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G. M. King
University of Maine

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Land use impacts on atmospheric carbon monoxide consumption by soils

Gary M. King

Darling Marine Center, University of Maine, Walpole

Abstract. Seasonal analyses of in situ CO fluxes from forested and agricultural soils in Maine and Georgia, and more limited comparisons in Hawai'i indicated that agricultural land use consistently enhanced CO consumption. Soils at an agricultural site in Maine consumed approximately 1.9 g CO m^{-2} yr^{-1}while uptake in a nearby mixed forest was about 70% lower, 0.6 g CO m^{-2} yr^{-1}. A similar trend was observed for sites in Georgia, where annual uptake by agricultural sites was approximately 1.0 g CO m^{-2} while net emission (about –0.5 g CO m^{-2}) was observed for neighboring pine stands. Net CO fluxes in Maine and Georgia were generally aseasonal. Accordingly, seasonal changes in temperature and water content played variable but often minimal roles as determinants of net fluxes and gross CO uptake and production. However, comparisons among sites suggested that soil organic matter contents were an important control of the magnitude of CO fluxes. In particular net CO consumption for a given soil type increased with decreasing organic matter content associated with forest to agriculture transitions in land use. Although interactions among soil organic matter and various microbiological, physical and chemical parameters in soils are complex, changes in organic matter at the sites described here appear to affect net CO fluxes primarily by reducing the relative rate of abiological CO production

1. Introduction

The CO budget commands considerable interest [e.g., *Bekki et al.*, 1994; *Khalil and Rasmussen*, 1994; *Novelli et al.*, 1994; *Bergamaschi et al.*, 2000a, b] for several reasons. Reactions involving CO dominate tropospheric chemistry [*Logan et al.*, 1981; *Crutzen and Gidel*, 1983]. Recent analyses also indicate that current and projected CO concentrations could result in indirect radiative forcing from CO comparable to direct radiative forcing by N_2O [*Daniel and Solomon*, 1998]. Moreover, CO dynamics may play a significant role in strategies to mitigate greenhouse warming since CO affects the fate of methane.

The global annual tropospheric CO flux [~2800 Tg yr^{-1}] includes numerous natural and anthropogenic sources but only two sinks: tropospheric oxidation and consumption by soils [*Seiler and Conrad*, 1987; *Khalil and Rasmussen*, 1990; *Taylor et al.* 1996]. The tropospheric sink is reasonably well known, but net CO consumption by soils is poorly characterized, with estimates ranging from 15 to 650 Tg yr^{-1} [*Bartholemew and Alexander*, 1981; *Conrad*, 1988; *Badr and Probert*, 1995; *Potter et al.*, 1996]. The substantial uncertainty in this estimate arises from the limited number of studies assessing controls of activity and from the relatively small number of field sites for which consumption has been assayed in situ [*King*, 1999].

In addition, impacts of land use on net CO consumption are poorly known. Comparisons among tropical savanna soils indicate that agricultural land use significantly enhances CO consumption [*Scharffe et al.*, 1990; *Sanhueza et al.*, 1994a, b]. However, data from temperate soils suggest minimal effects from agriculture or even decreased CO consumption [*Moxley and Smith*, 1998a, b]. Resolution of the response of CO fluxes to land use is essential since changes in the CO budget due to changes in land use could either ameliorate or exacerbate the well-known, greenhouse-reinforcing impacts of agriculture on methane and nitrogen oxides [*Prather et al.*, 1995; *Steudler et al.*, 1996; *King*, 1997].

I report here results from seasonal in situ CO flux assays in agricultural and forested soils in Maine and Georgia and from a more limited comparison of such sites in Hawai'i. CO fluxes from tilled soils consistently exceed those from forested soils. Differences in flux rates between land uses at each site correlate with organic concentrations. In general, higher organic concentrations in forested soils support greater CO production, which reduces net atmospheric CO consumption. Seasonal variations in temperature and water content within forested sites correlate weakly with net CO fluxes, although elevated temperatures tend to increase CO production. Temperature and water content explain a greater level of seasonal variation in tilled site CO fluxes. Net deposition velocities for all sites are lower than values reported for European soils but compare favorably with data from boreal forests [*Zepp et al.*, 1997] and Japanese soils [*Yonemura et al.*, 2000], suggesting that estimates of global net atmospheric CO consumption by soils should be revised downward from previously published ranges [e.g., *Sanhueza et al.*, 1998].

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2. Materials and Methods

Two field sites were established in a forest at the Darling Marine Center (DMC) [*Adamsen and King*, 1993; *King and*

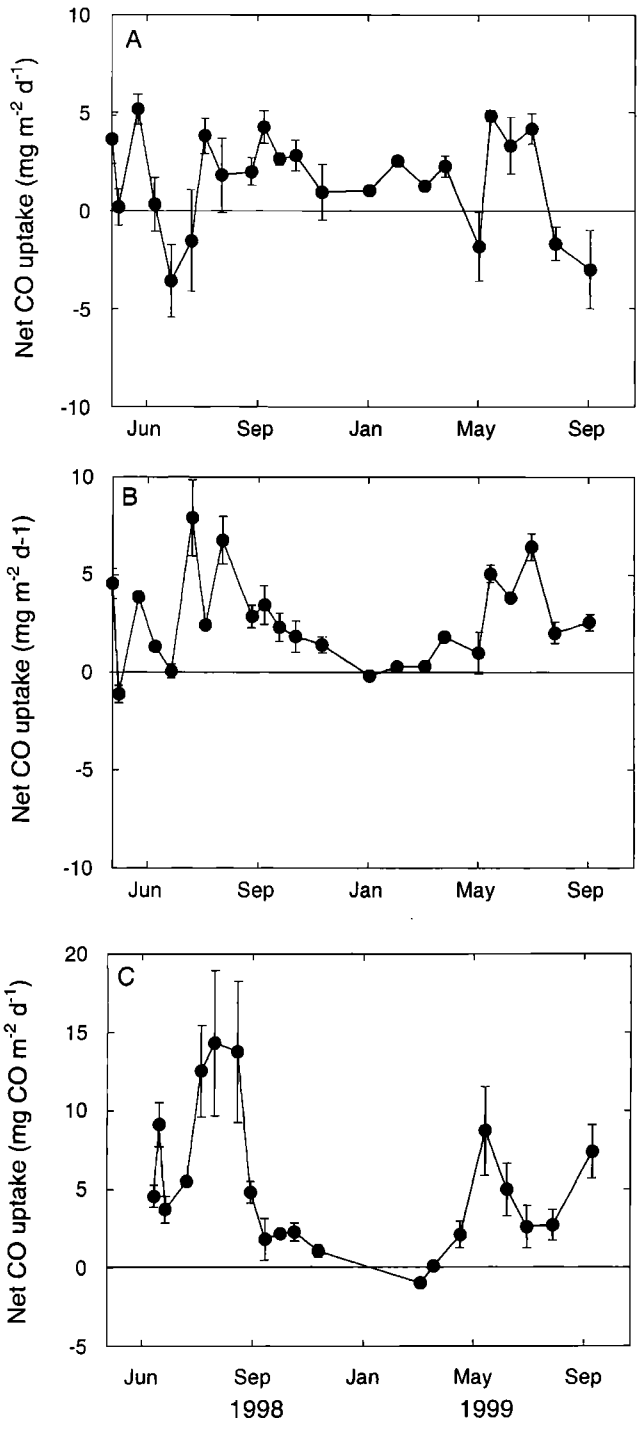

Figure 1. Net CO uptake rates for (a) mixed forest soils, (b) planted pine stand soils, and (c) agricultural soils in Maine. All values are means of triplicates ± 1 standard error. Values < 0 indicate net CO emission.

Adamsen, 1992; *King and Schnell*, 1994] and at Sproul Farm, Walpole, Maine. The first forest site was in a relatively undisturbed mixed hardwood-coniferous stand containing oak, maple, and fir with a sparse understory. Litter layer thickness at this site was variable, typically extending for ~5 cm; the soils have been classified as typic haplorthods. The second forest site was in a planted pine stand ~40 years old. Vegetation existing at the time of planting was cleared and the original litter layer removed. The litter layer at present consists only of pine needles with a thickness of ~2 cm. The agricultural site has been cultivated continuously for > 25 years. It was tilled, planted in corn prior to initiation of flux assays (May 1998) and harvested in September 1998; a similar cycle was repeated in the spring and summer of 1999. Soils at this site have been classified as typic fragiorthods.

Additional sites were established at the University of Georgia Agricultural Research Station, Griffin, Georgia, in a field managed for crop production for > 25 years. At the time of the assays (1997-1999) the field was used in a sorghum and wheat rotation. An adjacent unmanaged pine stand was used for comparison. Soils at both sites have been classified as red-yellow podzols of the Lloyd series. Sites were also established at the University of Georgia Agricultural Research Station, Tifton, Georgia, in a field used in a rotation of cotton, peanuts, winter wheat, and soybeans and in an unmanaged pine stand (> 50 years old). Soils at both of these sites have been classified as plinthic paleudults. Sites in Hawai'i were established on cultivated fields west of Hilo, Hawai'i at an elevation of ~500 m. The specific history of these fields is unknown, but the area had been used extensively for sugar cane production for about 50 years. At the time of observation, one field had been tilled and recently planted with cucumber following a ginger crop; the second field had been planted for Macedemia nut production and consisted of mature trees (10-20 years old) and a sparse, mowed grass understory. Separate forested stands dominated by *Acacia koa* or *Eucalyptus signa* near the cultivated fields were used for comparison. Temperatures and precipitation regimes at these sites are largely aseasonal [*Chadwick et al.*, 1999]. Soils at all of the Hawaiian sites have been classified as acurdoxic hydrudands.

CO fluxes at all sites were measured using triplicate collars constructed from sharpened stainless steel tubes [9.2 cm inner diameter x 10 cm] with welded aluminum flanges. At all sites other than DMC, collars were deployed 6-24 hours prior to use after which a 1 L quartz chamber fitted with septum ports for syringe sampling was inverted and secured to a collar with a nylon washer that allowed the chamber to be sealed on a silicone O-ring. The chamber was covered with aluminum foil to minimize temperature variations during incubation. For DMC sites, collars were deployed permanently throughout the study. Initial analyses indicated that exposure of cultivated or forest soils to ambient light had little or no discernible effect on CO depth profiles or on rates of forest soil CO flux [*King*, 1999]. Thus dark incubations, typically in early afternoon to mid-afternoon, were used for routine assays. For sites in Georgia, assays were also conducted at intervals through a morning-night transition during July 1998.

CO fluxes were estimated from headspace CO concentrations determined using 3 cm^3 headspace samples obtained by needle and syringe from a sealed chamber at 3-4 min intervals over a period of 15-20 min. Headspace samples were assayed immediately in the field using a model RGA3 [Trace Analytical, Inc.] gas chromatograph equipped with a mercury vapor detector and operated according to the manufacturer's recommendations [*Rich and King*, 1998, 1999; *King*, 1999]. Detector response was standardized with zero grade air (Scott Specialty Gases, Inc.)

Table 1. Summary of Results from Mixed Forest, Planted Pine, and Agricultural Sites in Maine

Parameter	Mixed Forest	Planted Pine	Agriculture
Net CO flux rate	1.5 ± 0.5	2.7 ± 0.5	5.3 ± 1.0
Gross CO production rate	3.0 ± 0.7	1.5 ± 0.2	2.0 ± 0.3
Net deposition velocity, cm s^{-1}	0.006 ± 0.001	0.014 ± 0.002	0.021 ± 0.003
Gross uptake rate constant, $hour^{-1}$	5.1 ± 0.7	5.4 ± 0.6	7.5 ± 0.8
Compensation, ng CO cm^{-3}	2.7 ± 0.5	1.4 ± 0.2	1.5 ± 0.2
Ambient temperature, °C	15.6 ± 1.7	15.7 ± 1.7	20.8 ± 2.0
Water content, 0-2 cm, %	181.0 ± 19.8	100.2 ± 9.8	30.2 ± 2.9
Ambient CO, ppb	208 ± 16	192 ± 11	259 ± 212
Organic content, %	45.5	15.2	4.4
pH	3.9	4.5	7.1

All values are means ± 1 standard error (n = 21, forest and planted pine; n = 19 agricultural site) for the measurement period (May, 1998 – September, 1999) with the exception of single time point assays for organic content and pH. All rates are in mg CO $m^{-2} d^{-1}$.

containing 289.8 ppb CO as determined by comparison with a certified standard (National Oceanic and Atmospheric Administration-Climate Monitoring and Diagnostics Laboratory] containing 91.9 ppb CO in air. Net flux and deposition rates were estimated according to *Conrad and Seiler* [1980] using the following equation to describe CO concentration in a chamber headspace as a function of time:

$$CO(t) = CO_{comp} + (CO_{init} - CO_{comp})e^{-kt},$$

where CO_{init} is the initial or ambient CO concentration in a chamber, CO_{comp} is the final compensation CO concentration representing the balance between first-order CO uptake and a

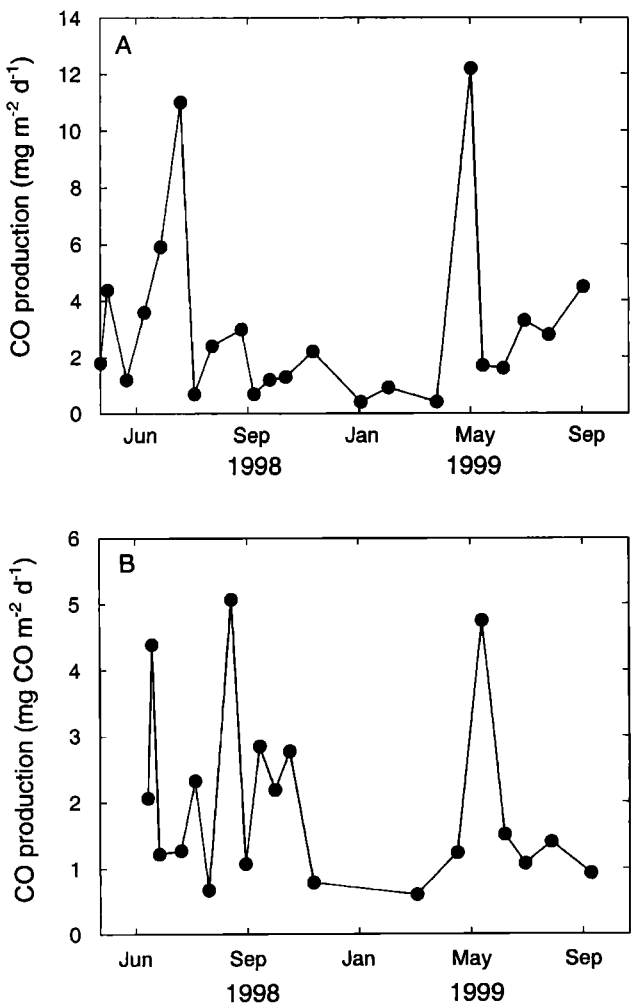

Figure 2. Gross CO production rates for (a) mixed forest and (b) agricultural soils in Maine. All values are means of triplicates ± 1 standard error.

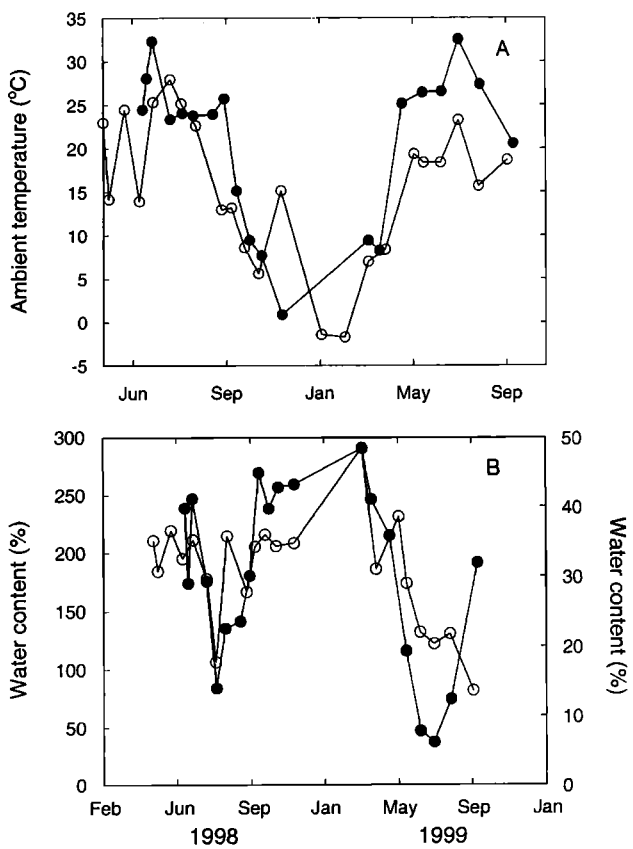

Figure 3. (top) Ambient temperatures for mixed forest (open circles) and agricultural soils (solid circles) in Maine. (bottom) Surface water contents (0-2 cm interval) for mixed forest (open circles) and agricultural soils (solid circles).

zero-order CO production term, and k is the gross uptake rate constant. Note that the product of k CO_{thresh} provides an estimate of the gross CO production rate. Rate constants and threshold CO concentrations were estimated using the nonlinear curve-fitting algorithm of Kaleidagraph software [see also *King*, 1999]. For this manuscript, net CO uptake is taken as a positive value and emission as negative.

Soil water contents were determined routinely at all sites using cores obtained with sharpened aluminum tubes (6.5 cm inner diameter). After removing the litter layer, cores were sectioned at 0-2, 2-5, and 5-10 cm intervals. Subsamples from these intervals were dried at 105°C to facilitate gravimetric water content assays. Ambient and soil temperatures (at 0, 1, 5, and 10 cm) were determined using thermistors with a digital output (Fisher Scientific, Inc.). Organic contents were measured for select samples using the modified Walkley-Black perchlorate digestion procedure [*Forster*, 1995]; pH was assayed for selected samples using a 1:1 dilution [by weight] of fresh soil with deionized water and a Beckman model 71 pH meter.

3. Results

3.1. Maine Forest and Agricultural Sites

Net CO fluxes in the mixed forest site varied from a maximum of 5.2 ± 0.8 mg CO m^{-2} d^{-1} to a minimum of −3.6 ± 1.9 mg CO m^{-2} d^{-1} but with no consistent seasonal trend (Figure 1a). Net fluxes for an adjacent planted pine stand varied from 6.8 ±1.2 mg CO m^{-2} d^{-1} to −1.1 ± 0.4 mg CO m^{-2} d^{-1}, with maxima during summer and minima during winter and spring (Figure 1b). At a nearby agricultural site, net CO fluxes were generally higher than at the forested sites (analysis of variance, ANOVA, $F = 7.24$; $p < .001$), ranging from 12.5 ± 2.9 mg CO m^{-2} d^{-1} to −1.0 ± 0.1 mg CO m^{-2} d^{-1} with a more pronounced seasonal trend (Figure 1c). Annual CO fluxes were 0.6, 1.0 and 1.9 g CO m^{-2} for the mixed forest, planted pine stand and agricultural site, respectively.

Trends in net deposition velocities and gross uptake rate constants were similar to those of net CO fluxes, with the highest values occurring at the agricultural site (Table 1). Seasonal trends in these parameters were also comparable to those of net CO fluxes at each site (data not shown). In contrast, compensation CO levels and gross CO production rates were greatest in the mixed forest site (ANOVA for compensation CO, $F = 4.26$; $p = .019$; ANOVA for CO production, $F = 3.26$; $p = .045$). Further, mixed forest gross CO production rates exhibited an early summer maximum, while rates were more variable on a seasonal basis at the other sites (Figure 2).

Physical parameters also differed among the sites. Soil organic matter and water contents were lowest in the agricultural soil and highest in the mixed forest soils, while pH showed the reverse trend (Table 1). Soil water contents at all sites were

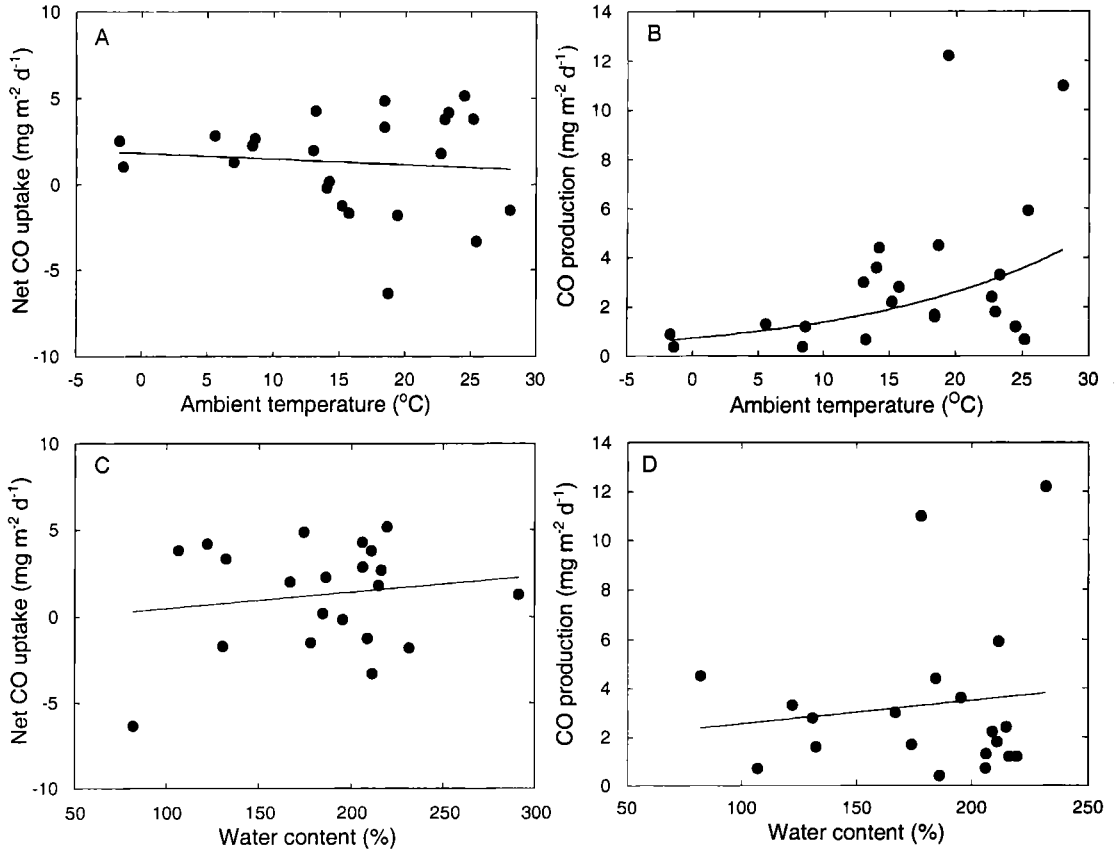

Figure 4. (a) Mixed forest net CO uptake rates (see Figure 1a) versus ambient temperature. (b) Mixed forest gross CO production rates (see Figure 2a) versus ambient temperature. (c) Mixed forest net CO uptake rates versus surface water content. (d) Mixed forest gross CO production rates versus water content. Lines indicate fits from regression analysis (see text for details).

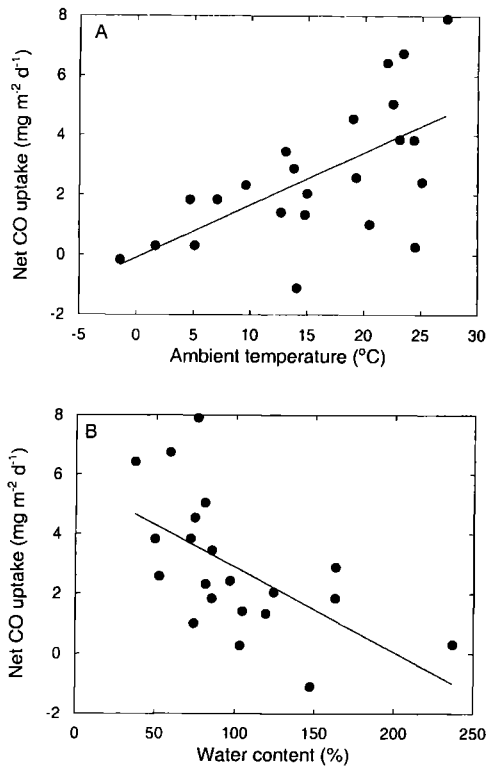

Figure 5. (a) Planted pine stand net CO uptake rates (see Figure 2b) versus ambient temperature. (b) Planted pine stand net CO uptake rates versus surface water content. Lines indicate fits from regression analysis (see text for details).

lowest in summer, but water content was more variable seasonally and as a function of temperature at the mixed forest site than at other sites (e.g., Figure 3). Ambient temperatures throughout the year were essentially equal at the mixed forest and pine sites but were somewhat warmer at the agricultural site, especially during summer ($T_{[2,\ 0.05,\ 19]} = 2.816$; $p = .011$). At all sites, ambient temperatures were highly correlated ($r > 0.9$) with temperatures at the soil surface and at depth (1 and 10 cm; data not shown). Likewise, surface water contents (0-2 cm) were highly correlated with water contents in deeper soils (2-5 and 5-10 cm; data not shown). Ambient CO concentrations did not vary consistently on a seasonal basis at any of the sites; values were somewhat elevated at the agricultural site, but the differences were not statistically significant ($p > 0.1$).

Net CO flux rates at the forest site did not vary significantly as a function of either ambient temperature or surface water content (Figures 4a and 4c; $r^2 < 0.05$; $p > 0.1$). Results were similar for net deposition velocities and gross uptake rate constants (data not shown). Gross CO production rates increased significantly with temperature, although the relationship was weak (Figure 4c; $r^2 = 0.21$; $p = 0.037$), but did not vary significantly as a function of soil water content (Figure 4d; $r^2 < 0.05$; $p > 0.1$). Net CO fluxes at the planted pine site increased and decreased significantly as a function of ambient temperature and water content, respectively (Figures 5a and 5b; $r^2 = 0.38$; $p = 0.002$ for temperature; $r^2 = 0.34$; $p = 0.005$ for water content), with net deposition velocities and gross uptake rate constants exhibiting similar patterns (data not shown). In contrast, gross CO production rates did not vary significantly as a function of either ambient temperature or water content ($r^2 \leq 0.1$; $p > 0.1$; data not shown).

A somewhat different pattern emerged for net CO fluxes and net deposition velocities at the agricultural site. Both increased linearly though weakly with temperature ($r^2 = 0.21$; $p = 0.041$) while varying parabolically ($r^2 = 0.61$) with water content (Figures 6a and 6b; data for net CO fluxes only). Gross uptake rate constants varied parabolically with temperature and water content (Figures 6c and 6d; $r^2 = 0.52$, 0.28 respectively), but gross CO production rates were correlated with neither parameter ($r^2 < 0.1$; $p > 0.1$; data not shown).

3.2. Georgia Forest and Agricultural Sites

Although the two agricultural soils in Georgia differed substantially in their physical characteristics (sandy loam versus clay), net CO fluxes were similar with mean rates of 2.5 ± 0.3 and 2.8 ± 0.3 mg CO m^{-2} d^{-1} (1.0 and 0.9 g CO m^{-2} yr^{-1}) for the Tifton and Griffin sites, respectively. A variety of other parameters were also similar, including net deposition velocities, gross uptake rate constants, compensation CO levels, and gross CO production rates (Table 2). Ambient temperatures and soil pH were somewhat higher and water contents and organic matter concentrations were somewhat lower for the Tifton than Griffin site (Table 2).

Pine stand net CO fluxes at both Griffin and Tifton (-0.5 ± 1.5 and –2.3 ± 2.1 mg CO m^{-2} d^{-1} and –0.2 and –0.8 g CO m^{-2} yr^{-1}, respectively) were significantly lower than for the agricultural sites (ANOVA, $F = 4.18$; $p = 0.016$), with net emission observed on average over the course of the study (Table 2). Net CO fluxes and net deposition velocities were least at Tifton but highly variable and not significantly different ($p > 0.1$ in comparisons of both variables) than values for Griffin. Similarly, gross uptake rate constants and compensation CO levels were somewhat higher but not statistically different ($p > 0.1$) for Tifton (Table 2). Soil organic matter concentrations and pH were also comparable for the two pine stands (Table 2). However, gross CO production rates were significantly higher for both pine stands than for the agricultural sites, with the greatest production occurring at Tifton (Table 2; ANOVA, $F = 11.96$; $p < 0.001$).

Net CO fluxes and gross CO production rates for the Griffin and Tifton sites were essentially aseasonal (Figure 7) and did not vary over a diurnal period during July (not shown). In addition, net CO fluxes were comparable for untilled soils and soils 2 and 24 hours after conventional tilling in November 1998 (not shown). Similar results were obtained for other Griffin and Tifton parameters (e.g., gross uptake rate constants and deposition velocities and compensation CO levels; data not shown). At the Griffin agricultural site, net CO fluxes increased with increasing temperature ($r^2 = 0.53$; $p = 0.042$), albeit with a small slope, while flux rates for the pine stand appeared to increase strongly over a small increment of temperature (e.g., 13°-20°C), with little increase at temperatures > 20°C (Figure 8a). In contrast, gross CO production at the agricultural site did not vary as a function of temperature ($p > 0.1$) and decreased with increasing temperature at the pine stand (Figure 8c). Weak inverse relationships between net flux and water content were observed for both the agricultural and pine sites in Tifton (Figure 8b), while either no response or a weak positive response was observed for gross CO production as a function of increasing water content (Figure 8d).

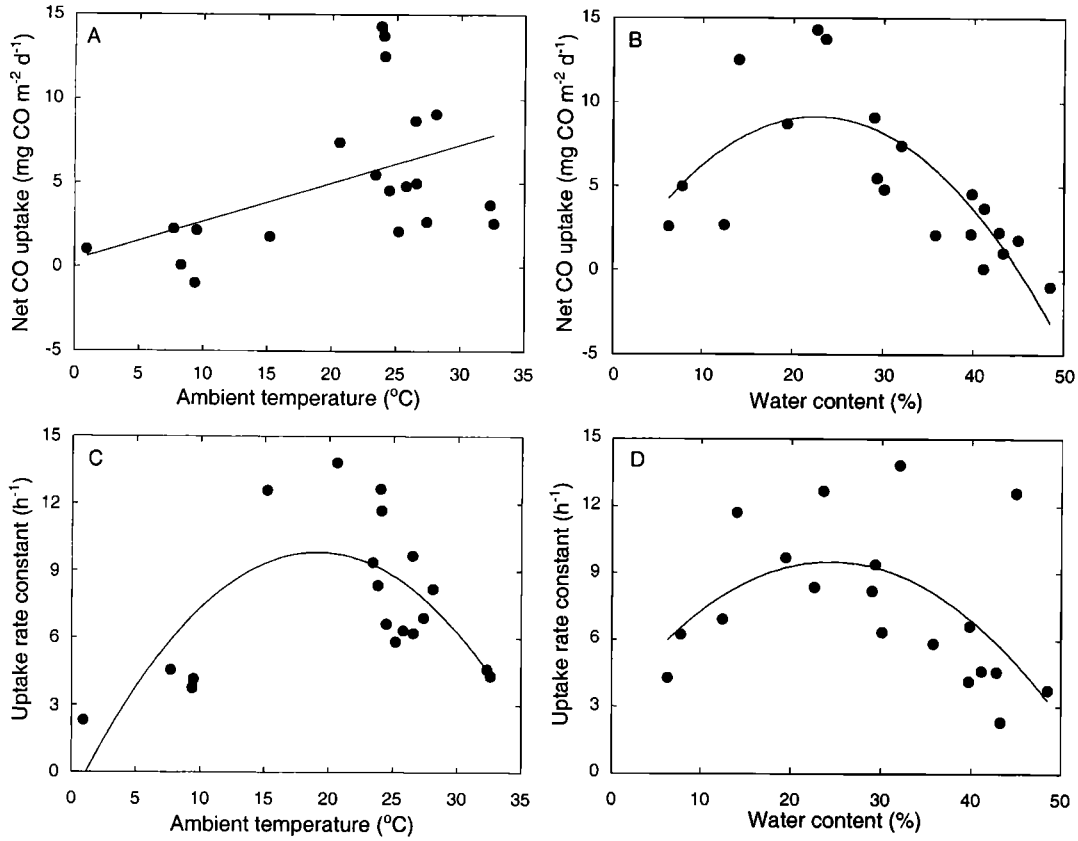

Figure 6. (a) Agricultural site net CO uptake rates (see Figure 1c) versus ambient temperature. (b) Net CO uptake rates versus surface water content. (c) Gross CO uptake rate constants versus ambient temperature. (d) Gross CO uptake rate constants versus water content. Lines indicate fits from regression analysis (see text for details).

At both agricultural and pine stand sites in Tifton, net CO fluxes and gross CO production rates responded inversely and directly, respectively, to increasing temperature (Figures 9a and 9c). In the latter case, the responses were highly significant (r^2 >0.70; $p < 0.01$), with the greatest slope for the pine stand site. No significant response was observed for net CO fluxes as a function of water content ($r^2 < 0.1$; $p > 0.1$), but CO production increased linearly ($r^2 = 0.66$; $p = 0.027$) at the agricultural site and may have varied parabolically at the pine stand (Figures 9b and 9d).

In general, net CO fluxes were higher for agricultural and forest sites in Maine than for comparable sites in Georgia (Tables 1 and 2). Conversely, gross CO production rates were substantially greater for pine stands in Georgia than for forested stands in Maine; CO production was similar among the various agricultural sites. Naturally, sites in Georgia were significantly warmer and drier than sites in Maine. Forest soil pH values were comparable between Georgia and Maine, but the Maine agricultural soil was the least acidic of the three agricultural sites examined (pH 5.2 and 6.2 versus 7.1; Tables 1 and 2). Surface organic matter

Table 2. Summary of Results from Pine Stands and Agricultural Sites in Georgia.

Parameter	Griffin		Tifton	
	Pine	Agriculture	Pine	Agriculture
Net CO flux rate	-0.5 ± 1.5	2.8 ± 0.3	-2.3 ± 2.1	2.5 ± 0.3
Gross CO production rate	5.2 ± 1.1	2.9 ± 0.6	11.2 ± 2.1	2.2 ± 0.5
Net deposition velocity, cm s^{-1}	-0.002 ± 0.005	0.013 ± 0.001	-0.012 ± 0.007	0.012 ± 0.001
Gross uptake rate constant, $hour^{-1}$	5.2 ± 0.7	4.9 ± 0.5	7.5 ± 2.1	5.1 ± 0.6
Compensation, ng CO cm^{-2}	6.9 ± 2.5	2.2± 0.4	9.9 ± 2.4	1.6 ± 0.3
Ambient temperature, °C	24.5 ± 2.3	23.7 ± 2.1	25.8 ± 1.8	28.4 ± 1.8
Water content (0-2 cm), %	44.3 ± 11.8	10.7 ± 1.9	59.4 ± 21.5	7.0 ± 1.2
Ambient CO, ppb	253 ± 23	270 ± 23	288 ± 26	229 ± 20
Organic content, %	24.9	0.7	21.5	0.5
pH	4.6	5.2	4.4	6.2

All values are means ± 1 standard error (n = 8, Griffin; n = 7, Tifton).

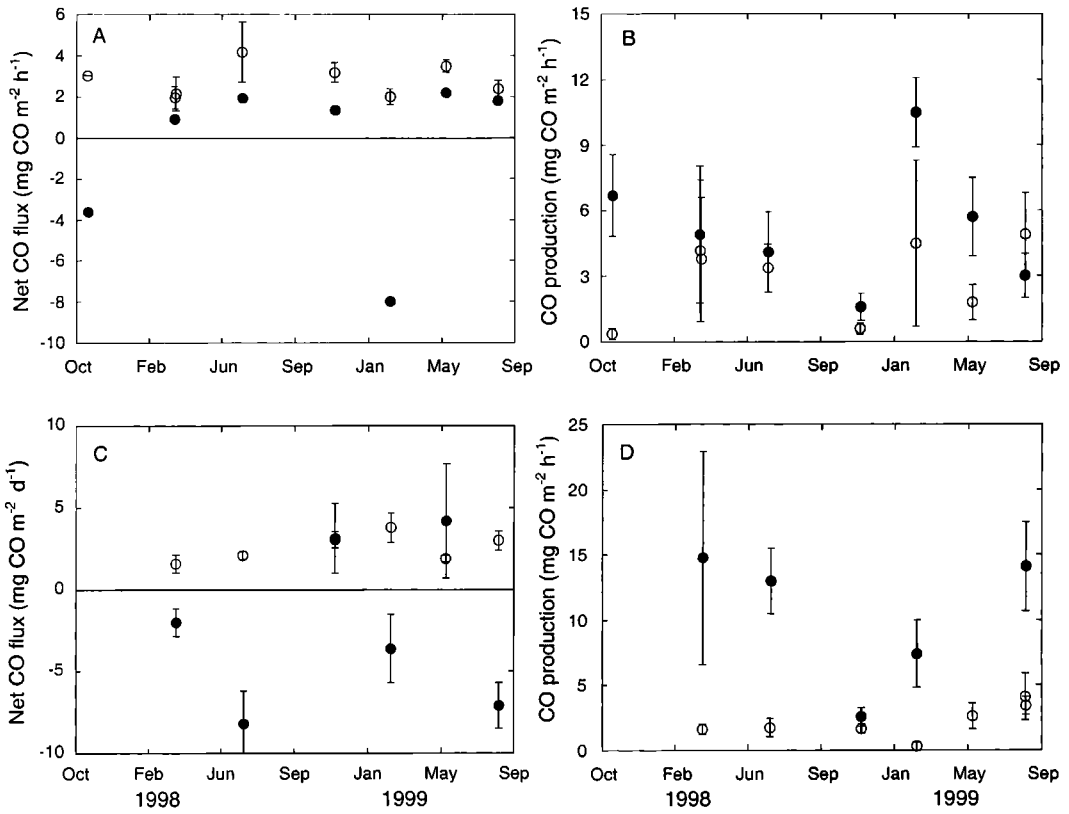

Figure 7. (a) Net CO fluxes for Griffin, Georgia agricultural (open circles) and pine stand sites (solid circles). (b) Gross CO production rates for Griffin, Georgia agricultural (open circles) and pine stand sites (solid circles). (c) Net CO fluxes for Tifton, Georgia agricultural (open circles) and pine stand sites (solid circles). (d) Gross CO production rates for Tifton, Georgia agricultural (open circles) and pine stand sites (solid circles). Flux values < 0 indicate net CO emission. All values are means of triplicates ± 1 standard error.

concentrations were least in the Georgia agricultural soils (0.5-0.7%) and increased from the Maine agricultural soil (4.4%) to the pine stands (15.2, 21.5 (Georgia) and 24.9% (Maine)) to the mixed hardwood-coniferous site in Maine (45.5%).

3.3. Hawaiian Forest and Agricultural Sites

The conventionally cultivated Hawaiian soils (tilled field and Macademia nut grove) neither consumed nor produced CO during in situ assays in December 1998 (Figure 10). In contrast, similar soils in *A. koa* and *E. saligna* forests produced CO at net rates of 1.9 ± 0.6 and 0.7 ± 0.3 mg CO m^{-2} d^{-1}, respectively (Figure 10). Owing to the low level of activity, gross uptake rate constants could not be estimated for the agricultural soils, but the calculated values for *A. koa* and *E. saligna* forests were 3.0 ± 0.1 and 2.1 ± 0.5 $hour^{-1}$, respectively, or about one-half the values for Maine and Georgia soils.

During April 1999 CO fluxes for the tilled and *E. saligna* sites sampled previously were compared using intact cores and an in vitro assay. Water contents for both sites were notably lower than values measured during December 1998 (46.1 versus 88.2% and 52.5 versus 240.7% for *E. saligna* and tilled sites, respectively). However, CO was emitted from *E. saligna* cores but consumed by the tilled soil cores at rates of -2.1 ± 0.4 and 1.5 ± 0.8 mg CO m^{-2} d^{-1}, respectively.

4. Discussion

The absence of distinct seasonal trends in CO fluxes at the Maine mixed forest site and Georgia forest and agricultural sites (Figures 1 and 7), and responses to temperature and soil water content (Figures 4-6 and 8) are consistent with results from several previous studies [*Conrad and Seiler*, 1980; *Moxley and Smith*, 1998a, b; *Sanhueza et al.*, 1998; *Yonemura et al.*, 2000]. Aseasonality at these sites can be attributed to several factors. Both CO consumption and production respond positively to increasing temperature [*Moxley and Smith*, 1998a, b; *King*, 1999], and in some cases comparable responses for each can minimize changes in net flux. Limited temperature sensitivity, especially for CO consumption, may also reflect diffusion limitation for CO transport from the atmosphere to sites of oxidation in the soil matrix [*Yonemura et al.*, 2000; see also *King and Adamsen*, 1992]. In addition, gas transport and responses to temperature vary with soil water content, the latter of which did not correlate consistently with temperature at the various sites in this study (r = 0.51 and –0.81 for Tifton and Griffin agricultural sites, respectively; r = -0.66 and -0.67 for Maine planted pine and agricultural sites, respectively; $-0.1 \leq r \leq 0.1$ for Maine and Georgia forest sites).

In contrast to all other sites, pronounced and consistent seasonal changes in net CO flux have been observed at the Maine agricultural site (Figure 1), where water content appears to play a substantial, albeit nonlinear role (Figure 6). Responses to water content similar to that of the Maine agricultural site have been reported for in vitro assays of Maine forest soils [*King*, 1999], but such assays may not reliably predict in situ behavior since water content was not a strong determinant of forest CO flux in the field studies.

A consistent though short-lived seasonal trend also appears in Maine forest gross CO production rates (Figure 2); production for other sites is aseasonal. However, the seasonal peaks in the Maine forest do not correspond to unusual conditions for temperature or water content (Figure 4), and are at present largely unexplained. Spring peaks in CO production might derive from a pulse of CO associated with leaf litter from the previous fall senescence. Litter is an important source of CO [*Sanhueza et al.*, 1998], the dynamics of which likely vary substantially in response to litter age, temperature and moisture, all of which may promote a strong CO source in early spring. The absence of such peaks in forested stands dominated by conifers suggests that the impact of deciduous leaf fall on CO dynamics deserves additional attention.

Although gross CO production rates do not vary seasonally at the Tifton sites (Figure 7), they show a strong positive relationship to temperature and water content (possibly parabolic for water content at the pine stand; Figure 9). At the pine stand in particular, the relationship between temperature and gross CO production appears to account for a decreasing trend of net CO flux as a function of increasing temperature (Figure 9). A relatively thick litter layer (~10 cm) comprised primarily of pine needles likely dominates the behavior of this system, distinguishing it from the other forest sites which have substantially thinner litter layers (~5 cm or less).

While CO flux patterns within each of the sites assayed respond variably to temperature and water content, a comparison among sites indicates that net CO flux rates vary consistently and inversely as a function of soil organic matter concentrations (Figure 11a). The absence of a litter layer, decreased carbon inputs, and the effect of tilling account for the substantially lower organic matter levels in cultivated versus forest soils [*Davidson and Ackerman*, 1993; *Scholes and Scholes*, 1995; *Franzluebbers and Arshad*, 1997; *Grant*, 1997]. However, the relationship between organic matter and CO fluxes is more complex and likely involves interactions with a variety of physiochemical and microbial parameters.

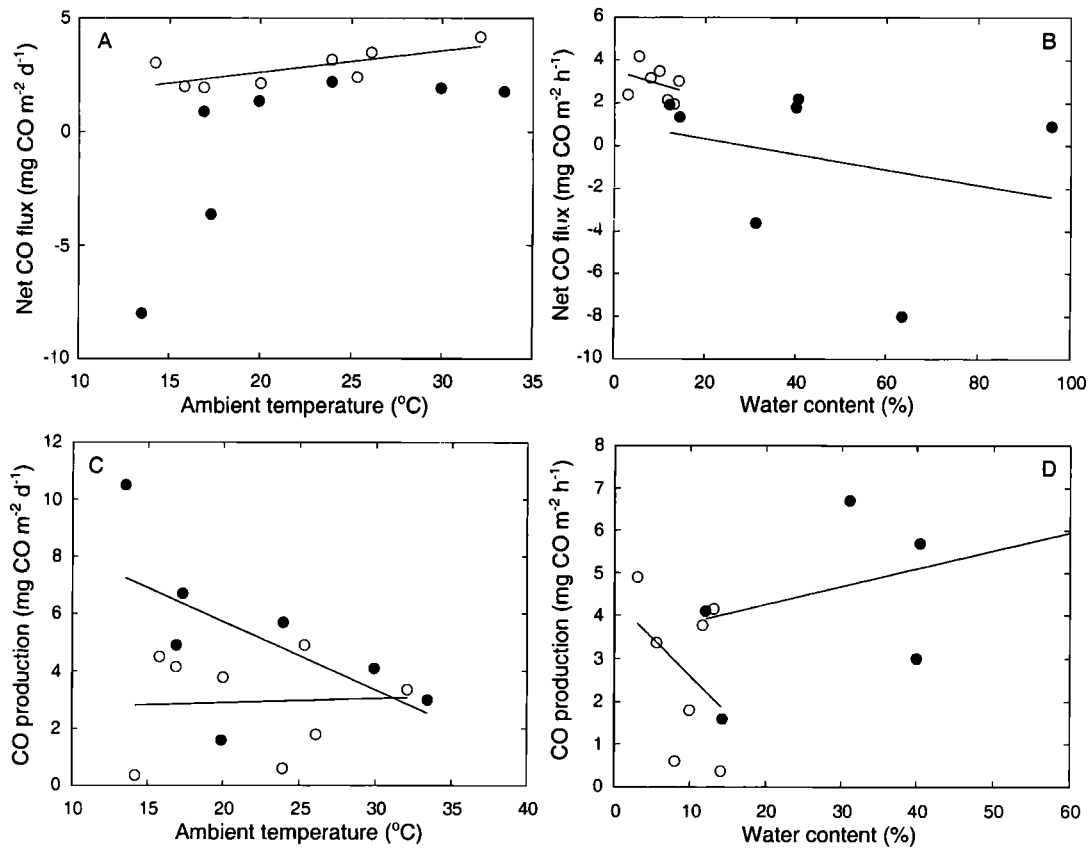

Figure 8. (a) Net CO fluxes for Griffin agricultural (open circles) and pine stand (solid circles) sites versus ambient temperature. (b) Net CO fluxes for Griffin agricultural (open circles) and pine stand (solid circles) sites versus surface water content. (c) Gross CO production rates for Griffin agricultural (open circles) and pine stand (solid circles) sites versus ambient temperature. (d) Gross CO production rates for Griffin agricultural (open circles) and pine stand (solid circles) sites versus surface water content. Lines indicate fits from regression analysis (see text for details).

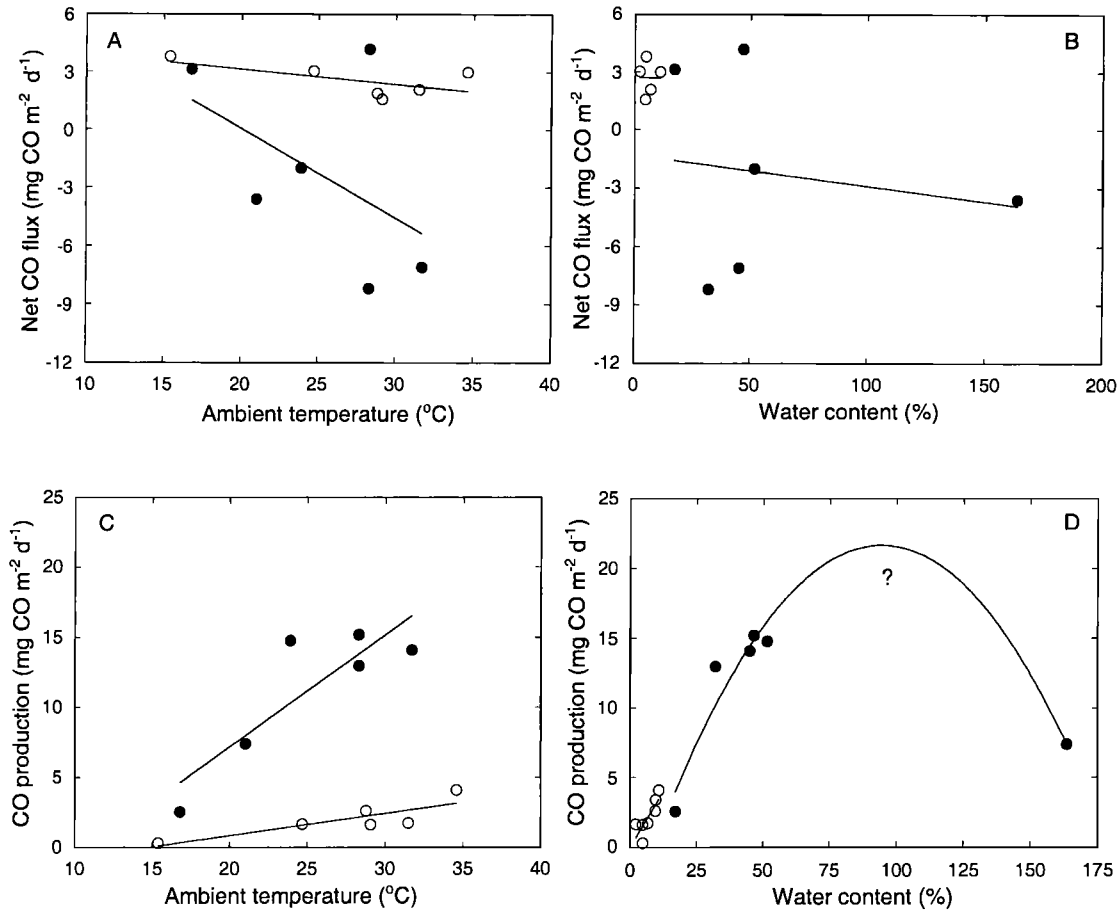

Figure 9. (a) Net CO fluxes for Tifton agricultural (open circles) and pine stand (solid circles) sites versus ambient temperature. (b) Net CO fluxes for Tifton agricultural (open circles) and pine stand (solid circles) sites versus surface water content. (c) Gross CO production rates for Tifton agricultural (open circles) and pine stand (solid circles) sites versus ambient temperature. (d) Gross CO production rates for Tifton agricultural (open circles) and pine stand (solid circles) sites versus surface water content. Lines indicate fits from regression analysis (see text for details); question mark indicates a possible hyperbolic relationship.

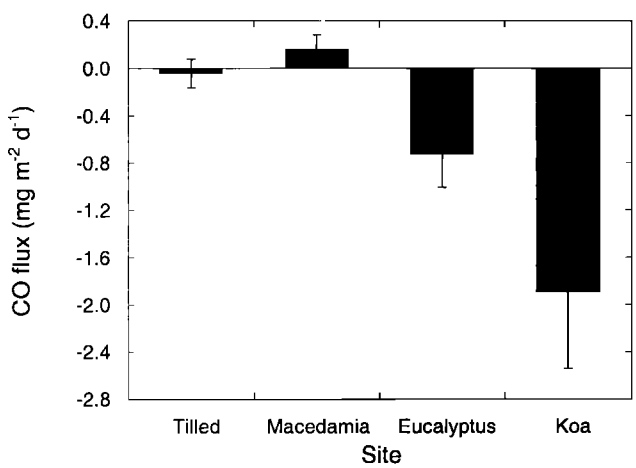

Figure 10. Net CO fluxes for agricultural (tilled and Macademia) and forested (Eucalyptus and Koa) sites in Hawai'i during December 1998. Values < 0 indicate net CO emission. All values are means of triplicates ± 1 standard error.

Although organic matter correlates positively with microbial biomass [*Hedges and Oades*, 1997], increases in which may result in elevated CO uptake [*Moxley and Smith*, 1998a], abiological CO production increases as a function of organic matter concentrations (Figure 11b), with organic matter lability, temperature, pH, and water content important determinants of specific production rates [*Conrad and Seiler*, 1982; *Conrad and Seiler*, 1985a, b; *Zepp et al.*, 1996; *Zepp et al.*, 1997; *Moxley and Smith*, 1998b]. Since the balance between simultaneously occurring microbial consumption and abiological production determines the magnitude and direction of CO fluxes between soil and the atmosphere, relative changes in either process can shift flux regimes from net uptake to emission or vice versa. Such shifts have been observed in temperate and tropical soils in vitro and in situ as a function of varied water contents, elevated temperatures and tilling [*Conrad and Seiler*, 1985a; *Scharffe et al.*, 1990; *Sanhueza et al.*, 1994a, b; *Moxley and Smith*, 1998a]. Results from this study suggest that land use change may lead to long-term changes in soil-atmosphere CO fluxes, with conversion of forests or grasslands to conventional agricultural uses in

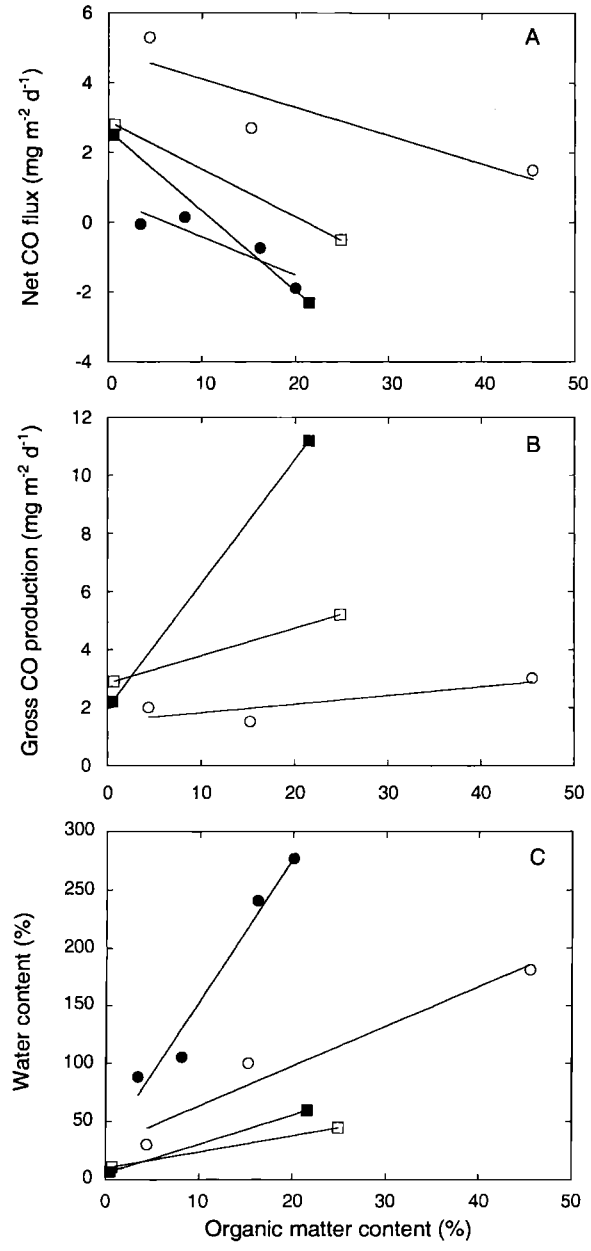

Figure 11. (a) Seasonally averaged net CO flux rates for sites in Maine (see Table 1) and Georgia (open squares for Griffin and solid squares for Tifton; see Table 2) and values from December for Hawai'i (see Figure 10) versus soil organic matter contents (0-2 cm interval). (b) Seasonally averaged gross CO production rates for sites in Maine (see Table 1 and Georgia (open squares for Griffin and solid squares for Tifton; see Table 2) versus organic matter contents. (c) Water contents (0-2 cm) versus organic contents for surface soils as in Figure 11a.

particular promoting lower soil organic matter concentrations, lower CO production, and increased CO consumption.

The distribution of soil organic matter correlates with and likely determines patterns for additional key regulatory parameters, among them water content (e.g., Figure 11c). In comparisons among sites, net CO fluxes decrease with increasing water content (not shown). However, since water content is not a major determinant of fluxes within the various sites, it appears that the relationship among sites may be coincidental to that of organic matter.

Organic matter concentrations also correlate strongly and inversely with soil pH (r = 0.78, p = 0.004; n = 11), and comparisons among sites indicate that CO fluxes increase with increasing pH. This trend may indicate that CO oxidizer population size, cell-specific activities, or both increase in response to physiologically less stressful conditions resulting from forest to agriculture transitions. Nonetheless, since elevated pH stimulates abiological CO production [*Conrad and Seiler*, 1985b], the significance of pH shifts derived from landuse change deserve additional attention, with an emphasis on changes in susceptibility of organic matter to abiological CO production.

Land use dramatically affects numerous soil-atmosphere trace gas fluxes [*Schlesinger*, 1997]. Changes in flux may have important consequences for atmospheric chemistry and climate. Greenhouse amplification results from land uses [e.g., deforestation] that elevate nitrous or nitric oxide emissions or increase atmospheric methane by inhibiting soil methane consumption [*Prather et al.*, 1995; *King*, 1997]. In contrast, greenhouse negative changes may result from land uses that significantly increase net CO consumption, thereby lowering atmospheric CO which in turn can lead to reductions in both methane and ozone [*Logan et al.*, 1981; *Crutzen and Gidel*, 1983; *Guthrie*, 1989]. Although agriculture accounts for >10% of current land use [*Schlesinger*, 1997] and has clearly contributed to the rise in atmospheric methane and nitrogen oxides [*Prather et al.*, 1995; *Steudler et al.*, 1996; *King*, 1997], the effects of agriculture on these gases may have been partially mitigated by increased CO consumption.

Results from four distinct systems indicate that conventional agriculture enhances net CO consumption in response to soil organic matter losses and accompanying changes in soil water and pH regimes. Owing to the central role of organic matter, agricultural impacts on CO fluxes likely vary temporally in response to rates of organic matter loss. However, practices that decrease or reverse organic matter losses, such as no-till or conservation methods [*Rasmussen et al.*, 1998] may limit the extent to which CO consumption is enhanced by agriculture or potentially lead to net CO emission. Likewise, increased carbon sequestration in forest or grassland soils as a consequence of elevated CO_2 and climate change [*Fan et al*, 1998; *Houghton et al.*, 1999] could alter the role of these systems in CO budgets and regional, if not global atmospheric chemistry.

Results from the four forest sites in this study also raise doubts about previous estimates of the global soil CO sink strength [*Badr and Probert*, 1995]. These reports have been based primarily on data from a small number of temperate European forests, a limited survey of tropical savanna systems, and an assumption that all such systems are permanent CO sinks. This assumption may not be generally valid since CO emission occurs frequently at all sites in this study. In addition net deposition velocities (Tables 1 and 2) from this study are markedly lower than values used for extrapolations (> 0.02 cm s^{-1}), even with corrections for CO production, but are comparable to recent reports for boreal forests [*Zepp et al.*, 1997]. Consequently, the global soil CO sink may have been overestimated, and even the most recent downward revision, 115-230 Tg yr^{-1} [*Sanhueza et al.*, 1998] could be an upper limit.

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Gary M. King, Darling Marine Center, University of Maine, Walpole, ME, 04573. (gking@maine.edu)

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