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Abstract. There is debate on the potential release of the tundra's immense carbon stocks into the atmosphere in response to global warming. We present here results obtained with a model of CO_2 exchanges, coupled to a model of the soil thermal and hydrological regime in the tundra. We show that, because of the partial thawing of permafrost and subsequent increase in nutrient availability, the ecosystem's response to warming may be a long-lasting increase in C accumulation, following a temporary increase in CO_2 emissions. Our study also provides a consistent picture of CO_2 exchanges in tundra ecosystems, reconciling the short-term experimental response to warming, recent field measurements, and Holocene C accumulation estimates.

Introduction

Tundra ecosystems contain about 200 GtC, 80% of which is in the soil as partly decomposed organic matter (*Oechel and Vourlitis*, 1994). This is an amount equivalent to 27% of the present carbon content of the atmosphere. Therefore, a modification of carbon exchanges between the tundra and the atmosphere could significantly affect the atmospheric CO_2 concentration. Moreover, the increase in greenhouse gas concentrations resulting from human activities is expected to induce a larger increase in surface air temperature at high latitudes than at low latitudes (*Kattenberg et al.*, 1995).

Tundra's carbon cycle is particularly vulnerable to climate change because biological processes (e.g., decomposition, growth) are strongly affected by the presence of permafrost and the duration of the snow-free season. Although the possibly large impact of changes in active layer thickness (or depth to the permafrost) on arctic ecosystems has been recognized by several authors (*Miller et al.*, 1983; *Shaver et al.*, 1992), existing tundra models do not account for them (*Miller et al.*, 1983, 1984; *Rastetter et al.*, 1991; *Kane et al.*, 1991). We present here a new coupled model of CO_2 exchange and soil physics in the tundra and summarize the main results concerning the impact of climate change on tundra's C balance and its potential feedback on atmospheric CO_2 accumulation.

The model

The complete model consists of coupled biogeochemical and soil physics units. It is 1-dimensional (vertically, from the soil surface down to 20m) and has a time step of 1 day. It is designed to simulate average C fluxes on a regional scale and to be easily coupled to an atmospheric GCM with a grid of 2.5° x 2.5°. The soil physics unit, fully described in *Waelbroeck* (1993), computes the daily soil temperature and moisture content. Because the soil thermal coefficients are moisture dependent, soil moisture affects soil temperature, which in turn affects soil moisture through the changes in active layer thickness and drainage conditions. The mean annual runoff and drainage are implicitly accounted for by re-initializing the soil moisture content at the beginning of each year to a value which decreases as the depth to permafrost increases. This submodel is driven by the surface climatic conditions, by the leaf area index (LAI) and organic layer thickness. The LAI is taken as proportional to the leaf biomass, and the organic layer thickness is assumed to increase linearly with amounts of seasonally thawed soil organic matter. The biogeochemical submodel, which is described in *Waelbroeck and Louis* (1995), computes the daily C and N fluxes in the soil-plant-atmosphere system, as well as the biomass and soil C and N pools, as a function of the surface climatic conditions and soil temperature and moisture regime. This submodel includes a formulation of the relationship linking the active layer thickness to its C content and hence, to its effective decomposition and mineralization rates. In short, the complete model allows us to simulate not only the *direct* impact of a given climatic change on CO_2 exchange, but also the *indirect* impact resulting from the induced changes in the growing season length, snow cover, depth to the permafrost, and soil temperature and moisture.

The model has been validated by comparing computed and measured CO_2 fluxes in several sites on the Alaskan North Slope. Two different versions of the model, defined by a set of five biological parameters, correspond to the two main types of tundra, i.e., wet sedge and tussock tundra. Within a given tundra type, each site is defined by its geographical location and soil physical properties, i.e., the mineral soil texture, organic soil specific dry weight, and organic layer thickness at the beginning of the run (*Waelbroeck*, 1993). Fig. 1 shows computed and measured fluxes in two different wet sedge tundra sites and one tussock tundra site. In wet sedge sites, the measurements are too scarce to provide a test for the ability of the model to reproduce day to day variations in CO_2 fluxes. However, data from the tussock site (Fig. 1D) allowed us to verify that the model faithfully reproduces the measured CO_2 fluxes, not only at the seasonal scale, but also at shorter time scales (2-3 days). Furthermore, the comparison between measurements and simulations at Prudhoe Bay in 1990 and 1991 indicates that the interannual variability at a given site is also well reproduced. In conclusion, the very good agreement

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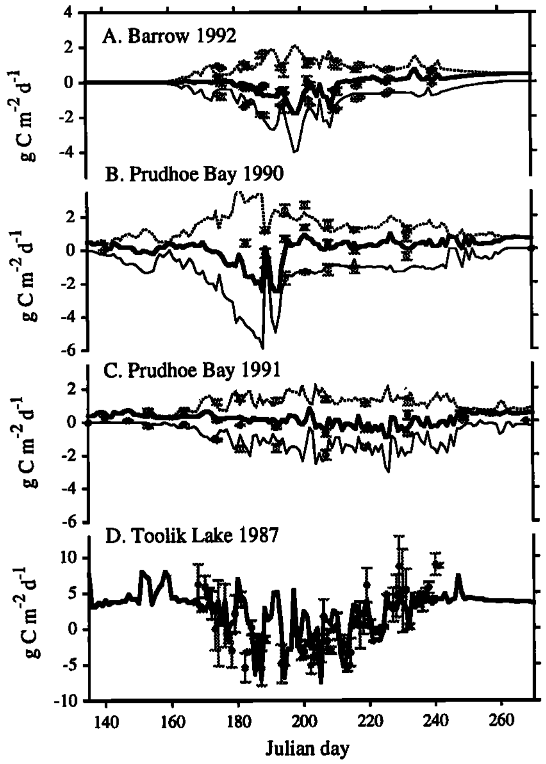

Figure 1. Computed and measured CO_2 fluxes. Continuous lines represent model results (······ plant respiration + decomposition, ▬ net flux, — photosynthesis), symbols represent the mean value and standard deviation of the fluxes measured in n chambers per site. A: Barrow (71°30'N, 156°78'W) in 1992, n = 2; - B: Prudhoe Bay (70°22', 148°45') in 1990, n = 6; - C: Prudhoe Bay in 1991, n = 4; - D: Toolik Lake (68°38', 149°35') in 1987, n=2. Positive fluxes are directed from the ecosystem toward the atmosphere. Measurements were made in wet sedge tundra sites using a portable ecosystem gas exchange system (*Oechel*, 1992), and in Toolik Lake, using a CO_2LT chamber system (*Vourlitis et al.*, 1993).

obtained between computed and measured CO_2 fluxes, on time scales ranging from a few days to two successive years, shows that the processes responsible for CO_2 exchanges are correctly formulated for those time scales.

Results

Response to a step increase in air temperature

We first describe the response to a 3°C step increase in air temperature. Although this case is not realistic, it gives useful insight into the processes triggered by an increase in temperature. The model simulates an increase in CO_2 emissions during approximately the first 5 years, followed by a long-lasting increase in CO_2 uptake (Fig. 2, coupling ON). Decomposition first increases more than net primary production (NPP) in response to increased temperatures. Subsequently, the thawing of the upper part of permafrost and concomitant deepening of the active layer (Fig. 2) releases organic matter, making it available to decomposers. Because the soil C/N ratio (≈ 18) is much lower than the average tundra plant C/N ratio (≈ 30 to 40) (*Shaver et al.*, 1992), and because the level of nutrients available in the tundra is essentially controlled by mineralization of soil organic matter (SOM) (*Nadelhoffer et al.*, 1991), decomposition of additional SOM can substantially increase the mineral N pool. Moreover, tundra ecosystems are currently nutrient-limited (*Shaver and Kummerow*, 1992), and thus an increase in mineral N stocks leads to an increase in NPP if the climatic conditions are favorable. The contrast between short-term and long-term responses comes from the fact that the total mineralization rate does not evolve proportionally to the total decomposition rate because soil organic matter pools of low C/N ratios contribute more to mineralization than pools of higher C/N ratios. Assuming that the permafrost volumetric C content is equal to the average volumetric C content of the active layer (the upper *permafrost* contains about 130 kg C m^{-2}; *Brown and Tedrow*, 1996) and that the C/N ratio of the permafrost SOM is equal to that of the active layer bottom SOM (i.e., ≈ 18), we estimate the net effect of a 3°C air temperature increase on the C budget after 50 years to be a C fixation of about 210 g C m^{-2}. This effect could be somewhat smaller if better drainage results in increased N losses to aquatic and marine systems.

Not accounting for the coupling between soil physics and biogeochemical cycles has drastic consequences on this response (Fig. 2, coupling OFF): the net effect of a 3°C warming is then a *loss* of 30 g C m^{-2} after 50 years. Note that the increase in active layer thickness is about twice as large in

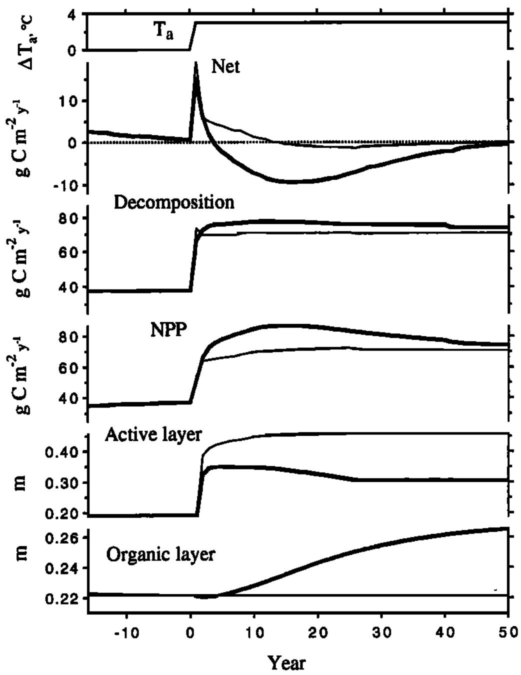

Figure 2. Response to a 3°C step increase in air temperature. In order to reach a quasi-equilibrium, the model is first run for 100 years under constant climatic conditions given by climatological data averaged over 1921-1990 at Barrow. The air temperature is then increased by 3°C. A - Coupling ON: the biogeochemical and soil physics units are coupled, as described in the text. B - Coupling OFF: variations of the active layer thickness do not induce any transfers of SOM between the permafrost and the active layer, nor any changes in drainage conditions; the LAI, organic layer thickness and soil thermal coefficients remain constant.

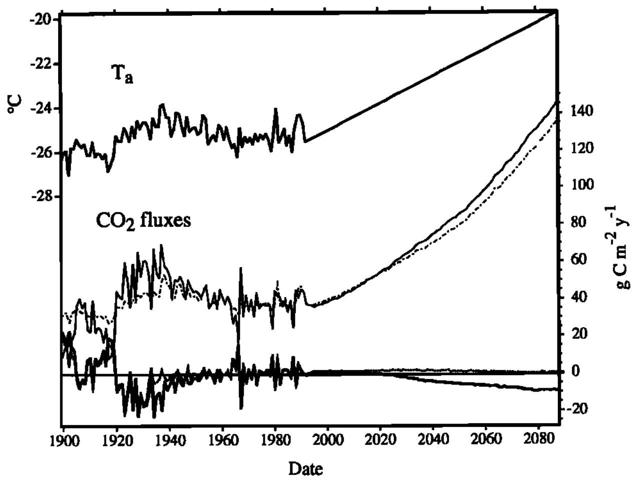

Figure 3. Simulation obtained by forcing the model with annual mean temperatures and using the seasonal pattern given by the climatology. The model is first initialized by a 20-year run under constant climatic conditions, the temperature being the measured annual mean temperature averaged on the latitudinal band 64-90°N over 1880-1900 (*Hansen and Lebedeff*, 1987). From 1900 to 1992, the model is forced with annual mean temperature averaged on the latitudinal band 64-90°N (*Hansen and Lebedeff*, 1987; *Angell*, 1994). From 1993 on, the model is submitted to a steady air temperature increase of 0.06 °C y^{-1}. A - Coupling ON (— · — decomposition, ▬ net flux, — NPP), B - Coupling OFF (······ net flux).

this latter case than in the coupled run because the LAI shading effect resulting from increased biomass, and the organic layer insulating effect caused by increased litter input (*Dyrness*, 1982; *Waelbroeck*, 1993) are suppressed.

Response to the XXth century temperature anomalies

Based on temperature records, we have calculated the CO_2 fluxes for the period 1900-1992 (Fig. 3A). This scenario allows us to verify that the model reproduces the net CO_2 source observed from 1983 to 1992 on the Alaskan North Slope (*Oechel et al.*, 1993), and leads us to use the model to simulate the CO_2 fluxes' response to a progressive increase in temperature over the next century. From 1900 to 1920, because of low air temperatures, the simulated NPP and plant N uptake are low. Because mineral N stocks in tundra ecosystems are determined by the balance between mineralization and plant uptake (*Nadelhoffer et al.*, 1991), these nutrient stocks tend to increase when poor climatic conditions keep plant uptake lower than mineralization. Therefore, after 1920, the computed mineral N stocks are sufficient to allow NPP to increase in response to increasing temperatures, and thus creating a net CO_2 sink. From 1920 to about 1940, the annual N uptake is larger than the annual mineralization so that the simulated soil mineral N decreases until it becomes too low to sustain the plant N uptake rate determined by the climatic conditions. After 1940, our results indicate that the ecosystem becomes nutrient-limited, i.e., the climatic conditions would lead to higher photosynthesis and NPP than permitted by nutrient availability, so that NPP levels are actually controlled by the mineralization rate. This situation persists until the warming leads to sufficient thawing of the permafrost and subsequent increase in mineralization. Hence, our results suggest that the response of the net CO_2 flux to climatic changes depends on the ecosystem's current nutrient status, which is itself determined by the climate of the previous decades. A comparison of Fig. 3A and 3B also shows that the impact of the variations in the active layer thickness on the biological processes contributes to increase the net CO_2 flux decadal variability.

In addition, Fig. 3A shows that, as a result of this large interannual and decadal variability, the long-term response of the net CO_2 flux to climate change can be masked during certain periods. Accordingly, although the temperature has been increasing over the last century in northern Alaska (*Lachenbruch et al.*, 1986; *Chapman and Walsh*, 1993), simulations predicting an increase in C fixation, shortly after the onset of warming (*Rastetter et al.*, 1991; this work) appear consistent with the net CO_2 source observed from 1983 to 1992 on the Alaskan North Slope (*Oechel et al.*, 1993). Because the model in this example is forced by air temperatures alone and all other climatic inputs are kept constant, we do not expect that the simulated fluxes should faithfully reproduce the measurements. However, as tundra's net CO_2 flux is more sensitive to air and soil surface temperature than to solar radiation or precipitation (*Waelbroeck and Louis*, 1995), the present results should capture the main features of the C dynamics simulated with a full set of climatic inputs. Equally important, sensitivity tests showed that these results are robust with respect to the initial conditions. Thus, even though we do not have flux data sets long enough to thoroughly validate the model over 10 to 50 years, the fact that it has been validated over seasonal and interannual time scales, and that it successfully reproduces a net CO_2 source from 1983 to 1992, speaks for its ability to correctly simulate the ecosystem's dynamic behavior on periods ranging from 1 to about 100 years. Still, our model, like other existing models of gas exchange in the tundra, does not simulate vegetation dynamics, and therefore the correctness of our simulations relies on the hypothesis that the changes in vegetation composition that might occur over the duration of the simulations would have no major impact on the average C and N fluxes.

The simulated response to a progressive increase in temperature, starting in 1993 (Fig. 3A) indicates that the long-term increase in C storage described in the case of a step increase in temperature also occurs in the case of a gradual warming. Here again, the absence of coupling transforms the net CO_2 flux cumulated over the duration of the warming experiment, from a significant sink to a weak source.

Discussion and conclusion

The simulated short-term increase in CO_2 emissions is supported by earlier modeling and experimental studies (*Billings et al.*, 1982; *Rastetter et al.*, 1991). A long-term response similar to the one we obtain with our coupled model has also been obtained with a biogeochemical model that includes a parameterization of the C/N ratio's response to environmental conditions (*Rastetter et al.*, 1991), but does not account for the coupling between the C and N cycles and the soil physics. In both studies, the mechanisms described (i.e., the impact of changes in the C/N ratio, or in the depth to permafrost) increase the ecosystem's capacity to fix atmospheric CO_2. In the real world, one therefore expects that the combination of these two processes should lead to an even higher ecosystem's fixing capacity.

Finally, our results can be compared to data on past climates. Measurements of soil C accumulation rates in northern Alaska during the mid- and late-Holocene (from about 7000 to 500 BP) indeed demonstrate that higher soil C accumulation rates correspond to warmer climatic conditions (*Marion and Oechel*, 1993). However, it is unclear whether this is directly caused by climate, or to altered vegetation and soils. Because our model does not simulate vegetation dynamics, our results suggest that climate change alone could explain the observed change in soil C accumulation rate between the warmer mid-Holocene and colder late-Holocene. Thus, the present study provides a coherent link between short-term experimental results and measurements of accumulation rates during the recent geological past.

In conclusion, our simulations are consistent with the short-term experimental response to warming, recent field measurements, and Holocene C accumulation estimates. Our work shows that permafrost can play a decisive role with respect to C dynamics in the tundra. More specifically, we show that within the context of climatic decadal variability, the impact of the variations in the active layer thickness on the biological processes can contribute to increase the net CO_2 flux decadal variability. On the other hand, we show that, in the presence of a sustained warming, permafrost thawing may be responsible for a delayed long-lasting increase in C storage. The order of magnitude of the predicted sink can be assessed by extrapolating our estimate of the cumulated sink induced by a 0.06°C y^{-1} warming over 100 years to the entire tundra biome. This leads to a total sink of only ≈ 2.9 GtC, an amount equal to 1% of the expected increase in atmospheric C (if its present accumulation rate remains constant). Therefore, despite initial outgasing of CO_2, tundra's response to warming may ultimately exert a modest negative feedback on atmospheric C accumulation and cannot be invoked as a mechanism capable of compensating the anthropogenic CO_2 emissions. Improving present estimates of the future C balance in the tundra requires (1) long-term monitoring of CO_2 exchange, nutrient status, and depth to the permafrost in order to validate the computed active layer and ecosystem dynamics, (2) additional measurements of the amount and C/N ratio of organic matter located in the permafrost, (3) a better understanding CO_2 fertilization effects under elevated temperature and nutrient availability.

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