



Vegetation and soil respiration: Correlations and controls

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Abstract. Soil respiration rates vary significantly among major plant biomes, suggesting that vegetation type influences the rate of soil respiration. However, correlations among climatic factors, vegetation distributions, and soil respiration rates make cause-effect arguments difficult. Vegetation may affect soil respiration by influencing soil microclimate and structure, the quantity of detritus supplied to the soil, the quality of that detritus, and the overall rate of root respiration. At the global scale, soil respiration rates correlate positively with litterfall rates in forests, as previously reported, and with aboveground net primary productivity in grasslands, providing evidence of the importance of detritus supply. To determine the direction and magnitude of the effect of vegetation type on soil respiration, we collated data from published studies where soil respiration rates were measured simultaneously in two or more plant communities. We found no predictable differences in soil respiration between cropped and vegetation-free soils, between forested and cropped soils, or between grassland and cropped soils, possibly due to the diversity of crops and cropping systems included. Factors such as temperature, moisture availability, and substrate properties that simultaneously influence the production and consumption of organic matter are more important in controlling the overall rate of soil respiration than is vegetation type in most cases. However, coniferous forests had ~10% lower rates of soil respiration than did adjacent broad-leaved forests growing on the same soil type, and grasslands had, on average, ~20% higher soil respiration rates than did comparable forest stands, demonstrating that vegetation type does in some cases significantly affect rates of soil respiration.

Introduction

Carbon dioxide emissions from soils (i.e., soil respiration) exceed all other terrestrial-atmospheric carbon exchanges with the exception of gross photosynthesis (Raich & Schlesinger 1992). Almost 10% of the atmosphere's CO₂ passes through soils each year (Raich & Potter 1995); this is more than 10 times the CO₂ released from fossil fuel combustion. Due to the magnitude of this soil-to-atmosphere CO₂ flux and the large pool of potentially mineraliz-

able C in soils (e.g., Bohn 1982; Eswaran et al. 1993, 1995), any increases in soil CO₂ emissions in response to environmental change have the potential to exacerbate increasing atmospheric CO₂ levels and to provide a positive feedback to global warming (e.g., Schleser 1982; Jenkinson et al. 1991; Raich & Schlesinger 1992; Kirschbaum 1995). Identifying the environmental factors that control soil CO₂ emissions, and their effects on emission rates, is a necessary step in assessing the potential impacts of environmental change.

Rates of soil respiration are largely dependent upon soil temperature and moisture conditions (e.g., Singh & Gupta 1977; Schlentner & Van Cleve 1985; Carlyle & Than 1988). Seasonal changes in soil microclimate play an important role in defining seasonal differences in soil-CO₂ emissions within sites, and climatic differences generate different soil respiration rates among distant sites (e.g., Raich & Potter 1995). Other soil factors potentially influencing rates of soil respiration *in situ* include the availability of C substrates for microorganisms (e.g., Seto & Yanagiya 1983), plant root densities and activities (e.g., Ben-Asher et al. 1994), soil organism population levels (e.g., Singh & Shukla 1977; Rai & Srivastava 1981), soil physical and chemical properties (e.g., Boudot et al. 1986) and soil drainage (e.g., Luken & Billings 1985; Moore & Knowles 1989; Freeman et al. 1993).

Soil respiration also varies with vegetation. Respiration rates vary significantly among major biome types (e.g., Schlesinger 1977; Singh & Gupta 1977; Raich & Schlesinger 1992), and side-by-side comparisons of different plant communities frequently demonstrate differences in soil respiration rates (e.g., Lundegårdh 1927; Lieth & Ouellette 1962; Ellis 1974). Such findings indicate that vegetation type is an important determinant of soil respiration rate, and therefore that changes in vegetation have the potential to modify the responses of soils to environmental change.

Our overall objectives are to consider the mechanisms that might cause soil respiration rates to change in response to changes in vegetation, and to quantify the magnitude of differences observed. Vegetation affects soil respiration by influencing soil microclimate and structure, the quantity of detritus supplied to the soil, the quality of that detritus, and the overall rate of root respiration. Hence, changes in vegetation resulting from human activities or global environmental change have the potential to modify the soil-to-atmosphere CO₂ flux. We specifically undertake three tasks. First, we seek to identify predictable differences in soil respiration rates between contrasting vegetation types, focusing on plant communities that are structurally or functionally different. Our assumption is that if dramatic differences in vegetation type do not substantially influence soil respiration rates, then less obvious changes due to species differences alone are unlikely to be important. Second, we review the available literature for evidence of vegetation's effect on soil

respiration rates via its influence on detritus production and root respiration rates. Third, we consider vegetation-soil microclimate interactions and their potential role in affecting soil respiration rates.

Vegetation type and soil respiration

To determine if predictable differences in soil-CO₂ emissions occur as a result of differences in vegetation type, we tallied published comparisons of soil respiration in different vegetation communities. We included all data where soil respiration was measured in two or more plant communities located on the same soil parent material and in similar topographic positions. Only measurements that were collected at the same times by the same authors with the same methods were included so as to eliminate extraneous variables (Table 1). Each comparison was considered a single independent estimate of a difference in soil respiration directly attributable to vegetation type. All data were converted from their original (published) units to g C m⁻² d⁻¹ prior to testing for differences among sites with paired *t*-tests. In those cases where more than two vegetation types were compared, each pair-wise comparison was used in the final analysis. We found sufficient data to compare soil respiration rates between cropped and fallowed sites, between broad-leaved and coniferous forests, between grasslands (including pastures) and forests, between grasslands and croplands, and between forests and croplands (Table 1).

On average, actively cropped fields had ~20% higher rates of soil respiration than did adjacent fields without plants (mostly fallow fields), but this difference was not significant (Figure 1(A), $n = 11$, $P = 0.13$). In some cases (e.g., Rochette et al. 1992), higher soil temperatures in the fallow fields stimulated soil respiration, despite the lack of live root respiration. Such situations cannot be maintained over long terms because soil C pools would become depleted, but fallow plots are not generally maintained for more than a year.

We also found no significant differences between croplands and nearby forests (Figure 1(B), $n = 7$, $P = 0.50$) or between grasslands and nearby croplands (Figure 1(C), $n = 8$, $P = 0.13$), although grasslands had, on average, about 25% higher soil respiration rates than did adjacent cropped fields (Figure 1(C)). These latter results are in contrast to Lundegårdh's (1927) observations that soil respiration is consistently greater in forests than in grasslands, and is consistently greater in grasslands than in croplands. The lack of significant trends in our compilation is probably due to the variety of crops and cropping systems included in the analysis. For instance, Beyer (1991) reported much higher soil respiration rates in environmentally tilled crop fields than in conventionally tilled fields. Our summary indicates

Table 1. Sources of data for paired tests of vegetation influences on soil respiration. All soil respiration (SR) values are converted to common units from the original source. Some numbers have been estimated from figures. 'Period' refers to the length of the comparison.

Location	Vegetation	Period	SR g C m ⁻² d ⁻¹	Reference
Brazil	Evergreen forest	1 d	2.96	Goreau and Mello (1988)
Brazil	Pasture	1 d	4.19	"
Brazil	Evergreen forest	1 d	3.53	"
Brazil	Pasture	1 d	3.58	"
Brazil	Cowpeas	1 d	2.71	"
Brazil	Fallow	1 d	1.07	"
Brazil	Pastures I	Annual	4.76	Steudler et al., in review
Brazil	Forest I	Annual	3.66	"
Brazil	Pastures II	Annual	4.94	"
Brazil	Forest II	Annual	3.72	"
New Brunswick	Grass meadow	5 d	0.90	Lieth and Ouellette (1962)
New Brunswick	Fir forest	5 d	0.31	"
New Brunswick	Grass meadow	5 d	0.77	"
New Brunswick	Alder forest	5 d	0.65	"
Ontario	Maple forest	Growing season	2.31	Ellis (1974)
Ontario	Pine forest	Growing season	2.17	"
Ontario	Maple forest	Growing season	2.32	"
Ontario	Pasture	Growing season	2.06	"
Ontario	Barley	69 d	3.94	Rochette et al. (1992)
Ontario	Fallow	69 d	5.20	"
Ontario	Deciduous forest	Growing season	2.33	Lessard et al. (1994)
Ontario	Corn	Growing season	1.00	"
Saskatchewan	Cereal, top slope	Growing season	0.16	de Jong (1981)
Saskatchewan	Fallow, top slope	Growing season	0.23	"
Saskatchewan	Prairie, top slope	Growing season	0.41	"
Saskatchewan	Cereal, mid	Growing season	0.30	"
Saskatchewan	Fallow, mid	Growing season	0.30	"
Saskatchewan	Prairie, mid	Growing season	0.66	"
Saskatchewan	Cereal, lower	Growing season	0.57	"
Saskatchewan	Fallow, lower	Growing season	0.45	"
Saskatchewan	Prairie, lower	Growing season	0.82	"
Costa Rica	Forest	1 d	4.88	Raich et al. (1985)
Costa Rica	Cassava	1 d	3.46	"
Costa Rica	Fallow	1 d	2.51	"
Germany	Forest on luvisol	Annual	1.30	Beyer (1991)
Germany	Crops on luvisol	Annual	1.13	"
Germany	Crops on luvisol	Annual	1.71	"
Germany	Forest on podzol	Annual	0.80	"
Germany	Crops on podzol	Annual	1.80	"
Germany	Crops on podzol	Annual	1.52	"
India	Oak forest	Annual	1.82	Rout and Gupta (1989)
India	Pine forest	Annual	1.42	"
India	Oak forest	Annual	1.28	Joshi et al. (1991)
India	Cedar forest	Annual	1.05	"
Russia	Fallow	Growing season	0.45	Belkovskiy and Reshetnik (1981)
Russia	Pasture	Growing season	0.94	"
Russia	Rye	Growing season	0.97	"
Russia	Potato	Growing season	0.70	"

Table 1. Continued.

Location	Vegetation	Period	SR g C m ⁻² d ⁻¹	Reference
Malaysia	Young forest	Several days	2.54	Ceulemans et al. (1987)
Malaysia	Rubber plantation	Several days	1.37	"
Malaysia	Fallow	Several days	0.98	"
Sweden	Fallow	Short	1.75	Lundegårdh (1927)
Sweden	Oats	Short	2.61	"
U.K.	Crops	Growing season	1.77	Monteith et al. (1964)
U.K.	Fallow	Growing season	1.09	"
Alaska	Poplar	139 d	0.93	Ruess et al. (1996)
Alaska	White spruce	139 d	0.89	"
Alaska	Birch-aspen	139 d	1.08	"
Alaska	White spruce	139 d	0.85	"
Hawaii	Pasture, 800 m	Annual	2.17	Townsend et al. (1995)
Hawaii	Forest, 900 m	Annual	1.97	"
Hawaii	Pasture, 1700 m	Annual	1.69	"
Hawaii	Forest, 1500 m	Annual	1.79	"
Iowa	Switchgrass	231 d	3.70	Tufekcioglu et al., in press
Iowa	Soybean	231 d	2.70	"
Iowa	Mixed grass	231 d	4.55	"
Iowa	Corn	231 d	2.40	"
Maine	Deciduous forest	Growing season	2.10	Fernandez et al. (1993)
Maine	Conifer forest	Growing season	2.10	"
Missouri	Prairie	Annual	1.34	Buyanovsky et al. (1987)
Missouri	Wheat	Annual	1.75	"
New York	Red pine	Annual	0.41	Hudgens and Yavitt (1997)
New York	Pasture	Annual	0.36	"

only that the conversion of forest or grassland to croplands does not have a predictable impact on soil respiration rates; management of the croplands is an important variable that will influence the direction and magnitude of any resulting changes.

Soil respiration rates are consistently greater in grasslands than in forests growing under similar conditions (Figure 2, $n = 10$, $P = 0.053$). The differences observed were $\sim 20\%$ on average, suggesting that forest conversion to grassland would stimulate soil CO₂ emissions to the atmosphere. This finding does not explain the reasons for the difference, but physiological and structural differences between grasslands versus forests are likely involved. With virtually no allocation of C to wood production, grasses may have more photosynthate available to allocate belowground than do forest trees. We emphasize that the observed difference is based on studies in only six locations (Figure 2), but these include both tropical and temperate locations. In contrast to our results, Griffiths et al. (1997) found that riparian soils under forest had more organic C and N, more fungi, and higher C miner-

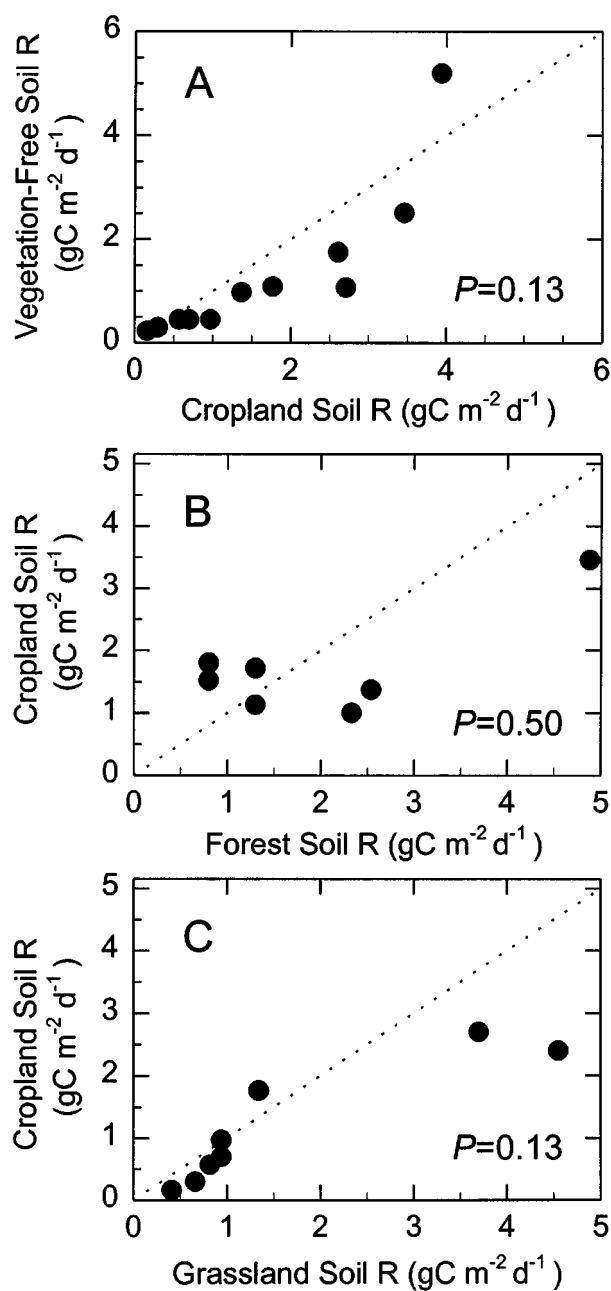


Figure 1. Paired comparisons of soil respiration rates in contrasting vegetation communities. In each figure the dashed line shows the 1:1 relationship. Data sources are shown in Table 1. All soil respiration values have been converted to $\text{gC m}^{-2} \text{d}^{-1}$ for comparative purposes. (A) cropped soils compared with nearby vegetation-free (mostly fallow) plots. (B) forest stands compared with adjacent croplands. (C) grasslands (including pastures) compared to adjacent croplands.

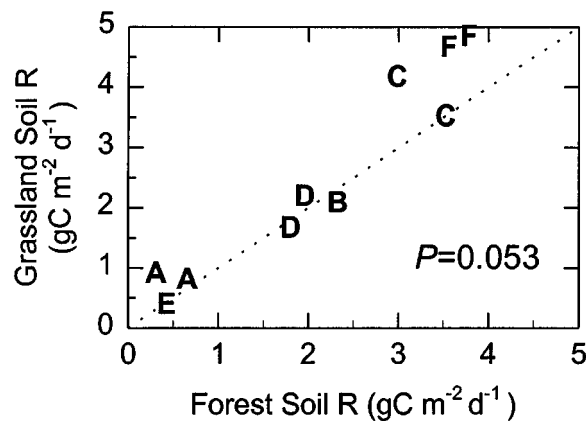


Figure 2. Paired comparisons of soil respiration rates in grasslands and comparable forest stands. The dashed line shows the 1:1 relationship. Data are converted from their original units to $\text{g C m}^{-2} \text{ d}^{-1}$. Sources of data: **A**, Lieth and Ouellette (1962); **B**, Ellis (1974); **C**, Goreau and Mello (1988); **D**, Townsend et al. (1995); **E**, Hudgens and Yavitt (1997); **F**, Steudler et al. (in review).

alization rates than did comparable riparian soils under pasture, but they did not measure *in situ* soil respiration rates.

The available data also suggest that soil respiration rates in coniferous forests are lower than those in broad-leaved forests located on the same soil types (Figure 3, $n = 6$, $P = 0.034$), by an average of 10%. These results are supported by Weber's (1985, 1990) findings that aspen stands in Ontario had higher soil respiration rates than did nearby jack pine stands, and Hudgens and Yavitt's (1997) findings of higher soil respiration rates in a New York hardwood forest than in a nearby pine plantation. In these latter cases it is likely that soil characteristics varied among stands, but our analysis (Figure 3) suggests that the observed differences may not be due to soils alone.

Our finding is in contrast to that of Raich and Potter (1995), who found no consistent differences between soil respiration rates in coniferous and broad-leaved forests when respiration rates were plotted in relation to mean monthly air temperatures. Their approach included data from many more sites, but they did not control for substrate type, moisture conditions, measurement techniques, or location. Our current analysis is based on direct comparisons of sites where forest type is the principal variable differing among pairs, but is limited to only six comparisons in five temperate locations. Additional direct comparisons of broad-leaved and coniferous forests on the same soil type would be valuable, particularly if coupled with measurements of C cycling properties that might elucidate the reasons for any observed differences.

The data we collected do not provide a mechanism for the difference observed between broad-leaved and coniferous forest respiration rates, but

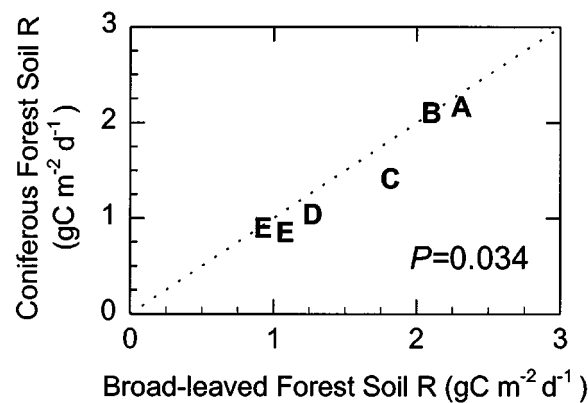


Figure 3. Paired comparisons of soil respiration rates in paired coniferous and broad-leaved forest stands. The dashed line shows the 1:1 relationship. Data are converted from their original units to $\text{g C m}^{-2} \text{ d}^{-1}$. Sources of data: A, Ellis (1974); B, Fernandez et al. (1993); C, Rout and Gupta (1989); D, Joshi et al. (1991); E, Ruess et al. (1996).

differences in C allocation patterns, litter production rates, litter quality, or root respiration are all possible. Tewary et al. (1982) found that soil respiration rates beneath coniferous trees were lower than those beneath broad-leaved trees in a mixed forest in northern India, and that these micro-habitat differences correlated with higher N and lower lignin contents in the oak litter. Tewary suggested that substrate quality affected soil respiration rates, but this has not been demonstrated clearly in any study. Cole and Rapp (1981) inferred that nutrient cycling rate was an inherent property of deciduous and coniferous tree species, with deciduous species having faster nutrient cycling rates. Our result (Figure 3) suggests that this is true, too, of C.

Plant production and soil respiration

A principal mechanism by which vegetation may control soil respiration rates is via the production of plant detritus, which feeds soil organisms. Raich and Nadelhoffer (1989) found that soil respiration increased with increasing litterfall in relatively mature forest ecosystems. We tallied published data not included in Raich and Nadelhoffer's analysis, using the same selection criteria (i.e., relatively mature forests, and measurement chambers not inserted >6 cm into the ground). These data also support the conclusion that litter production and soil respiration are positively correlated ($n = 22$, $r = 0.90$, $P < 0.0001$; Figure 4(A)).

There are insufficient data to make similar comparisons for most other biomes, but we did compare directly measured rates of aboveground net

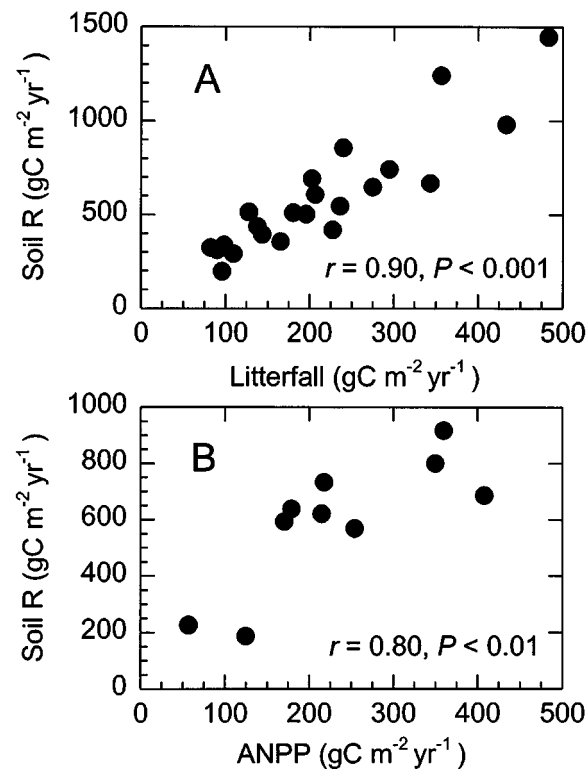


Figure 4. (A) Soil respiration shown in relation to litterfall in relatively mature forests of the world. Included are data from: Tulaphitak et al. (1983) and Tsutsumi et al. (1983); O'Connell (1987) and O'Connell and Menagé (1982); Piñol et al. (1995); Bowden et al. (1993a, b); Edwards et al. (1989); Kursar (1989); Jurik et al. (1991); Gunadi (1994); Haynes and Gower (1995); Ruess et al. (1996); Raich (1998). (B) Soil respiration in grasslands of the world, shown in relation to aboveground net primary productivity (ANPP). Included are data from: de Jong et al. (1974); Lamotte (1975); Coleman et al. (1976); Tesarova and Gloser (1976); Risser et al. (1981); Upadhyaya and Singh (1981); Behara and Pati (1986); Buyanovsky et al. (1987).

primary production (ANPP) and soil respiration in grasslands of the world. We included in this analysis data from burned, mowed, grazed, and unmanaged grasslands where both soil respiration and aboveground plant production were measured over the same time intervals. We assumed grassland biomass to be 45% C when converting to units of carbon. Despite variations in management, *in situ* soil respiration and ANPP in grasslands were positively correlated ($n = 10$, $r = 0.80$, $P < 0.01$; Figure 4(B)).

Both of these findings (Figure 4) suggest that soil respiration is greater in sites with greater rates of detritus production, which would be expected if plant detritus is providing the energy that drives soil respiration. Raich and

Schlesinger (1992) previously reported that soil respiration and NPP were linearly correlated at the biome scale. Hence, there is strong evidence that rates of plant production and soil respiration are linked processes. Broad-scale C limitations to microbial activity in mature terrestrial ecosystems (e.g., Zak et al. 1994) support the conclusion that plants control heterotrophic activity via their control over C supply. However, correlations between plant production and soil N mineralization (e.g., Pastor et al. 1984; Raich et al. 1997; Reich et al. 1997) provide equally strong evidence that microbial activity controls plant production via effects on nutrient availability.

Several reports suggest that soil respiration and plant production in forests are poorly correlated at local scales (e.g., Reiners 1968; Ellis 1969). Weber (1985, 1990) found that soil respiration rates were only somewhat greater in aspen stands than in much-less-productive jack pine stands of similar ages in Ontario. The most productive of three Hawaiian forests had 86% higher aboveground NPP but only 36% more soil respiration than did the least productive stand (Raich 1998). In both northern lower Michigan (Jurik et al. 1991) and boreal Alaska (Ruess et al. 1996) soil respiration rates were similar among forest stands that differed widely in aboveground production. Local factors such as soil type, inter-site habitat variability, species composition, or land use history may obscure correlations that are obvious at broader geographic scales, but all these studies are consistent in suggesting that soil respiration rates vary less among nearby stands than do rates of plant production.

Root respiration and soil respiration

Root respiration is a primary contributor to the soil CO₂ pool, and hence a major factor influencing soil respiration rates *in situ*. The proportion of the total soil respiration flux that is attributable to live root respiration appears to be very high in cold, northern biomes, ranging from 50–93% in arctic tundra (Billings et al. 1977, 1978; Chapin et al. 1980) and from 62–89% in boreal forests (Bonan 1993; Ryan et al. 1997). In temperate zones, estimated proportions of the total soil respiration flux that is derived from live root respiration range from 33–50% in broad-leaved forests (Edwards & Sollins 1973; Nakane 1980; Bowden et al. 1993b); from 35–62% in pine forests (Nakane et al. 1983; Ewel et al. 1987; Striegl & Wickland 1998) and from 17–40% in grasslands (Kucera & Kirkham 1971; Coleman 1973; Herman 1977; Buyanovsky et al. 1987). Root respiration is generally a lesser contributor to the annual soil-CO₂ efflux from crop fields, due to the short duration of live roots in annual crop fields and the relatively low biomass of roots during the early part of the growing season. Root respiration inputs to crop fields

are estimated to range from 12–38% of the total soil-CO₂ flux (Monteith et al. 1964; Singh & Shekhar 1986; Buyanovsky et al. 1987; Singh et al. 1988; Paustian et al. 1990; Buyanovsky & Wagner 1995). These estimates are consistent with our finding that fallow fields have on average 20% less soil respiration than do adjacent, cropped fields.

Given the difficulties of estimating live root contributions to total soil respiration, it is not possible to identify predictable differences among vegetation types. Nevertheless, vegetation composition is potentially important. Caldwell et al. (1977) developed C budgets for two desert shrub communities, and found that *Ceratoides* communities had less root biomass production but the same soil respiration rate as did *Atriplex* communities. They concluded that *Ceratoides* had higher root maintenance respiration rates than did *Atriplex*. Tissue-specific construction and maintenance respiration rates vary among species (e.g., Penning de Vries 1975; Amthor 1984; Ryan 1995), at least in part due to differences in N content (e.g., Ryan 1991, 1995). Such differences among plant species have the potential to influence overall soil respiration rates. However, the importance of physiological differences among plant species on *in situ* soil respiration rates remains poorly known.

Vegetation and soil microclimate

It is not our goal to review the various ways by which plants can and do modify the soil environment, but three related points are important. A plant cover alters soil temperature and moisture conditions, and these effects often differ among vegetation types (Gates 1980). Soil temperature and moisture conditions significantly influence soil respiration rates (e.g., Singh & Gupta 1977). As a result, observed differences in soil respiration among plant communities can frequently be attributed directly to plant-mediated effects on soil microclimate.

We provide an example from central Iowa (Tufekcioglu et al. in press). Soil respiration was measured approximately monthly over two growing seasons in two agricultural fields, using the soda-lime method. Temperatures and gravimetric moisture contents of the surface 0–5 cm of soil were measured whenever soil respiration was monitored. One field was planted in spring to soybeans and the other was planted 7 years earlier to switchgrass (*Panicum virgatum* L.), a native C₄ prairie grass that has not since been cultivated. Both fields were in the same soil mapping unit and had long histories of annual row crop agriculture.

Over the growing season, soil respiration in the soybean field averaged 520 g C m⁻², and respiration in the switchgrass field averaged 790 g C m⁻², and these rates were significantly different as determined by ANOVA followed by

a least significant difference test ($P < 0.05$). Seasonal variations in the soil respiration rate closely followed those of temperature in each site (Figure 5). Considering each site alone, mean monthly soil respiration correlated highly with surface-soil temperature but not with moisture (stepwise multiple linear regression, $n = 11$, $P < 0.004$). However, if data from both sites are combined ($n = 22$) then soil respiration rate was significantly affected by both soil temperature ($P < 0.001$) and moisture content ($P < 0.001$), with an $r^2 = 0.78$. In this case soil respiration rates were lower in the site with the warmest soil temperatures (Figure 5), suggesting that another factor was overriding the temperature effect. The observed differences in soil respiration between the two fields could be explained by their different soil moisture regimes (Figure 5).

Higher soil moisture contents in the switchgrass site are probably due to the denser cover of living and dead plant matter, and the higher soil C contents in uncultivated switchgrass field. Our point is that the difference between these two contrasting vegetation types can be explained by plant-mediated effects on soil microclimate alone, irrespective of differences in tissue quality, detritus production, or root respiration rate. Vegetation may impact soil respiration rates in many ways; we must explain both how and why if we are to predict the consequences of vegetation changes on soil respiration rates. This will require a better understanding of within-soil C cycling.

General discussion

Humans have dramatically altered the vegetation cover of Earth (e.g. Olson et al. 1983; Hannah et al. 1994; Houghton 1994; Imhoff 1994), and further changes in vegetation cover are expected as human impacts on Earth continue, particularly if climate change also occurs (e.g., Emanuel et al. 1985; Overpeck et al. 1991; Davis & Zabiniski 1992; Cramer & Solomon 1993). The obvious changes in vegetation that have already occurred, and future changes in land cover that are likely to occur, have the potential to alter the global C cycle. Approximately 10% of the atmosphere's C passes through soils each year. Our goal was to evaluate the effect of vegetation type on this important C flux.

The direct paired comparisons that we found indicate that vegetation type alone does not predictably influence soil respiration rates in many cases (Figure 1). Even sites without plants had, in some cases, greater respiration rates than vegetated plots, despite a complete absence of root respiration or root exudates in the fallow plots (Figure 1(A)). In several cases the complete felling or removal of forest vegetation has had no measurable impact on

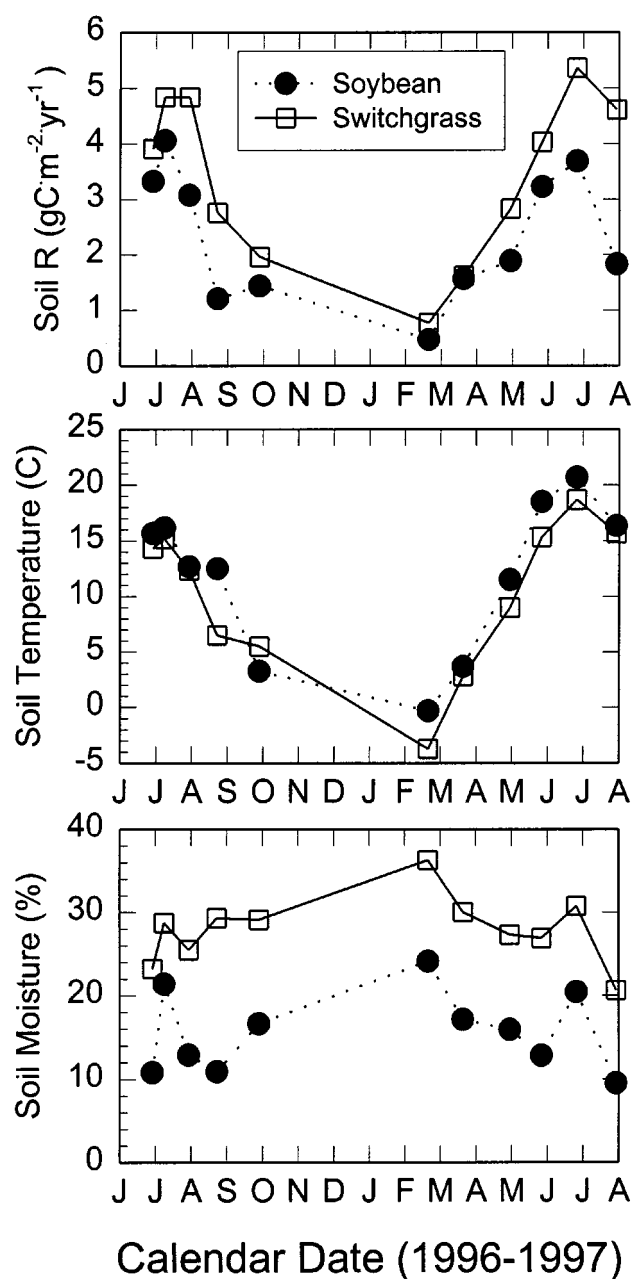


Figure 5. In situ soil respiration (top), surface-soil temperatures (middle), and surface-soil gravimetric moisture content (lower) in central Iowa agricultural fields planted to soybean (solid symbols) and switchgrass (open squares). Shown are mean values, each based on an average of three plots with three chambers per plot.

annual soil-CO₂ emissions (e.g., Edwards & Ross-Todd 1983; O'Connell 1987; Bowden et al. 1993a; Toland & Zak 1994; Marra & Edmonds 1996). These results support the conclusion that vegetation type has relatively little influence on soil respiration rates, but also highlight some of the difficulties in interpreting soil respiration measurements. Because soil respiration is a net flux derived from several different processes, changes occurring in any single process can be masked by opposite changes in another (e.g., Buyanovsky & Wagner 1995). Soil respiration is most useful as a measure of CO₂ fluxes from soils; its value as a measure of other ecosystem processes is very much limited. Additional research focused on disentangling the various sources of CO₂ within the soil is needed.

Our comparisons do suggest that grasslands and forests growing under the same conditions have different soil respiration rates (Figure 2), and that coniferous and broad-leaved forests growing under the same conditions have different soil respiration rates (Figure 3). Hence, conversions of land cover among these vegetation types would potentially alter the soil-to-atmosphere C flux. These findings suggest fundamental differences in C cycling between these vegetation types. Further evaluation of the specific reasons why grasslands have higher soil respiration rates than do forests, and why deciduous forests have higher respiration rates than do broad-leaved forests, is warranted. Our findings support the generalizations that grasslands allocate large proportions of their photosynthate belowground, and that C cycles more slowly through coniferous forest soils than through broad-leaved forest soils. Suggestions that differences in the quality of detritus produced by coniferous versus broad-leaved forests are in part responsible for this latter difference (e.g., Tewary et al. 1982) require additional study. Given the very real structural, physiological, and phylogenetic differences between grasses and trees, and between conifers and angiosperms, the relatively small respiration differences observed between these vegetation types (Figures 3 and 4) support the conclusion that soil respiration rates are controlled primarily by climatic and substrate factors, with vegetation having a secondary effect only.

The natural distribution of vegetation over Earth's surface is largely dependent upon climate, and in particular on the interplay between moisture availability and temperature (e.g., Holdridge 1947; Walter 1973; Stephenson 1990). Similarly, soil respiration rates are largely determined by the climate, and particularly by the interplay between moisture availability and temperature (e.g., Kowalenko et al. 1978; Schlentner & Van Cleve 1985; Carlyle & Than 1988; Raich & Potter 1995). As a result, distinguishing vegetation from climatic controls over soil respiration is problematic, as we found in our comparison of soybean and switchgrass plots in Iowa (Figure 5). It is probable that global-scale summaries demonstrating differences in soil

respiration rates among biome types are more representative of climatic differences among biomes than of inherent respiration differences among vegetation types *per se*. We suggest that interactions among climatic and substrate conditions generate fundamental limitations to the potential rates of soil respiration, in the same way that they limit rates of plant productivity (e.g., Lieth 1973; Box 1978; Webb et al. 1978). It may be these factors, which are largely independent of vegetation, that drive global-scale correlations between soil respiration and vegetation type, and between soil respiration and plant productivity (Figure 4). Plants produce the organic matter that feeds soil organisms, and soil biota transform organically bound nutrients into forms that can be utilized by plants. The production and consumption of organic matter are inextricably linked processes that together are controlled by temperature, moisture availability, and substrate conditions that are largely independent of the plants present.

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