand Reinhold, New York
- National Oceanic and Atmospheric Administration (1970–1989) Climatological data, Georgia, Volumes 74–93. U.S. Department of Commerce, Washington, DC
- Pulliam WM (1991) Carbon dioxide and methane exports from a southeastern floodplain swamp: patterns, pathways, and sensitivity to climate. Ph.D. dissertation, University of Georgia, Athens, Georgia
- Revelle RR & Waggoner PE (1983) Effects of a carbon dioxide-induced climatic change on water supplies in the western United States. In: Changing Climate: Report of the Carbon Dioxide Assessment Committee (pp 419—432). National Academy Press, Washington, DC
- Rodin LE, Bazilevich NI & Rozov NN (1975) Productivity of the world's main ecosystems. In: Lieth H & Whittaker RH (Eds) Primary Productivity of the Biosphere, Ecological Studies 14 (pp 13—26). Springer-Verlag, New York
- Schlesinger ME & Mitchell JFB (1987) Climate model simulations of the equilibrium climatic response to increased carbon dioxide. Rev. Geophys. 25: 760—798
- Seiler W (1984) Contribution of biological processes to the global budget of CH₄ in the atmosphere. In: Klug M & Reddy C (Eds) Current Perspectives in Microbial Ecology (pp 468–447). American Society of Microbiologists, Washington, DC
- Thornthwaite CW & Mather JR (1957) Instructions and tables for computing potential evapotranspiration and the water balance. Drexel Inst. Technol. Lab. Climatol. Publ. Climatol. 10: 183–311
- U.S. Geological Survey (1951–1960) Surface water supply of the United States Part 2-B: South Atlantic slope and eastern Gulf of Mexico basins, Ogeechee River to Pearl River. Geological Survey Water-Supply Papers 1204, 1234, 1274, 1284, 1334, 1434, 1504, 1554, 1624, 1704. U.S. Department of the Interior, Washington, DC
- U.S. Geological Survey (1954) Compilation of records of surface waters of the United States through September 1950. Part 2-B: South Atlantic slope and eastern Gulf of Mexico basins, Ogeechee River to Pearl River. Geological Survey Water-Supply Paper 1304. U.S. Department of the Interior, Washington, DC
- U.S. Geological Survey (1966) Surface water supply of the United States, 1961—1965. Part
 2: South Atlantic slope and eastern Gulf of Mexico basins; Vol. 2: Basins from Ogeechee
 River to Carrabelle River. Geological Survey Water-Supply Paper 1905. U.S. Department of the Interior, Washington, DC
- U.S. Geological Survey (1965–1989) Water resources data for Georgia. U.S.G.S. Water-data Reports GA-65-1 to GA-89-1. U.S. Department of the Interior, Washington, DC
- Wallace JB, Benke AC, Lingle AH & Parsons L (1987) Trophic pathways of macro-invertebrate primary consumers in subtropical blackwater streams. Arch. für Hydrobiologie (Supplementband) 74: 423–451
- Washington WM & Meehl GA (1984) Seasonal cycle experiment on the climate sensitivity due to a doubling of CO₂ with an atmospheric general circulation model coupled to a simple mixed-layer ocean model. J. Geophys. Res. 89: 9475—9503
- Weather Bureau (1937–1969) Climatological data, Georgia, Volumes 41–73. U.S. Department of Commerce, Washington, DC
- Wetherald RT & Manabe S (1986) An investigation of cloud cover change in response to thermal forcing, Clim. Change 8: 5–23

- Wharton CH, Kitchens WM, Pendleton EC & Sipe TW (1982) The ecology of bottomland hardwood swamps of the southeast: A community profile. U.S. Fish and Wildlife Service, Biological Services Program, FWS/OBS-81/37.
- Whittaker RH & Likens GE (1975) The biosphere and man. In: Lieth H & Whittaker RH (Eds) Primary Productivity of the Biosphere, Ecological Studies 14 (pp 305-328). Springer-Verlag, New York
- Wieder RK, Yavitt JB & Lang GE (1990) Methane production and sulfate reduction in two Appalachian peatlands. Biogeochem. 10:81–104.
- Wigley TML & Jones PD (1985) Influences of precipitation changes and direct CO₂ effects on streamflow. Nature 314: 149—152
- Wilson JO, Crill PM, Bartlett KB, Sebacher DI, Harriss RC & Sass RL (1989) Seasonal variation of methane emissions from a temperate swamp. Biogeochem. 8: 55–71