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Comparison of atmospheric carbon dioxide concentration and metabolic activity in Boreal Forest ecosystems

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ABSTRACT

The increasing seasonal amplitude of atmospheric CO_2 concentrations may reflect biotic influences such as increased photosynthesis due to higher CO_2 concentrations or increased winter respiration due to warmer temperatures. Boreal forests have a large rôle in the seasonal dynamics of atmospheric CO_2 in the Northern Hemisphere, and if terrestrial ecosystems contribute to the greater amplitude, such a signal should appear in the metabolic activity of boreal forests. Analyses in which a mechanistic model of photosynthesis, respiration, and decomposition was driven with the observed annual increase in atmospheric CO_2 concentration and observed daily air temperature and precipitation show that from 1974 to 1982 the seasonal amplitude in metabolic activity in boreal forests near Fairbanks, Alaska, increased by $0.52 \pm 0.03\%$ year^{-1}. The increasing amplitude was due to increased tree photosynthesis as CO_2 concentration increased. However, the increase in annual aboveground biomass production was so small (3 g m^{-2} year^{-1} year^{-1}) that it is undetectable given field sampling errors. The small biomass growth increase indicates that a larger seasonal amplitude of atmospheric CO_2 can occur without large changes in net primary production, nutrient availability, or nutrient use efficiency. The increase in CO_2 concentration that produced the higher biomass production was also small (1.1 ppm year^{-1}), suggesting more attention should be paid to the ecological effects of small changes in CO_2 concentrations.

1. Introduction

Since continuous measurements were first begun at Mauna Loa, Hawaii, the concentration of carbon dioxide in the atmosphere has shown a persistent annual increase due to the combustion of fossil fuels. For example, from 1958 to 1989 mean annual CO_2 concentration measured at Mauna Loa increased by 12%, from 315 ppm to 352 ppm (Keeling et al., 1989a). Atmospheric CO_2 concentrations also show a seasonal cycle that reflects photosynthesis and respiration by terrestrial plants (Tucker et al., 1986; D'Arrigo et al., 1987; Fung et al., 1987) and in which the amplitude varies geographically from 1 to 15 ppm (Komhyr et al., 1985). While these signals dominate the modern CO_2 record, there are important interannual variations on the order of a few tenths ppm in the annual CO_2 increase and the seasonal cycle that may reveal important features of the carbon cycle.

In particular, the seasonal amplitude of atmospheric CO_2 concentrations has increased over time (Table 1). This increasing amplitude is thought to reflect terrestrial biotic influences such as increased photosynthesis due to "CO_2 fertilization" or increased winter respiration due to warmer temperatures (Pearman and Hyson, 1981; Cleveland et al., 1983; Gammon et al., 1985; Keeling et al., 1985, 1989b; Bacastow et al., 1985; Enting, 1987; Chan and Wong, 1990). The issue of CO_2 fertilization is extremely controversial. While laboratory studies show that photosynthesis increases with higher ambient CO_2 concentrations when other resources are in adequate supply, less is known about the long-term acclimation of plants to higher CO_2 concentrations, how increased CO_2 assimilation affects dry matter growth, nutrient availability, and nutrient use efficiency, how species-specific responses to increased CO_2 concentrations affect stand structure and composition, and whether growth increases

Table 1. *Annual increase in the amplitude of atmospheric CO_2 concentrations (mean ± SE% year^{-1})*

Amplitude	Years	Source
	Mauna Loa (20° N, 156° W)	
0.75 ± 0.09	1958–1982	Bacastow et al. (1985)
0.45 ± 0.19	1959–1977	Pearman and Hyson (1981)
0.54†	1958–1978	Cleveland et al. (1983)
	Ocean Weather Station P (50° N, 145° W)	
0.79 ± 0.31	1969–1981	Keeling et al. (1985)
0.72 ± 0.78	1970–1978	Pearman and Hyson (1981)
1.40 ± 0.73	1971–1979	Chan and Wong (1990)
	Barrow (71° N, 157° W)	
0.58 ± 1.24	1975–1981	Chan and Wong (1990)
0.57 ± 0.87‡	1973–1982	Peterson et al. (1986)

† No SE available.
‡ ±95% confidence interval.

will be realized in the field where factors such as temperature, moisture, and nutrients limit plant growth (Strain and Cure, 1985; Kienast and Luxmoore, 1988; Eamus and Jarvis, 1989; Bazzaz, 1990; Graumlich, 1991; Mooney et al., 1991; Woodward et al., 1991). Moreover, the changes in metabolism needed to produce the observed amplitude increase may be too large to be explained by CO_2 fertilization or increased respiration (Houghton, 1987; Kohlmaier et al., 1989).

Boreal forests appear to have a major rôle in the seasonal dynamics of atmospheric CO_2. The seasonal amplitude of atmospheric CO_2 concentrations is most pronounced at 65° N, near the northern edge of the boreal forest (Komhyr et al., 1985). Uptake and release of CO_2 by boreal forests may account for 50% of the seasonal amplitude in atmospheric CO_2 at Barrow, Alaska, and 30% of the seasonal amplitude at Mauna Loa (D'Arrigo et al., 1987). If terrestrial ecosystems are contributing to the increasing amplitude, such a signal should appear in the metabolic activity of boreal forests.

Bonan (1991b) has developed a detailed, process-oriented biophysical and physiological model that simulates daily photosynthesis, respiration, and decomposition in boreal forests. Using climatic parameters for a "typical meteorological year", this model has been applied to examine seasonal and annual CO_2 fluxes in 23 mature forest ecosystems located along a soil moisture, soil temperature, and soil nutrient gradient near Fairbanks, Alaska. Here, the model is combined with observed daily weather data from 1974 to 1982 and the observed increase in mean annual atmospheric CO_2 concentration during this period to test whether higher CO_2 concentrations or interannual climatic variability have produced changes in the metabolic activity of these forests that are consistent with the increased seasonal amplitude of atmospheric CO_2.

2. Methods

2.1. Site description

The simulations were performed for 9 black spruce (*Picea mariana* (Mill.) B.S.P.), 5 white spruce (*Picea glauca* (Moench.) Voss), 3 balsam poplar (*Populus balsamifera* L.), 2 birch (*Betula papyrifera* Marsh.), 2 aspen (*Populus tremuloides* Michx.), and 2 mixed conifer mature stands growing on sites ranging from cold, wet, nutrient-poor, soils underlain with permafrost to warm, well-drained, nutrient-rich soils without permafrost. These forests and the ecological controls of production and decomposition have been described in detail by Viereck et al. (1983) and Van Cleve et al. (1983a, 1986, 1991). Aboveground tree biomass ranges from 2.6 to 24.6 kg dry matter [DM] m^{-2}, and aboveground tree production ranges from 72 to 952 g DM m^{-2} year^{-1} (Van Cleve et al., 1983a). Forest floor mass ranges from 1.7 to 10.5 kg DM m^{-2} (Van Cleve et al., 1983b) and forest floor decomposition ranges from 116 to 298 g DM m^{-2} year^{-1} (Flanagan and Van Cleve, 1983). Mosses are common in the conifer stands, and moss production is as high as 126 g DM m^{-2} year^{-1} (Oechel and Van Cleve, 1986). Detailed simulations of energy, moisture, and CO_2 exchange for these forests based on a "typical meteorological year" have been presented elsewhere (Bonan, 1991a, 1991b).

2.2. The model

Given estimates of the biomass and nutrient status of the forest canopy and forest floor, the model combines the biophysics of energy exchange between the forest and the atmosphere, heat and moisture flow in the soil, and physiological and

ecological principles to simulate daily tree photosynthesis and respiration, moss photosynthesis and respiration, and microbial respiration during decomposition (Fig. 1). Tree photosynthesis is a function of the CO_2 diffusion gradient and the boundary layer, stomatal, and mesophyll resistances. Boundary layer resistance is directly proportional to leaf size and is inversely proportional to wind speed. Stomatal resistance is a function of irradiance, foliage temperature, vapor pressure deficit, and foliage water potential. Mesophyll resistance includes rate limitations imposed by the diffusion of CO_2 within cells and the effects of foliage temperature, irradiance, and foliage nitrogen on the biochemical reactions of photosynthesis. Tree respiration is calculated separately for foliage, stem, and root biomass. These respiration fluxes are each partitioned into maintenance and growth respiration. Maintenance respiration is an exponential function of tissue temperature. Growth respiration is a function of the efficiency with which new tissue is synthesized.

Mosses form a significant component of many boreal forests. Moss photosynthesis is limited by irradiance, temperature, and moisture. Moss respiration is an exponential function of temperature and the efficiency with which new tissue is synthesized. Microbial respiration is a function of soil moisture, soil temperature, and substrate quality. Bonan (1991b) provides more details on the CO_2 fluxes.

Bonan (1991a) described the calculation of required biophysical parameters such as stomatal and boundary layer resistances, absorbed photosynthetically active radiation, foliage temperature, soil temperature, and soil moisture. The forest canopy is divided into three layers: an upper canopy, a lower canopy, and the ground surface. The components of the energy budget at each canopy layer are each written in terms of the upper and lower canopy temperatures and the temperature of the ground surface. At each canopy layer, the energy budget must sum to zero, and these three equations are solved simultaneously for

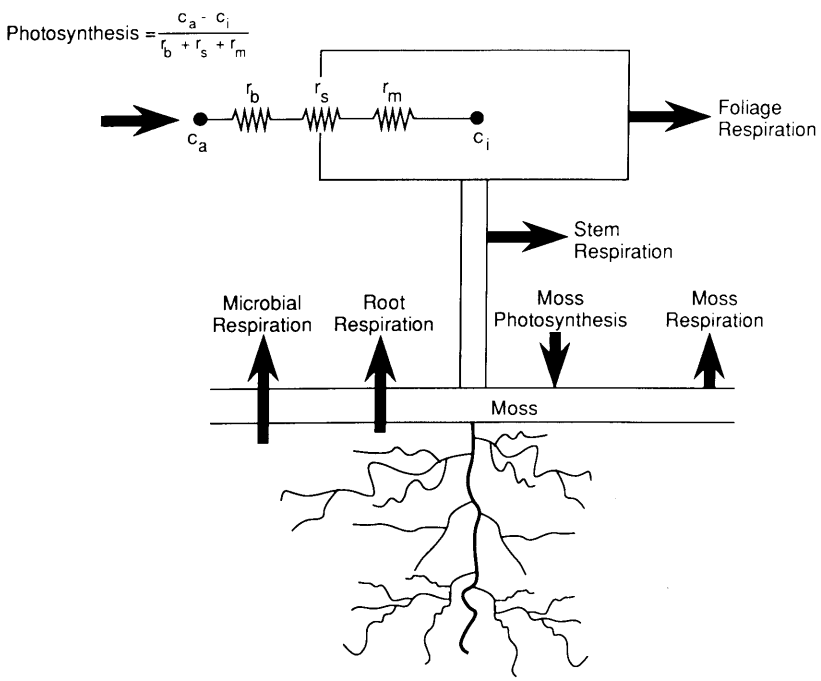

Fig. 1. CO_2 fluxes simulated by the model. Tree CO_2 fluxes are calculated separately for foliage photosynthesis and foliage, stem, and root respiration. Moss CO_2 fluxes are calculated separately for photosynthesis and respiration. Ecosystem flux is the sum of the tree, moss, and microbial CO_2 fluxes.

the three unknown temperatures. Then, with ground surface temperature, evapotranspiration, and snow melt known, soil temperature and soil moisture in a multi-layer soil are updated.

Required stand parameters for this model are: canopy height, leaf area index, foliage nitrogen, forest floor mass and nitrogen, moss and humus thickness, and green moss, tree sapwood, and tree root biomass. Site parameters are: aspect, slope, elevation, drainage, and soil color. Based on observed stand and soil descriptions, these parameters were estimated for the 23 stands previously described. Using daily-averaged parameters for a "typical meteorological year", simulated solar radiation, soil temperature, foliage water potential, evapotranspiration, and snow melt were consistent with observed data (Bonan, 1991a). Simulated annual soil respiration, moss production, forest floor decomposition, and aboveground tree production were also consistent with observed data (Bonan, 1991b). The model also simulates the appropriate seasonal dynamics of carbon uptake and release. The seasonal cycle of the Normalized Difference Vegetation Index, which is thought to reflect canopy photosynthesis (Sellers, 1985; Tucker et al., 1986; Running and Nemani, 1988), accounted for 85% of the seasonal variation in simulated tree photosynthesis (Bonan, 1991c).

2.3. *Simulation analyses*

The model was driven with observed meteorological data and atmospheric CO_2 concentrations for the period 1974 to 1982 to simulate interannual variability in the metabolic activity of the 23 forest ecosystems. For a given year, the seasonal amplitude in metabolic activity was defined as the deviation of maximum daily ecosystem CO_2 uptake and maximum daily ecosystem CO_2 loss about the mean daily CO_2 flux for that year. This is consistent with the definition of seasonal amplitude in atmospheric CO_2 concentrations used by Bacastow et al. (1985) and Keeling et al. (1985), except they used CO_2 concentration rather than flux.

The simulations were limited to a nine year period because of the availability of atmospheric CO_2 data, but also because the simulated CO_2 fluxes depend on the biomass and nutrient characteristics of the forests. Bonan's (1991b) model is a static canopy model in which biomass and nutrient availability are not updated at the end of the growing season. Thus, over the nine years of simulation the parameters that described the biomass and nutrient status of the forests were held constant to the values given in Bonan (1991a, 1991b). This is a reasonable assumption because (1) the 23 forests are all mature stands in which changes in forest structure and the forest floor occur slowly and (2) demographic processes such as mortality and regeneration become important only at time scales of ten years or longer.

Ambient CO_2 concentration is required to simulate tree photosynthesis (cf. Bonan, 1991b). Peterson et al. (1986) published observed CO_2 concentrations at Barrow from 1974 to 1982. Over this nine year period, mean annual CO_2 concentration at Barrow increased from 333 to 343 ppm (Fig. 2). These mean annual concentrations were used to drive the model in response to increasing atmospheric CO_2 concentrations.

Required surface meteorological parameters for the model are: air temperature, precipitation, cloudiness, relative humidity, wind speed, and air pressure. Daily air temperature and precipitation for the period 1974 to 1982 were obtained from the National Oceanic and Atmospheric Administration's co-operative data for Fairbanks (NOAA, 1987). This record does not include daily cloudiness, relative humidity, wind speed, and air pressure. For these parameters, data for a "typical meteorological year", as described in Bonan (1991a, 1991b), were used. Thus, the simulations

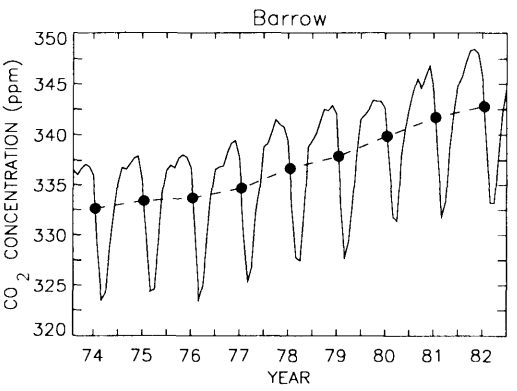

Fig. 2. Monthly atmospheric CO_2 concentration at Barrow from 1974 to 1982. Solid circles indicate mean annual concentrations used to drive the model. Tick marks indicate 6 month intervals from 1 January 1974 to 31 December 1982. Data are from Peterson et al. (1986).

examined the effects of only ambient CO_2, air temperature, and precipitation on metabolic activity.

To isolate whether the simulated interannual changes in metabolic activity were due to the increase in annual atmospheric CO_2 concentration or due to interannual climate variability, a second analysis was performed in which ambient CO_2 was held at 337 ppm for the nine year period (i.e., the average of the observed data). Additional analyses examined the sensitivity of the simulated trends in metabolic activity to the assumption of constant cloudiness, relative humidity, air pressure, and wind speed from year-to-year.

The snowpack, soil temperature, and soil moisture profiles must be initialized for each of the 23 stands with data appropriate for 1 January 1974. These initial conditions were obtained based on appropriate start-up conditions for 1 October 1973 (cf. Bonan, 1991a, 1991b). Observed daily weather data for 1 October to 31 December 1973 were then used to simulate initial conditions appropriate for 1 January 1974.

For the purposes of the current analyses, it is important to note how atmospheric CO_2 affects the simulated CO_2 fluxes. The simulated moss and microbial CO_2 fluxes are independent of ambient CO_2. While moss photosynthesis might be expected to increase with higher CO_2 concentrations, net CO_2 uptake by mosses represents

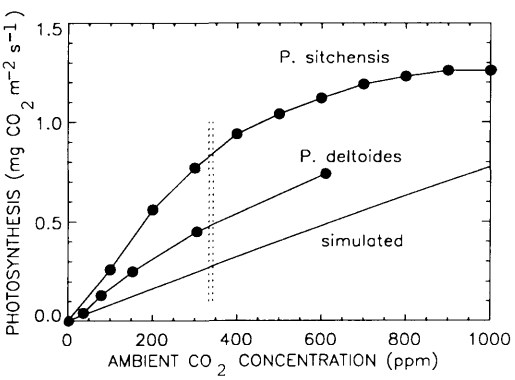

Fig. 3. Observed and simulated gross photosynthesis as a function of ambient CO_2. Observed data are for unstressed *Picea sitchensis* and *Populus deltoides* and were taken from Beadle et al. (1981) and Regehr et al. (1975), respectively. Simulated data are based on the parameters and equations given in Bonan (1991b) for an unstressed tree (i.e., with a resistance to CO_2 diffusion of 2000 s m^{-1}). The vertical dashed lines indicate photosynthesis over the range 333 to 343 ppm.

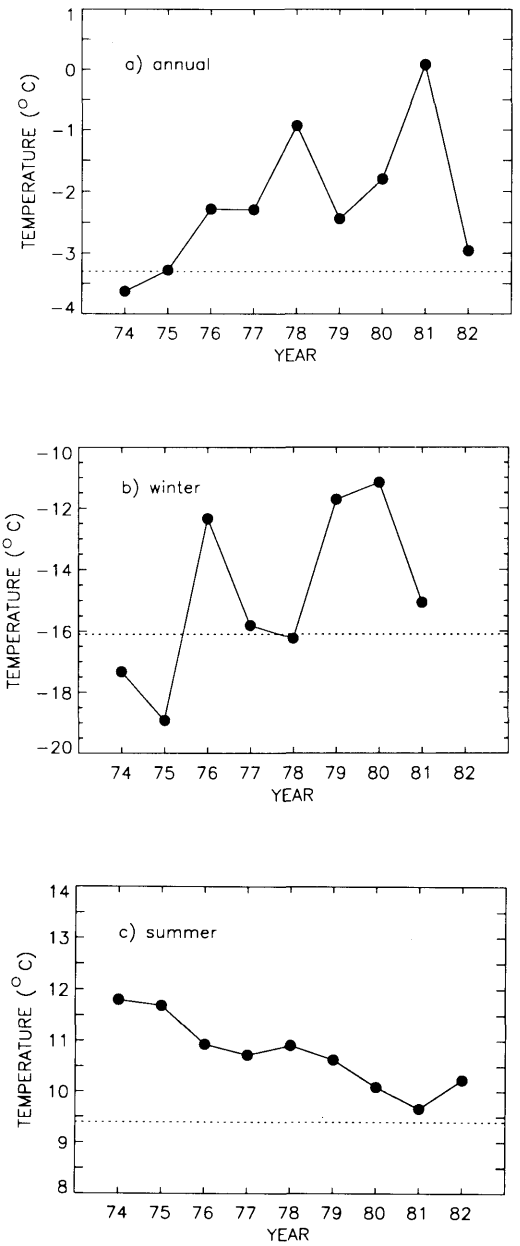

Fig. 4. Air temperature for Fairbanks from 1974 to 1982. Dotted lines indicate long-term means (Hare and Hay, 1974). (a) Mean annual air temperature. (b) Mean winter temperature. For a given year, winter was defined as October to December of the current year and January to March of the following year. (c) Mean summer temperature. Summer was defined as April to September of the current year.

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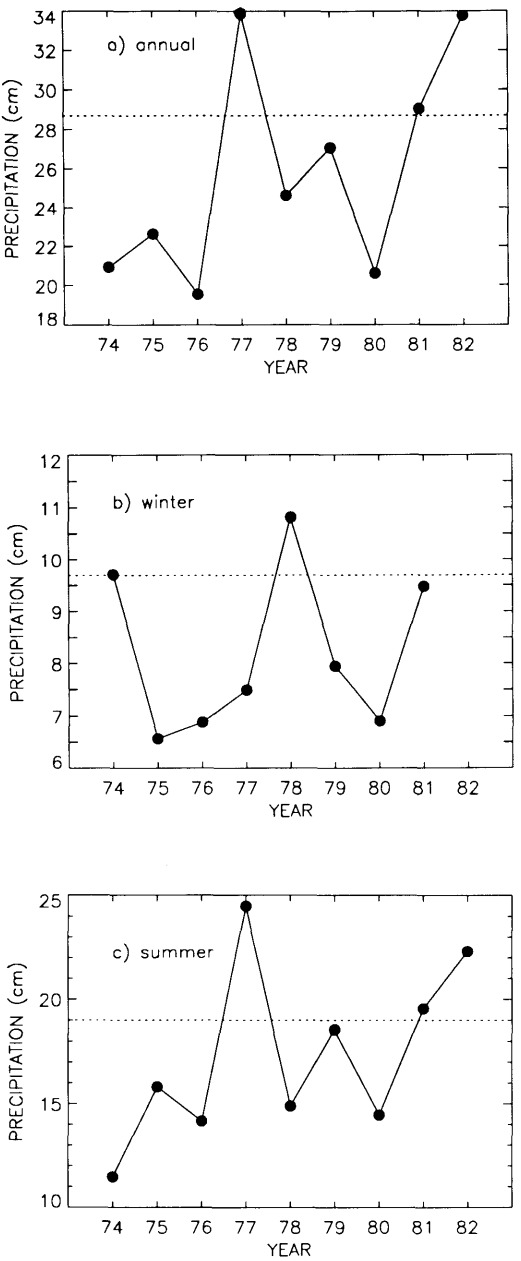

Fig. 5. Precipitation data for Fairbanks from 1974 to 1982. Dotted lines indicate long-term means (Hare and Hay, 1974). (a) Annual precipitation. (b) Winter precipitation. For a given year, winter was defined as October to December of the current year and January to March of the following year. (c) Summer precipitation. Summer was defined as April to September of the current year.

only 12% of the total CO_2 uptake by the 23 stands (Bonan, 1991b). Tree photosynthesis is directly proportional to the CO_2 diffusion gradient (Bonan, 1991b). Short-term experiments indicate that the rate of CO_2 assimilation increases asymptotically with higher ambient CO_2, reaching saturation at concentrations greater than 600 ppm (Fig. 3). Over the range of 0 to 1000 ppm, Bonan's (1991b) representation of photosynthesis results in a linear increase in photosynthesis with higher ambient CO_2. While this response is not consistent with the observed saturation response, over the range of 333 to 343 ppm the simulated rate of change of photosynthesis with respect to ambient CO_2 is consistent with observed data (Fig. 3).

2.4. Weather

Over the period 1974 to 1982, mean annual air temperature ranged from 0.3°C cooler to 3.4°C warmer than the long-term annual mean (Fig. 4a). The period 1976 to 1982 was 0.3 to 3.4°C warmer than average. This warming showed a pronounced seasonality in which most of the warming occurred in the months of October to March. From 1976 to 1981, these months were warmer than average, by as much as 5°C (Fig. 4b). The months of April to September were 0.3 to 2.4°C warmer than average over the period 1974 to 1982. Summer temperature decreased during this period (Fig. 4c).

There were no discernable trends in precipitation over the period of record. Annual precipitation ranged from 92 mm below average to 51 mm above average (Fig. 5a). Winter precipitation ranged from 31 mm drier to 11 mm wetter (Fig. 5b). Summer precipitation ranged from 75 mm drier to 55 mm wetter (Fig. 5c).

3. Simulated CO_2 fluxes

Monthly tree, moss, microbial, and ecosystem CO_2 fluxes averaged over the 23 stands are shown in Fig. 6 for the simulations in which ambient CO_2 increased from year-to-year. Over the period 1974 to 1982, these fluxes showed a regular seasonal cycle in which metabolic activity was low during the winter months and increased during the summers. Based on linear regressions of CO_2 flux versus time, over the nine years of simulation annual CO_2 uptake by trees increased by (slope $\pm$ SE) 9690 ± 1092 mg CO_2 m^{-2} $year^{-1}$ $year^{-1}$. This

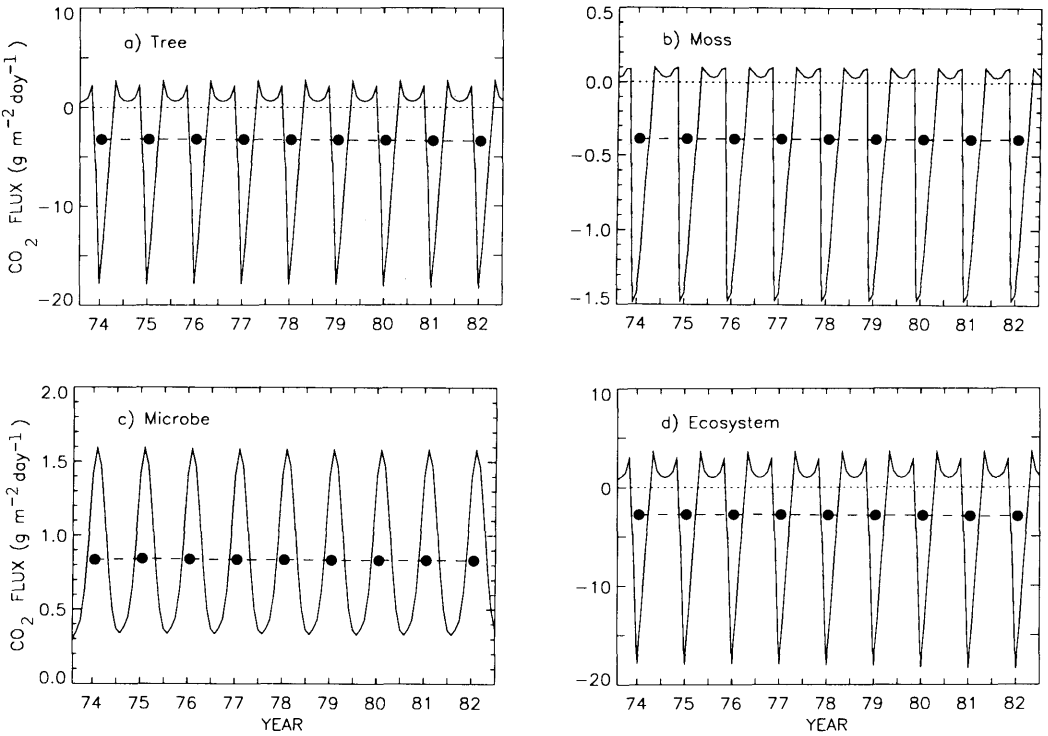

Fig. 6. CO_2 fluxes averaged over the 23 stands for simulations in which ambient CO_2 concentration increased yearly. Solid lines indicate mean daily fluxes for each month. Solid circles indicate mean daily fluxes for each year. Negative fluxes indicate CO_2 uptake. Tick marks indicate 6 month intervals from 1 January 1974 to 31 December 1982. (a) Net tree flux, i.e., the difference between photosynthesis and the respiration fluxes. (b) Net moss flux. (c) Microbial respiration. (d) Ecosystem flux, i.e., the difference between CO_2 uptake during tree and moss photosynthesis and CO_2 loss during tree, moss, and microbial respiration.

reflected an increase in annual CO_2 uptake during photosynthesis of 9305 ± 1211 mg CO_2 m^{-2} $year^{-1}$ $year^{-1}$. Total CO_2 loss from foliage, stem, and root biomass during maintenance and growth respiration was unchanged (-386 ± 378 mg CO_2 m^{-2} $year^{-1}$ $year^{-1}$). Annual net CO_2 uptake by moss did not change significantly over time (4 ± 16 mg CO_2 m^{-2} $year^{-1}$ $year^{-1}$). Annual microbial respiration decreased by 415 ± 110 mg CO_2 m^{-2} $year^{-1}$ $year^{-1}$. The net effect of these fluxes was an increase in annual ecosystem CO_2 uptake of $10{,}100 \pm 1168$ mg CO_2 m^{-2} $year^{-1}$ $year^{-1}$.

Maximum daily ecosystem CO_2 uptake, based on a 5-day average, consistently occurred from 30 June to 4 July over the 9-year record (Fig. 7). Maximum daily ecosystem CO_2 loss always occurred from 28 September to 2 October (Fig. 7). Over the nine year period, the deviation of maximum daily ecosystem CO_2 uptake from the

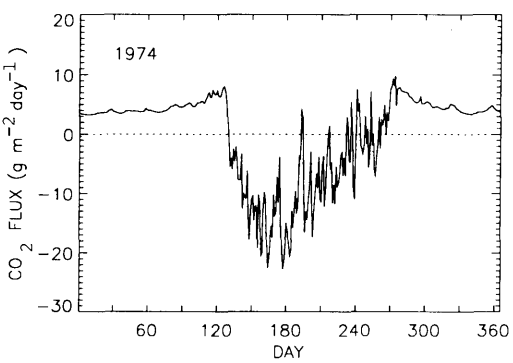

Fig. 7. Daily ecosystem CO_2 flux averaged over the 23 stands from 1 January 1974 to 31 December 1974. Ecosystem flux is the difference between CO_2 uptake during tree and moss photosynthesis and CO_2 loss during tree, moss, and microbial respiration. Fluxes are expressed as a deviation from the mean annual flux (-2.73 g CO_2 m^{-2} day^{-1}). A negative flux indicates CO_2 uptake.

annual mean daily flux increased by 120 ± 8 mg CO_2 m^{-2} day^{-1} $year^{-1}$ (Fig. 8). The deviation of maximum daily ecosystem CO_2 loss from the annual mean increased by 22 ± 1 mg CO_2 m^{-2} day^{-1} $year^{-1}$ (Fig. 8). The seasonal amplitude in metabolic activity, defined as the difference between maximum daily ecosystem CO_2 uptake and maximum daily ecosystem CO_2 loss, increased by 142 ± 8 mg CO_2 m^{-2} day^{-1} $year^{-1}$, or 0.52 ± 0.03 % $year^{-1}$ relative to 1974 (Fig. 8).

When ambient CO_2 was constant from year-to-year, annual tree photosynthesis and respiration decreased by 4181 ± 338 and 2327 ± 309 mg CO_2 m^{-2} $year^{-1}$ $year^{-1}$, respectively. Ecosystem CO_2 uptake decreased by 1445 ± 572 mg CO_2 m^{-2} $year^{-1}$ $year^{-1}$. When the annual decrease was removed (i.e., expressed as a deviation about the mean daily flux), maximum daily ecosystem CO_2 uptake increased by 17 ± 1 mg CO_2 m^{-2} day^{-1} $year^{-1}$. Maximum daily ecosystem CO_2 loss decreased by 5 ± 1 mg CO_2 m^{-2} day^{-1} $year^{-1}$. The seasonal amplitude increased by 12 ± 2 mg CO_2 m^{-2} day^{-1} $year^{-1}$, or 0.04 ± 0.01 % $year^{-1}$, relative to 1974.

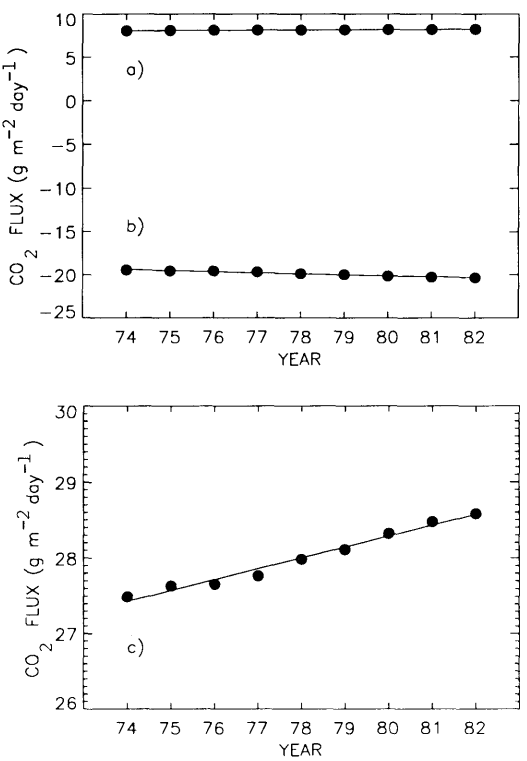

Fig. 8. Extreme annual ecosystem CO_2 fluxes and the seasonal amplitude. For each year, extreme fluxes were defined as the deviation of daily ecosystem CO_2 flux, based on 5-day averages, from the mean daily flux for that year (i.e., after the annual increase in ecosystem flux was removed). (a) Maximum CO_2 loss. (b) Maximum CO_2 uptake. (c) Amplitude, i.e., the difference between the maximum CO_2 loss and the maximum CO_2 uptake.

4. Discussion

The seasonal amplitude of atmospheric CO_2 concentrations measured at Mauna Loa and Ocean Weather Station P has significantly increased by 0.45 to 0.75 % $year^{-1}$ and 0.79 % $year^{-1}$, respectively (Table 1). The current analyses show that year-to-year differences in mean annual atmospheric CO_2 concentration, daily air temperature, and daily precipitation can produce an increased seasonal amplitude of metabolic activity in boreal forests that is consistent with the observed increase in the seasonal amplitude of atmospheric CO_2, and that CO_2 fertilization has a causal role. Without an annual increase in atmospheric CO_2 concentration, interannual variability in air temperature and precipitation caused the seasonal amplitude of ecosystem CO_2 flux to increase by 0.04 ± 0.01 % $year^{-1}$, relative to 1974, for the period 1974 to 1982. With higher ambient CO_2 concentrations, the amplitude increased by 0.52 ± 0.03 % $year^{-1}$. This increased seasonal amplitude was primarily due to increased summer drawdown during tree photosynthesis: while maximum daily CO_2 uptake increased by 120 ± 8 mg CO_2 m^{-2} day^{-1} $year^{-1}$, maximum daily CO_2 loss increased by only 22 ± 1 mg CO_2 m^{-2} day^{-1} $year^{-1}$. Over the range of ambient CO_2 concentration from 333 to 343 ppm, the simulated sensitivity of photosynthesis to higher CO_2 was consistent with observed data (Fig. 3), indicating that the simulated response to higher CO_2 concentrations is real.

While these analyses indicate boreal forests contribute to the increasing seasonal amplitude of atmospheric CO_2, this does not necessarily mean that boreal forests are a major contributor to interannual CO_2 variation. The occurrence of El Niño events also affects atmospheric CO_2 (Bacastow, 1976; Bacastow et al., 1980, 1985; Gammon et al., 1985; Komhyr et al., 1985; Thompson et al., 1986;

Conway et al., 1988; Keeling et al., 1985, 1989a), either through temperature dependent changes in solubility that cause oceanic CO_2 to be released during warmer El Niño events (Bacastow et al., 1980; Gammon et al., 1985; Komhyr et al., 1985; Keeling et al., 1989a) or through El Niño-related climatic changes that affect photosynthesis and respiration in terrestrial ecosystems (Keeling et al., 1989a; Elliot et al., 1991; Marston et al., 1991).

Moreover, the annual increase in maximum daily CO_2 uptake, which caused the higher seasonal amplitude in metabolic activity, was so small (120 mg CO_2 m^{-2} day^{-1}) that it may be very sensitive to the assumption of no inter-annual variability in daily cloudiness and relative humidity. When daily cloudiness and daily relative humidity were changed by $\pm 1.5\%$ and $\pm 2.5\%$ from values for a "typical meteorological year", the change in maximum daily CO_2 uptake from that of a "typical meteorological year" ranged from 113 to 121 mg CO_2 m^{-2} day^{-1} (Table 2). Maximum CO_2 uptake was not sensitive to the likely range of air pressure and was only sensitive to large changes in wind speed (Table 2). This sensitivity to small changes in cloudiness and relative humidity prevent the quantification of their effects on metabolic activity over the period 1974 to 1982. For example, with a maximum daily cloudiness of 10 tenths, the absolute change in cloudiness is at most ± 0.1 tenth, which may be beyond sampling accuracy. Likewise, with a maximum daily relative humidity of 100%, the absolute change is at most $\pm 2.5\%$.

Table 2. *Sensitivity of maximum daily ecosystem CO_2 uptake to changes in daily cloudiness, relative humidity, wind speed, and air pressure*

Percent change in meteorological parameter	Change in maximum daily ecosystem flux (mg CO_2 m^{-2} day^{-1})
cloudiness†	
+1.5%	−118
−1.5%	+113
relative humidity†	
+2.5%	+115
−2.5%	−121
wind speed†	
+60%	−120
−55%	−143
air pressure‡	
+5%	+16
−5%	+3

Data are deviations from a control simulation for a "typical meteorological year". Maximum daily ecosystem CO_2 uptake is a 5-day average for the 23 stands. A positive deviation indicates greater uptake than in the control simulation.

† Minimum change needed to produce a change in maximum daily ecosystem CO_2 uptake of approximately 120 mg CO_2 m^{-2} day^{-1}.

‡ Response to a prescribed change of $\pm 5\%$.

While it is impossible to rule out year-to-year changes in cloudiness or relative humidity that might obscure the signal produced by CO_2, air temperature, and precipitation, these analyses provide some important insights to the CO_2 fertilization debate. First, the annual atmospheric CO_2 growth increment that caused the increased amplitude in metabolic activity was small, only 1.1 ppm $year^{-1}$ on average (Fig. 2). Most studies of the photosynthetic response of plants to higher ambient CO_2 have focused on large (350 to 700 ppm) increases in CO_2 (Eamus and Jarvis, 1989). The current simulations indicate that more attention should be focused on the response of vegetation to small changes in CO_2 concentrations.

Second, much of the CO_2 fertilization debate has concerned how or whether the laboratory growth increment will be realized in the field (Strain and Cure, 1985; Kienast and Luxmoore, 1988; Eamus and Jarvis, 1989; Bazzaz, 1990; Graumlich, 1991; Mooney et al., 1991; Woodward et al., 1991). The current simulations identify higher tree production as a causal factor in the observed increased seasonal amplitude. However, the growth increase was small: average aboveground tree production for the 23 stands increased by only 3 g DM m^{-2} $year^{-1}$ $year^{-1}$, or 0.8% of the observed aboveground tree production (Van Cleve et al., 1983a). Aboveground tree biomass averages 11,372 g DM m^{-2} for these stands (Van Cleve et al., 1983a). Moreover, the standard error of mean aboveground tree production ranges from 17 g DM m^{-2} $year^{-1}$ in black spruce stands to

206 g DM m^{-2} $year^{-1}$ in balsam poplar stands (Van Cleve et al., 1983a). Against this background, the simulated tree growth increase was neither very measurable nor very large.

The small increase in tree growth that produced the amplitude change suggests that the increasing amplitude can occur without large changes in net primary production, nutrient availability, or nutrient use efficiency. For example, the nitrogen needed to support the simulated tree growth increment is minor. Assuming a carbon fraction of 0.45 for tree biomass, observed data for these stands indicate that the carbon-to-nitrogen (C:N) ratio for aboveground tree biomass averages 213:1 (Van Cleve et al., 1983a). To preserve this ratio given a 3 g DM m^{-2} $year^{-1}$ increase in annual aboveground tree production requires an additional uptake of only 6 mg N m^{-2} $year^{-1}$. For comparison, the observed annual nitrogen requirement for aboveground biomass production is 3.4 g N m^{-2} $year^{-1}$ (Van Cleve et al., 1983a). Moreover, trees show a large degree of plasticity in terms of growth and development, and the large range in C:N ratios (Van Cleve et al., 1983a) should allow trees to absorb this growth increment without any additional nitrogen. If no additional nitrogen was available to support the additional growth, the C:N ratio for aboveground biomass would increase by only 0.03%.

There are some interesting similarities between the atmospheric CO_2 concentrations recorded at Barrow and the simulated ecosystem CO_2 flux. For example, the Barrow record shows within-day CO_2 variations of up to 50% of the annual range and day-to-day variations of 15 to 50% of the annual range (Halter and Peterson, 1981). Over the nine years of simulation, daily ecosystem CO_2 flux showed maximum day-to-day variations equal to 38% of the annual range in daily ecosystem CO_2 flux. Moreover, when the annual increases in atmospheric CO_2 at Barrow and the simulated ecosystem flux were removed, monthly ecosystem flux was significantly correlated with atmospheric CO_2 with a lag of two months and accounted for 93% of the variation in atmospheric CO_2 at Barrow from 1974 to 1982 (Fig. 9). The 2-month lag occurs because monthly ecosystem CO_2 uptake was greatest during June and declined during the remaining summer months, whereas CO_2 drawdown at Barrow increased from June to August, reaching maximum drawdown in August.

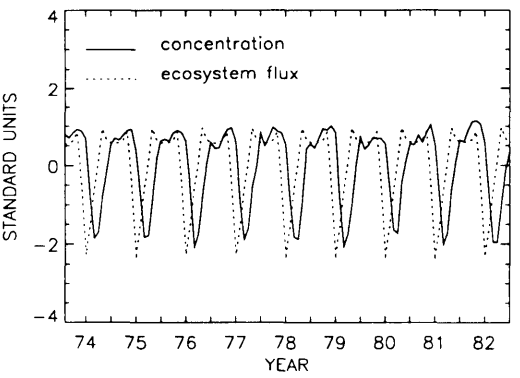

Fig. 9. Monthly atmospheric CO_2 concentration at Barrow and simulated ecosystem CO_2 flux. The annual increase in atmospheric CO_2 and ecosystem flux was removed from both data sets. Each data set was then standardized by subtracting the mean and dividing by the standard deviation. CO_2 concentration was significantly correlated with CO_2 flux with a lag of two months ($C_t = 0.96F_{t-2}$, $F = 1304$, $n = 106$, $\alpha < 0.001$, $r^2 = 0.93$).

Coupled models of biosphere CO_2 flux and atmospheric transport show a similar one to two month lag between maximum CO_2 uptake by high-latitude ecosystems and maximum drawdown in atmospheric CO_2 concentration at Barrow (Pearman and Hyson, 1980; Fung et al., 1983, 1987; Fung, 1986; Heimann et al., 1989).

However, the similarities between the Barrow data and ecosystem flux appear to be spuriously caused by the seasonal cycles of atmospheric CO_2 and ecosystem CO_2 flux. For example, over the nine year period ecosystem CO_2 flux for the months of January and July was not significantly correlated with CO_2 concentration at a 2 month lag (January: $F = 0.06$, $n = 9$, $r^2 = 0.01$, $\alpha > 0.05$; July: $F = 1.5$, $n = 9$, $r^2 = 0.18$, $\alpha > 0.05$). Moreover, whereas the seasonal amplitude of ecosystem CO_2 flux increased, two analyses have not found a significant increase in the amplitude of atmospheric CO_2 at Barrow (Table 1). In addition, whereas the simulated ecosystem CO_2 flux did not exhibit large year-to-year variation, the annual rate of CO_2 increase at Barrow ranged from 0.3 to 2.0 ppm $year^{-1}$ (Peterson et al., 1986). Analyses of the Barrow CO_2 record indicate that winter and summer variability in CO_2 concentrations reflects synoptic scale atmospheric flow that

modifies local sources and sinks of CO_2 (Peterson et al., 1980; Halter and Peterson, 1981; Halter and Harris, 1983; Halter et al., 1985).

Most analyses of interannual variability in atmospheric CO_2 concentrations have used crude assumptions and parameterizations of biosphere metabolism (Pearman and Hyson, 1980; Fung et al., 1983, 1987; Fung, 1986; Tucker et al., 1986; D'Arrigo et al., 1987; Kohlmaier et al., 1989; Keeling et al., 1989a, 1989b; Heimann et al., 1989). The current analyses indicate that mechanistic models of photosynthesis and respiration can provide useful information and need to be combined with atmospheric transport models to provide realistic interpretations of atmospheric CO_2 concentrations, regional terrestrial CO_2 sources and sinks, and the major contributors to interannual variation in atmospheric CO_2.

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