

Soil moisture regulates the biological response of elevated atmospheric CO₂ concentrations in a coupled atmosphere biosphere model

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Received 16 March 2005; received in revised form 5 February 2006; accepted 5 February 2006

Available online 23 June 2006

Abstract

Terrestrial biosphere models/land surface models are routinely used to study the effects of CO₂ doubling and climate change. The objective of this study is to show that the biological response associated with CO₂ doubling is important, and that the effects intrinsically depend on the soil moisture state. Therefore, using a coupled biosphere–atmosphere model, we tested the hypothesis that the biological effects of CO₂ changes in biosphere models are significantly coupled to the hydrological feedback via soil moisture availability in a terrestrial biosphere/land surface model. The results from a 15-day simulation of a photosynthesis-based land surface model, dynamically coupled to an atmospheric boundary layer and surface energy balance scheme, were analyzed to test the hypothesis. The objective was to analyze the biological effects of CO₂ doubling under high as well as limiting soil moisture conditions for prescribed changes to the vegetation/land use type. The approach was to analyze the results from a coupled land surface-atmosphere model obtained by changing the biome type for each run. Sensitivity for all of the nine global vegetation type changes, as defined through the Simple Biosphere Model ver. 2 (SiB2) land cover classification, were analyzed for evapotranspiration and net carbon assimilation. The results indicated that: (i) the soil moisture (and its interaction with CO₂) has a direct (first-order) effect on the biological effects of CO₂ changes and the terrestrial ecosystem response; (ii) the biological impacts associated with CO₂ changes in a biospheric model should be interpreted in consideration of the soil moisture status; and droughts or high soil moisture availability can enhance or completely balance or even reverse the effects associated with CO₂ changes; (iii) for each vegetation type, the model results indicated a different response to soil moisture and CO₂ changes; and resolving the direct and indirect effects explicitly, both C3 and C4 vegetation, appeared to be significantly affected by the biological effects of CO₂ changes, and (iv) the explicit coupling between soil moisture/hydrological state and the CO₂ changes need to be explicitly considered in projecting climate change impacts. The study results also indicated that feedback pathways can be efficiently determined by dissociating the direct and the interactive effects of CO₂ impacts.

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Keywords: Land–atmosphere interaction; CO₂ doubling; Soil moisture; Climate change; Net primary productivity

1. Introduction

Though a consensus exists that atmospheric CO₂ levels have been rising since the pre-industrial revolution, the effects of these changes are still under investigation. For example, [Diffenbaugh et al. \(2005\)](#) used a coupled

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regional climate model and showed that an increase in CO₂ levels can affect the severity of extreme precipitation and temperature patterns. Curtis and Wang (1998) performed a comprehensive meta-analysis of over 500 reports of elevated CO₂ impacts on plant response and concluded that enhanced CO₂ levels led to a significant increase in total biomass and plant net carbon assimilation rates. Levis et al. (2000) used a dynamic vegetation model to simulate climatic response to the radiative and biological effects of elevated CO₂ concentrations and associated simulated shifts in global vegetation patterns. Eastman et al. (2001) developed a regional-scale sensitivity study and concluded that the landuse land cover changes outweigh the CO₂ impacts and that biological impacts due to CO₂ changes are important and possibly even more dominant than the radiative effects of CO₂ changes in modulating the surface meteorology/regional climate.

Thus, the Levis et al. (2000) and Eastman et al. (2001) results suggest that the biological effects of CO₂ changes have a dominant impact on the terrestrial biosphere and should be considered in future regional climate studies. In this study, we further extend these analyses by testing the hypothesis that the simulated biological effects of the CO₂ changes are significant for different vegetation types used in land surface models and that the impact of CO₂ changes is intrinsically coupled with the hydrology via soil moisture availability. This assessment is important because the Curtis and Wang (1998) meta-analysis concluded that interacting stress, such as drought, had no effect on the magnitude of plant response under enhanced CO₂ conditions, while the Levis et al. (2000) results indicated that CO₂ fertilization can cause either an increase or a decrease in available soil moisture, depending on the associated changes in vegetation cover and the ability of the regional climate to recirculate water vapor. Thus, assessing the impact that soil moisture status can have on the modeled biological effects of CO₂ enhancement under different landuse/land cover conditions is the focus of this paper.

An analysis of field experiments and chamber studies also indicates that the effects of soil moisture availability on the impact due to CO₂ doubling are still uncertain. Data from experimental plots (Nie et al., 1992; Owensby et al., 1993; Clark et al., 1999) suggest that the photosynthesis response to the terrestrial ecosystem possibly correlates to soil moisture availability. Whereas some of the reported productivity assessments, such as Kimball's (1985), which evaluated 18 studies on enhanced CO₂ effects, concluded that on average, productivity is a function of soil moisture stress rather than free availability conditions. Studies such as Field et al. (1995) also suggested that a feedback exists between an increase in CO₂ and an increase in the soil moisture availability. This feature has been recorded in

some follow-up field experiments (Hungate et al., 1997; Niklaus et al., 1998; Jackson et al., 1998). Curtis and Wang (1998) speculated that increased CO₂ can lead to some reduction in the evapotranspiration and an increase in the photosynthesis. Such a combination can increase the water use efficiency (WUE) of the vegetated surface. Better WUE can increase the soil moisture storage for the vegetated surface (as seen in the field observations). However, higher soil moisture availability can often lead to higher evapotranspiration and eventually deplete itself through a feed forward loss mechanism. These observations suggest that soil moisture availability (and change) may affect the biological impacts of CO₂ changes on vegetation/biosphere response.

In controlling the biological effects on the terrestrial biosphere, leaf stomata occupy a central position in modeling and understanding the interactions (Jones, 1998). Therefore, CO₂-based biophysical models which consider explicit photosynthesis (stomatal conductance relations), dynamically coupled with the surface hydrology, provide a useful tool for addressing the issue of terrestrial responses to CO₂ doubling (Niyogi, 2000; Eastman et al., 2001; Zhan et al., 2003). In this study, we will use a coupled model to investigate the direct as well as the interactive effects of the soil moisture changes on the biological effects of CO₂ doubling for different landuse/vegetation types.

2. Experimental design

The experimental design considerations and tasks are as follows. The experiment should lead to a delineation of feedback processes that can be tested or compared with field or chamber-based observations; and the model results should *maintain* the impact or memory of the initial conditions on the coupled system. The approach involves the development of a hydrodynamically consistent model configuration followed by an alteration of the vegetation/biome type (as is done, for instance, in studies such as Copeland et al., 1996; Marshall et al., 2004).

We analyzed variations in the evapotranspiration (E_{tr}) and net carbon assimilation (A_n) rates using a coupled land surface model. The biophysical module is as such generic to the photosynthesis-based schemes coupled to land surface models and is similar to the parameterizations and scaling discussed in SiB2-Simple Biosphere Model, version 2; (Sellers et al., 1996a,b). The biophysical module was dynamically coupled with a prognostic two-soil layered soil moisture/soil temperature scheme (Noilhan and Planton, 1989), and an atmospheric boundary layer/meteorological model (Alapaty et al., 1997).

The vegetation module is based on the Ball–Woodrow–Berry stomatal model (Ball et al., 1987; Niyogi and

Raman, 1997) and the Collatz et al. (1991, 1992) photosynthesis scheme. The stomatal conductance (g_s) (inverse of stomatal resistance, R_s) is estimated as

$$g_s = m \cdot \frac{A_n \cdot rh_s}{C_s} + b$$

where A_n is the net carbon assimilation (photosynthesis) rate, rh_s is the relative humidity, and C_s is the CO_2 concentration at the leaf surface. The terms m and b are constants based on gas-exchange considerations (Ball et al., 1987) as a function of C3 or C4 vegetation and land use (Sellers et al., 1996a). The physiological variables such as A_n , C_s , and rh_s at the leaf surface are estimated using transpiration/photosynthesis relationships at the leaf scale.

Photosynthesis or carbon assimilation is taken as the residue of gross carbon assimilation (A_g) and loss due to respiration (R_d). Following Farquhar et al. (1980) and Collatz et al. (1991, 1992), A_g is taken as the minimum of three limiting rates: W_c , W_e , and W_s , which describe the assimilation rates as limited by the photosynthetic (Rubisco) enzyme efficiency, the amount of photosynthetically active radiation (PAR) captured by the leaf chlorophyll and the leaf capacity to transport or adopt the photosynthetic outcome.

The carbon assimilation limiting rates are estimated as a function of photosynthesis pathway. For C3 vegetation,

$$W_c = V_m \left\{ \frac{C_i - \Gamma}{C_i + K_c \cdot (1 + O_2/K_o)} \right\}$$

$$W_s = 0.5 V_m, \text{ and } W_e = PAR \cdot \varepsilon \cdot (1 - \omega_\pi) \cdot [(C_i - \Gamma)/(C_i + 2\Gamma)]$$

while for C4 vegetation,

$$W_c = V_m, \text{ } W_e = PAR \cdot \varepsilon \cdot (1 - \omega_\pi),$$

$$W_s = \frac{20,000 \cdot V_m \cdot C_i}{P}$$

In the above, V_m is the maximum catalytic Rubisco capacity for the leaf; C_i is the carbon dioxide concentration in the leaf intercellular spaces; Γ is the CO_2 compensation point (Collatz et al., 1992); O_2 is oxygen availability for the leaf; K_c and K_o are the Michaelis–Menten constant and the oxygen inhibition constant, respectively; PAR is the component of the total radiation available for photosynthetic activities; ε is the efficiency for carbon dioxide uptake; ω_π is the leaf-scattering coefficient for PAR (Sellers et al., 1996b); and P is the atmospheric pressure.

In the above, C_i is obtained through an iterative solution that includes net assimilation (A_n) and stomatal conductance (g_s). The respiration loss R_d is estimated following Calvet et al. (1998) as, $R_d = 0.11 A_m$ where A_m is the

maximum assimilation rate (Schulze et al., 1994) limited by mesophyllic conductance (g_m) as,

$$A_m = A_{m,max} \cdot \left\{ \frac{1 - \exp[-g_m \cdot (C_i - \Gamma)]}{A_{m,max}} \right\}$$

The mesophyllic conductance is related to the exchange potential for the ambient CO_2 , and it also provides a link between available soil moisture and evapotranspiration and their control on carbon assimilation. Thus g_m is parameterized as (Calvet et al., 1998),

$$g_m = g_{m,max} \cdot 2^{Q_t} \cdot \frac{1 + \exp(0.3(T_c - S_2))}{1 + \exp(0.3(S_1 - T_c))} \cdot \frac{(w_2 - w_{wilt})}{(w_{sat} - w_{wilt})}$$

where $g_{m,max}$ is typically $17.5 \times 10^{-3} \text{ ms}^{-1}$, Q_t is the ‘Q-10 term’ temperature-modulation of the biospherical characteristics, T_c is the surface temperature, S_1 and S_2 are land-use-based coefficients as described in Sellers et al. (1996a,b), and w_2 , w_{wilt} , and w_{sat} are the deep (\sim root-level) soil moisture and the wilting and saturation capacity of the soil, respectively. For the CO_2 concentration at the leaf surface (C_s) we use $C_s = C_a - (A_n \cdot R_b)$ where, C_a is the ambient CO_2 concentration. For closure, using an approach similar to that of Collatz et al. (1991), C_i is estimated as $C_i = C_s - (1.6 \cdot A_n \cdot P \cdot R_b)$. The scaling from leaf to canopy follows Sellers et al. (1996a) and considers calculations for sunlit and shaded leaves with an exponential extinction and solar zenith angle based variation.

The atmospheric core and the surface models are similar to those described in Alapaty et al. (1997) and Alapaty et al. (2001). The only changes to the model are (a) those related to the programming enhancement that were necessary for adding the photosynthesis and CO_2 effects, (b) to correct for the deep soil moisture and gravitational corrections to the force-restore method following Boone et al. (1999), and (c) the Jarvis-type stomatal model calculations were overridden by the photosynthesis scheme calculations within the land surface model. To achieve a fully coupled two-way interaction between the surface and the atmosphere, the photosynthesis module is linked to a detailed PBL and land surface process model (Noilhan and Planton, 1989; Alapaty et al., 1997). Five prognostic equations model the topsoil (0.1 m) and deepsoil (1 m) temperature (T_{g1} , T_{g2}) and moisture (W_{g1} , W_{g2}), and rainfall interception (W_r):

$$\begin{aligned} \frac{\partial T_{g1}}{\partial t} &= C_T(R_n - S_{hf} - L_{hf}) - \frac{2\pi}{\tau}(T_{g1} - T_{g2}) \frac{\partial T_{g2}}{\partial t} \\ &= \frac{(T_{g1} - T_{g2})}{\tau} \frac{\partial W_{g1}}{\partial t} = \frac{C_1}{\rho_w d_1} (P_g - E_g) - \frac{C_2}{\tau} (W_{g1} - W_{geq}) \frac{\partial W_{g2}}{\partial t} \\ &= \frac{(P_g - E_g - E_{tr})}{\rho_w d_2} \frac{\partial W_r}{\partial t} = (V_c P_r) - E_r \end{aligned}$$

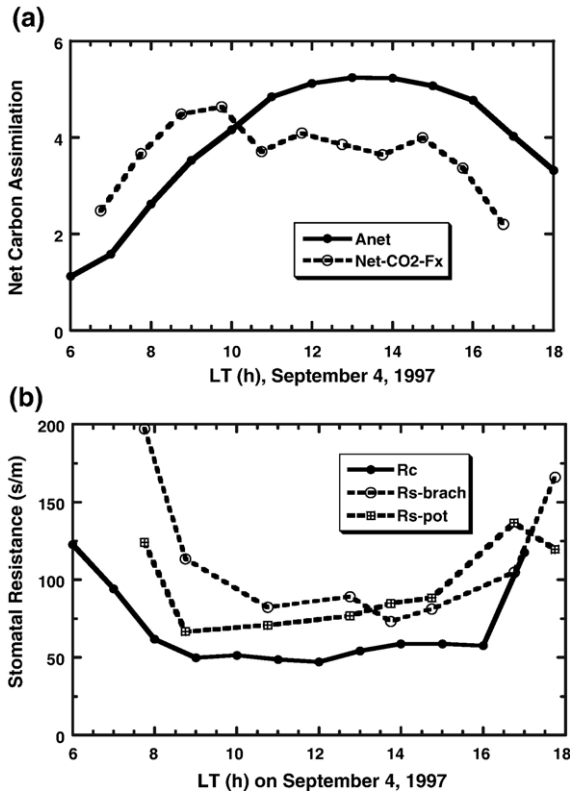


Fig. 1. Typical observed and modeled biophysical responses. The observations are from a field experiment and the model was run with default configurations as used in this study. (a) Observed (dashed line) and model estimated (solid line) net carbon assimilation (A_n , $\mu\text{mol}/\text{m}^2/\text{s}$). (b) Modeled (solid line) and observed (dashed lines) stomatal resistances for the same case. $R_{s\text{-brach}}$ and $R_{s\text{-pot}}$ refer to the stomatal resistance observations for two dominant vegetation (same biome type) species; *Brachypodium* sp. and *Potentilla reptans* over the study site. (Figure adapted from Niyogi, 2000).

In the above, C_T is the thermal transfer coefficient, while C_1 and C_2 are the soil moisture coefficients (Noilhan and Planton, 1989); R_n , S_{hf} and L_{hf} are the net radiation, sensible heat, and latent heat fluxes at the surface, τ is the total seconds in a day, ρ_w is the density of liquid water, d_1 and d_2 are the thicknesses of the two soil layers, P_g is the flux of liquid water reaching the soil surface, E_g is the evaporation at the soil surface, W_{geq} is the topsoil moisture when gravity balances the capillary forces, E_{tr} is the transpiration rate, V_c is the fractional vegetation cover, P_r is the precipitation rate at the top of the vegetation, and E_r is the evaporation rate from the wet parts of the canopy. Total evaporation from the surface is taken as the sum of E_g , E_{tr} , and E_r , and provides a surface boundary condition to the atmospheric model. In the atmospheric model, net radiation at the surface is the sum of incoming solar radiation (a function of solar zenith angle, surface albedo, and atmospheric turbidity), atmospheric longwave back-

scattering radiation, and outgoing longwave surface radiation (Anthes et al., 1987). Upward and downward longwave radiative fluxes are calculated as functions of soil emissivity, ground temperature, atmospheric longwave emissivity, and atmospheric temperatures. Additionally, the PBL model uses surface layer similarity relationships with a turbulent kinetic energy (TKE) approach for the mixed-layer parameterization. More details regarding these submodels can be found in Alapaty et al. (2001).

This model has been tested over various landscapes (agricultural, fallow, and forest) and the results have been typically 10 to 15% of the observations (Niyogi, 2000). Fig. 1 shows the model performance over a grassland site in France as part of the MUREX study site. As can be seen, both the transpiration and the photosynthesis values in a coupled model setup (identical to the one been used here) are in good agreement with the field measurements. Overall, when the model has been applied as a coupled, column model, the typical results indicate errors on the order of 10% for surface fluxes, 2 K for temperature, 20% for humidity, and about 100 m for convective boundary layer heights under “clear sky” conditions. The errors are much more significant for “cloudy” conditions and are dependent on the timing and occurrence of the modeled and the observed clouds. Another good measure of the model’s stomatal (canopy) resistance module is its application within a dry deposition velocity model (since the canopy resistance term is the dominant term). Niyogi et al. (2003, 2006) found that the model typically provided deposition values within 20% of measurements. The model has also been coupled within a 3D weather forecast modeling system by Holt et al. (2006) and Niyogi et al. (2002) to develop realistic simulations of convective precipitation events over the Great Plains.

2.1. Simulation setup

Using the coupled modeling system, we designed the experiment to test the sensitivity of soil moisture under current and doubled CO_2 levels on the terrestrial response of each of the nine SiB2 vegetation types. The description of each vegetation type is presented in Table 1. In the model, the changes in the vegetation type are obtained by altering biophysical and environmental control variables such as the maximum carboxylation rate, assimilation and respiration efficiency for carbon exchange, water use efficiency, optimum temperature and radiation functional ranges, leaf and canopy geometry, ‘Q-10 coefficients’, and radiative properties such as albedo and emissivity. All the biophysical as well as the soil parameters used in the model are based on SiB2 (Sellers et al., 1996a,b). The model was run in a forecast mode, and the time step (typically 30 s)

Table 1
Summary of the nine Vegetation Types (VTYP) used in the study (following Sellers et al., 1996b)

Vegetation Type	Description
1	Broadleaf–evergreen trees
2	Broadleaf–deciduous trees
3	Broadleaf–Needleleaf mixed trees
4	Needleleaf–evergreen trees
5	Needleleaf–deciduous trees
6	C4 grassland
7	Shrubs with bare soil
8	Dwarf trees and shrubs
9	Agriculture or C3 grassland

was constrained by the convergence for CO₂ equilibrium as part of the iterative stomatal conductance-photosynthesis scheme coupled within the two layers of soil and single layer vegetation model. Four sets of simulations were performed for each landuse/vegetation type (Table 2). In the first, the soil moisture was prescribed as limiting (water stressed, within 10% of wilting point). Simulation two was identical to simulation one except for a CO₂ doubling (68 Pa) scenario. For simulations three and four, the model configuration in tasks one and two was repeated, but with the soil moisture not limiting. For this, the initial soil moisture was prescribed within 10% of the field capacity for both the present day and the doubling of CO₂ conditions. In all the simulations, other biophysical and surface conditions were identical (cf. Eastman et al., 2001). The atmospheric boundary condition was provided by the Eta data assimilation system (EDAS), with three hourly updates and a single sounding initialization representative of a mid-latitude site for a non-advective, high-pressure boundary layer following Alapaty et al. (1997). The domain and sounding corresponded to the summer, mid-latitude region (Southern Great Plains). Thus, the simulations for the changes in the vegetation type/landuse type are similar to the approach generally taken by various regional modeling studies in which the landuse is altered for the same domain (Gero et al., 2006-this issue).

The simulated net carbon assimilation (A_n) and evapotranspiration (Etr) with respect to the changes in the prescribed soil moisture availability and atmospheric CO₂

for varying landuse/vegetation were evaluated. The model results were analyzed by plotting the outcome and deducing feedback relations in terms of the soil moisture and CO₂ availability. To extract the direct effect (due to CO₂ change or soil moisture change *alone*) and the interactive or indirect (due to CO₂ and soil moisture change *together*) effects, the model outcome was analyzed further using a statistical interaction explicit technique called Factor Separation Analysis (Stein and Alpert, 1993; Niyogi et al., 1998; Eastman et al., 2001).

In the factor separation technique, we analyzed the four combinations for two factors (soil moisture and carbon dioxide) at two levels (soil moisture limiting, and abundant; and present day and doubled CO₂ availability) corresponding to the various landuse/vegetation combinations to extract the main effects (f_{CO_2} and f_{Moist}) and their synergistic interaction ($f_{Moist:CO_2}$). We assign,

$$f_0 = F_0 \\ F_0 \equiv (CO_2^-, Moist^-) \quad (1a)$$

$$f_1 = f_{CO_2} = F_1 - F_0 \\ F_1 \equiv (CO_2^+, Moist^-) \quad (1b)$$

$$f_2 = f_{Moist} = F_2 - F_0 \\ F_2 \equiv (CO_2^-, Moist^+) \quad (1c)$$

$$f_{1,2} = f_{Moist:CO_2} = F_{1,2} - (F_1 + F_2) + F_0 \\ F_{1,2} \equiv (CO_2^+, Moist^+) \quad (1d)$$

In the above, CO₂⁺ and CO₂⁻ refer to the scenario with doubling (68 Pa) and the present day (34 Pa) climatological values of ambient carbon dioxide concentrations (e.g., Houghton et al., 1996); and Moist⁺, Moist⁻, refer to the model setup for near-field capacity, or near-wilting soil moisture, respectively, for different landuse/vegetation types.

In the following section, we discuss the results corresponding to different landuse/vegetation types.

3. Results

Though each of the landuse/vegetation types is unique in terms of its biological response and characteristics, they

Table 2
Model simulations performed for each of the nine SiB2 vegetation types (Sellers et al., 1996a) to study the interactive effect of CO₂ and soil moisture change

Simulation set	CO ₂ levels	Soil moisture state
I	Present day (34 Pa)	Limiting (near wilting)
II	Doubling (68 Pa)	Limiting (near wilting)
III	Present day (34 Pa)	High (near field capacity)
IV	Doubling (68 Pa)	High (near field capacity)

Typically the near wilting and near field capacity soil moisture was 0.23 m³ m⁻³ and 0.3 m³ m⁻³, respectively.

exhibit some broad similarities by which the various types can be grouped for the presentation of our results. We clustered the nine biome types into four categories: Broadleaf Trees (SiB2 Vegetation Types 1, 2, and 3), Needleleaf Trees (SiB2 Vegetation Types 4 and 5), C4 Grass (SiB2 Vegetation Type 6), and C3 Grass and Shrubs (SiB2 Vegetation Types 7, 8, and 9). The results pertaining to these four groups of vegetation changes made within the model configuration are discussed below. For each vegetation type category, we will present two sets of plots: one providing the typical daytime variations for the four soil moisture and CO₂ combinations, and the second corresponding to the direct and interactive effects of the soil

moisture and biological CO₂ impacts for different vegetation types.

3.1. Broadleaf trees

This section represents model results when the vegetation type was changed to the three Broadleaf tree biome types: Broadleaf–evergreens, Broadleaf–deciduous, and Broadleaf–Needleleaf mixed trees.

Fig. 2a–b shows the average daytime variations in the simulated evapotranspiration (Etr) and net carbon assimilation or photosynthesis (A_n) for Vegetation Type 1. Soil moisture dominated the Etr changes, while the CO₂ changes had a relatively small effect. Interestingly, the CO₂ impact on the Etr increased as soil moisture became limited. A_n variations were dominated by CO₂ levels (Fig. 2b), with higher CO₂ leading to higher A_n under abundant soil moisture availability. When soil moisture was limiting, A_n saturated around mid-day with the dip in the A_n curve generally corresponding to peak radiation values.

The model results showed different responses resulting from both CO₂ and soil moisture changes. This variability in the simulated outcome is due to both the direct effect as well as the interaction of CO₂ and soil moisture changes. Fig. 3a–b gives the relative contribution of the direct changes in CO₂ and soil moisture, and their interactive feedback on modeled Etr and A_n . In the figure, the first box-plot shows the direct biological effect of CO₂ changes, the middle corresponds to the direct effect of soil moisture changes, while the third corresponds to the interaction between soil moisture and CO₂. For Etr, some CO₂-based modulation was evident under limited soil moisture conditions. The corresponding factor separation results (Fig. 3a) suggest that the effect of doubling the CO₂ led to a reduction in Etr as a cumulative effect (interacting with soil moisture changes). Overall, the Etr changes were dominated by soil moisture availability, but the soil moisture–CO₂ interaction was antagonistic (i.e., opposite in sign as compared to the direct effects). The combined effects of soil moisture and CO₂ changes therefore suggest an overall reduction of the combined effect due to CO₂ rise and higher soil moisture availability. The magnitude of the interaction term is small, yet the reduction of the Etr due to the CO₂ increase (which is also seen in field studies, e.g., Owensby et al., 1997) is in response to the water use change and soil moisture effect rather than the CO₂ effect alone. Considering the A_n response (Fig. 3b), the effect of CO₂ levels on carbon assimilation is clearly demonstrated (about ten times more effective than soil moisture). Again, for this case, the interaction term is antagonistic and suggests that, for the Broadleaf Evergreen trees, the impact of soil moisture

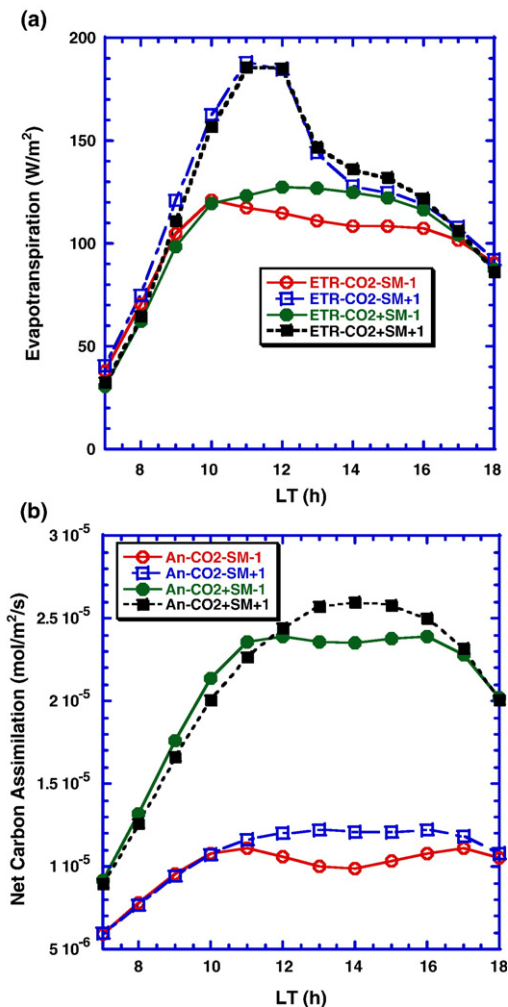


Fig. 2. Model predicted changes in (a) evapotranspiration (Etr, $W m^{-2}$), and (b) net carbon assimilation (A_n , $mol m^{-2} s^{-1}$) for Vegetation Type 1 (Broadleaf–evergreen trees). The high and low settings of the soil moisture and CO₂ values in the model initial conditions are represented by SM⁺, SM⁻, CO₂⁺, and CO₂⁻, respectively. Soil moisture has a dominant effect on ETR, while CO₂ changes are more important for A_n .

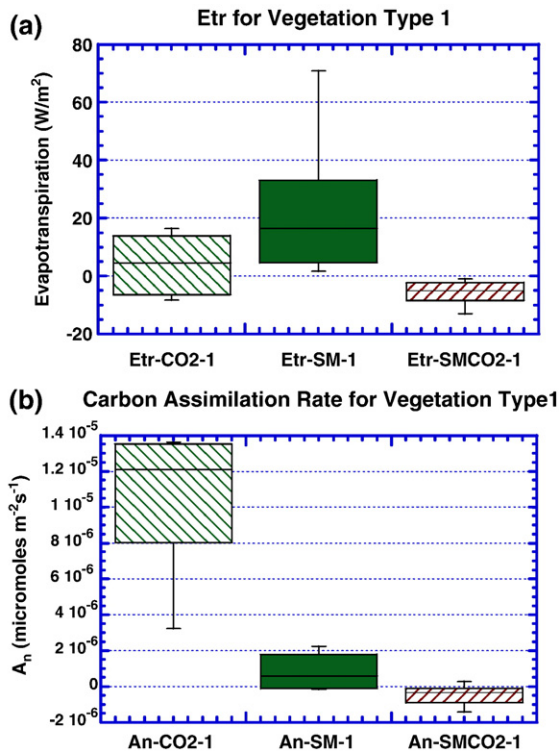


Fig. 3. Box plots for factor separated direct effects and interactions for (a) evapotranspiration (Etr, $W\ m^{-2}$), and (b) net carbon assimilation (A_n , $\mu mol\ m^{-2}\ s^{-1}$) corresponding to Fig. 2. The SM:CO₂ term corresponds to the interaction effect.

availability on the net primary productivity or evapotranspiration reduces as CO₂ levels increase.

The sensitivity of the soil moisture–CO₂ changes obtained for the SiB2 Vegetation Type 1 (Broadleaf–evergreen trees) is similarly seen for Vegetation Types 2 and 3 (Broadleaf deciduous trees, and Broadleaf and Needleleaf mixed trees). In general, changing from Vegetation Type 1 to 2, both the Etr and A_n values (not shown) were about 25% less. Also, for low soil moisture cases, the A_n showed a more pronounced mid-day dip, which can be related to the increase in the afternoon stomatal resistance. The factor-separated results for Etr, and A_n over Vegetation Type 2 were similar to those for Vegetation Type 1 biome. One notable difference was that the CO₂ dominance on A_n seen for Vegetation Type 1 decreased (by about 33%), and the soil moisture feedback became more pronounced (by about 25% as per the factor separation results).

For Vegetation Type 3 (Broadleaf and Needleleaf mixed trees), similar to Vegetation Types 1 and 2, soil moisture regulated evapotranspiration. However, a significant direct effect of CO₂ changes on Etr (larger than that realized for Vegetation Types 1 and 2) also occurred. The enhanced interaction between soil moisture and CO₂ was also more

apparent for A_n . Though the CO₂ doubling scenario led to increased A_n , the response was noticeably modulated by soil moisture availability. Overall, A_n values showed about a 50% difference depending on the soil moisture availability (with lower values under soil moisture limiting conditions).

The factor separation results for Vegetation Type 3 also suggest that the Broadleaf/Needleleaf mixed vegetation was more responsive to changes in both soil moisture and CO₂, rather than the relatively singular soil moisture or CO₂-based dominance seen for the Broadleaf trees (Vegetation Types 1 and 2). Soil moisture changes were three times as effective as CO₂ doubling for changing the Etr, while for A_n , the CO₂ changes were about three times more effective than the soil moisture changes. The interaction term between soil moisture and CO₂ was also significant and had about the same order of magnitude as the non-dominant term. Thus, an active synergistic interaction

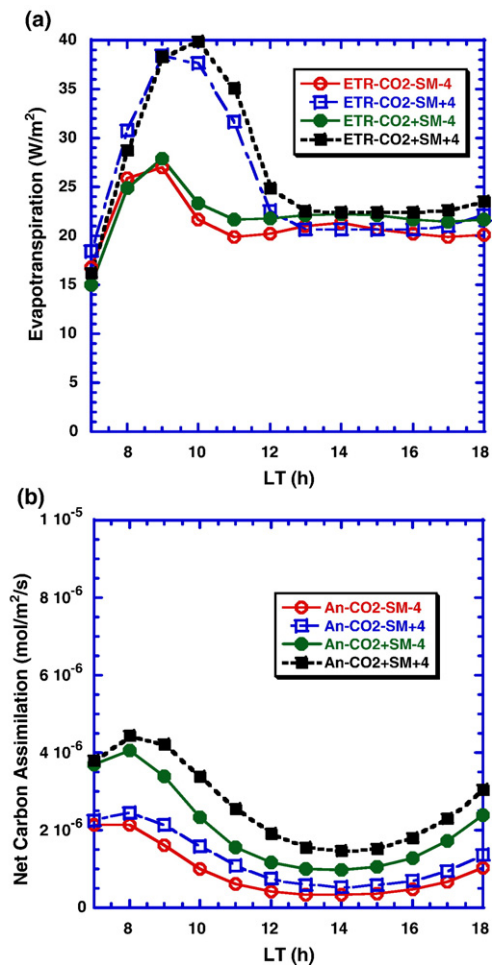


Fig. 4. Same as Fig. 2 except for Vegetation Type 4 (Needleleaf–evergreen trees).

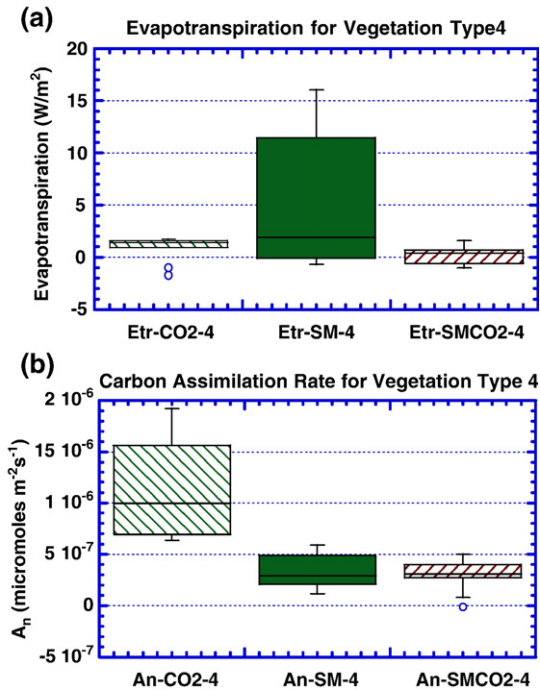


Fig. 5. Same as Fig. 3 except for Vegetation Type 4 (Needleleaf-evergreen trees).

between soil moisture and CO₂ availability for the modeled biological effects took place.

3.2. Needleleaf trees

We tested the model response for two vegetation types in this group: SiB2 Vegetation Types 4 (Needleleaf evergreens), and 5 (Needleleaf deciduous).

Fig. 4a–b shows the evapotranspiration and net carbon assimilation rates for the Needleleaf evergreen trees (SiB2 Vegetation Type 4). Both the Etr and A_n values were relatively small as compared to the Broadleaf plants (discussed in the previous section). This reduction could be largely attributed to the change in the leaf geometry, with the Broadleaf trees generally offering a better opportunity for water vapor and carbon exchange under similar environmental conditions (e.g., Nikolov et al., 1995). Despite the differences in the magnitudes, the change in model land use from Broadleaf to Needleleaf trees did not lead to very different CO₂ and soil moisture responses. Overall, an increase in soil moisture and high CO₂ values yielded both a higher Etr and a larger A_n . These results are consistent with various observational data for Needleleaf trees (Sun et al., 1995; Murthy et al., 1996; Roberntz and Stockfors, 1998; Laitjnen et al., 2000).

Fig. 5a–b shows the factor separation results for Etr and A_n , respectively. The results are generally similar to

those for the Broadleaf tree cases discussed earlier. Overall, the soil moisture and CO₂ interaction effect showed a relative increase for the Needleleaf trees compared to the results obtained for the Broadleaf trees. Additionally, the soil moisture–CO₂ change interaction was synergistic as against the antagonistic interactions obtained for the Broadleaf trees. Thus, for the Needleleaf A_n rates, the effect of CO₂ doubling appears to be four times more dominant than the soil moisture change. Also, similar to the Broadleaf trees, the interaction term was comparable to the less-dominant main effect. The reduction in the respiration loss due to increasing CO₂ and soil moisture changes discussed in Amthor (2000) and the enhanced biochemical interactions in the Needleleaves could aid A_n (Roberntz and Stockfors, 1998). Thus, for the model Needleleaf vegetation type, Etr was directly controlled by soil moisture availability. The effects of CO₂ changes were prominent under low soil moisture conditions. Overall, a CO₂ increase led to a positive impact on photosynthesis rates (or NPP) for the Needleleaf trees, and the soil moisture availability (non-limiting) aided the biospheric response.

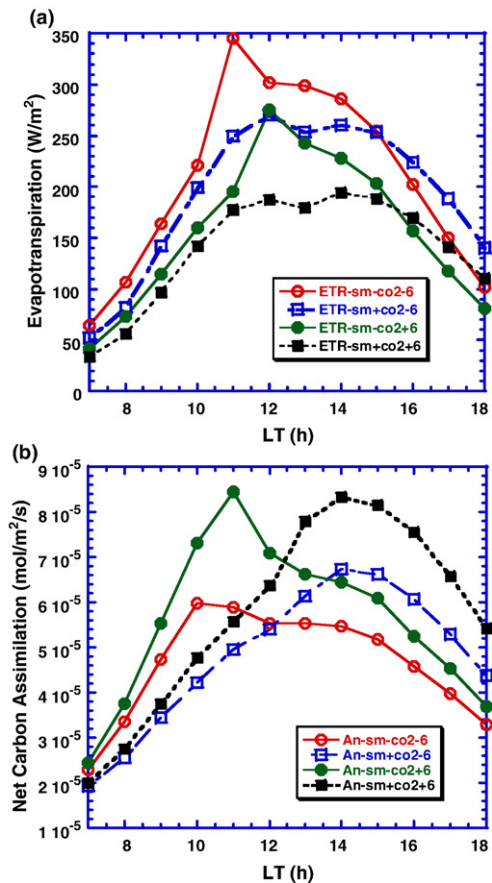


Fig. 6. Same as Fig. 2 except for Vegetation Type 6 (C4 grassland).

3.3. C4 grass

Studies by Owensby et al. (1997), Morgan et al. (1998), and Collatz et al. (1998) have yielded variable results regarding the effect of CO₂ doubling on C4 vegetation. Hence, studying the model response for this landuse/vegetation type to assess the biological impacts of CO₂ change with soil moisture change is of additional interest. The photosynthesis pathway for this vegetation type is known to be more conservative to CO₂ changes and is not expected to be affected significantly (Collatz et al., 1992).

Fig. 6a–b shows the modeled Etr and A_n for the C4 grasslands. Both soil moisture and CO₂ changes significantly modulate A_n and Etr. Increasing CO₂ decreased Etr and increased A_n. There was also strong interaction between CO₂ and soil moisture availability. In the factor separation results (Fig. 7a–b), the modeled Etr results indicated that a rise in CO₂ has a negative effect on evapotranspiration. Nie et al. (1992), Hungate et al. (1997), and Morgan et al. (1998) found a similar negative correlation in field studies with C4 vegetation. This conservative strategy is thus similar to the resource allocation optimization that the modeled landscape attains for equilibrium as discussed in Cowan (1982), Buckley et al. (2003), and Niyogi et al. (2002). The soil moisture–CO₂

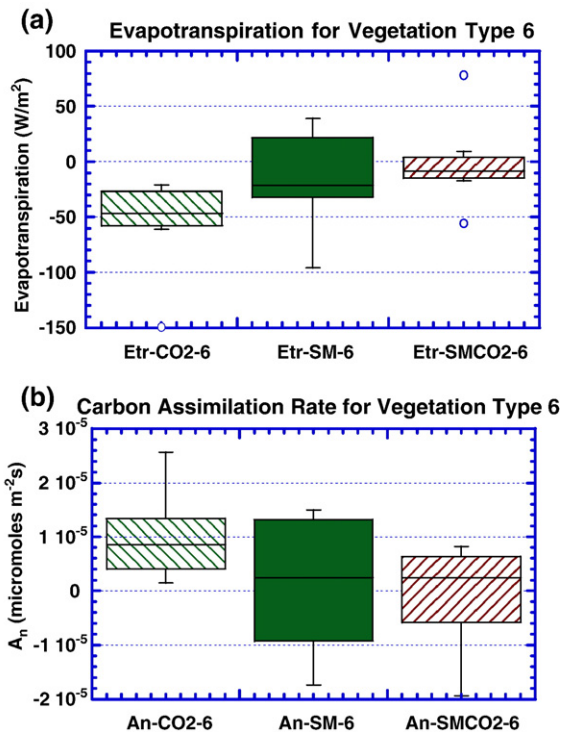


Fig. 7. Same as Fig. 3 except for Vegetation Type 6 (C4 grassland).

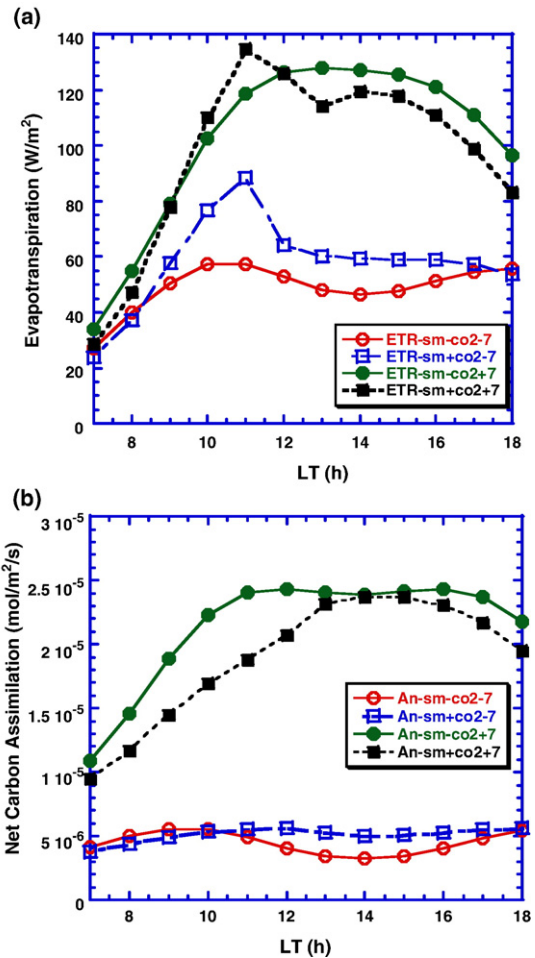


Fig. 8. Same as Fig. 2 except for Vegetation Type 7 (C3 shrubs with bare soil).

interaction is synergistic and relatively small for Etr but significantly active for A_n. Thus, soil moisture availability can contribute to differences in the modeled biological effects under doubled CO₂ levels for C4 vegetation. For example, as seen in Fig. 6b, the increase in CO₂ led to larger A_n, but an increase in soil moisture could also lead to an increase in A_n (Kirkham et al., 1991). Again, the interaction term is of nearly equal prominence and can modulate the model response of C4 vegetation as a source or sink for carbon. Note that unless the direct and interactive effects are explicitly obtained from the coupled outcomes, the combined effect can be dampened and could yield, in the model, the spurious conclusion that CO₂ changes do not affect C4 vegetation responses.

3.4. C3 grass, shrubs and crops

In this group, we included three biome types: SiB2 Vegetation Type 7 (shrubs with bare soil), SiB2 Vegetation

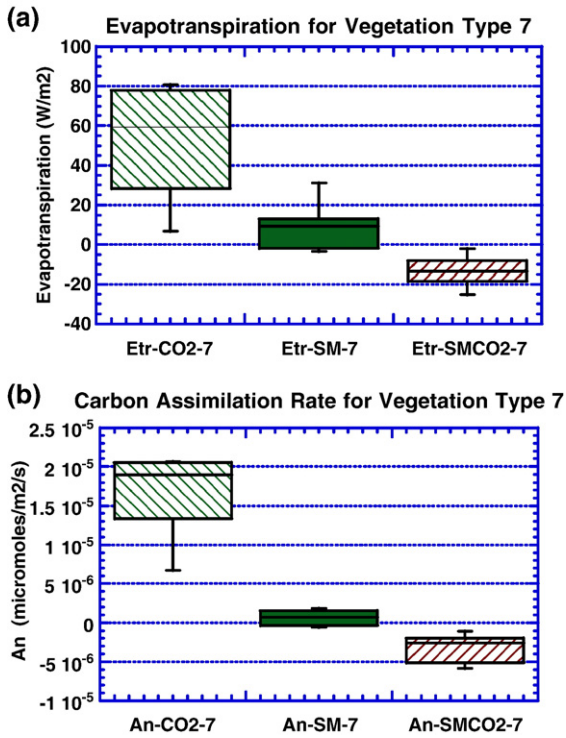


Fig. 9. Same as Fig. 3 except for Vegetation Type 7 (C3 shrubs with bare soil).

Type 8 (dwarf trees and shrubs), and SiB2 Vegetation Type 9 (agricultural or C3 grasslands).

Fig. 8a–b shows the model response for Vegetation Type 7. The results are somewhat similar to those obtained for C3 trees but almost opposite to those seen for C4 grass (Vegetation Type 6). For example, unlike C4 vegetation, Vegetation Type 7 resulted in higher Etr under high CO₂ availability. Further, in the case of C3 trees (Vegetation types 1 through 5), evapotranspiration was dominated by soil moisture availability, while for the C3 shrubs and bare ground, CO₂ availability was an equally important factor. Under low CO₂ conditions, soil moisture availability controlled the Etr rate (with larger Etr values for higher soil moisture availability). Under high CO₂ conditions, the soil moisture dominance was replaced by increasing CO₂ interactions. The model also yielded higher A_n for increasing CO₂ and limiting soil moisture conditions (cf. Idso and Idso, 1994). On the other hand, for low CO₂ cases, higher soil moisture availability was conducive to relatively larger modeled A_n.

Fig. 9a–b summarizes the factor separation results for Etr and A_n for Vegetation Type 7. CO₂ doubling has a dominant effect both on A_n and Etr. The interaction term shows an antagonistic response for the soil moisture changes (which was opposite to the feature seen for C4 vegetation). The A_n results are similar to those obtained for

C3 trees (particularly Vegetation Type 1). The main effects of CO₂ and soil moisture (to some extent) aid photosynthesis, but the interaction term assists respiration. This antagonistic interaction indicates that, unlike the C4 vegetation, the effect of soil moisture status may not significantly modulate the assimilative capacities for Vegetation Type 7 under elevated CO₂ conditions. Further, low CO₂–high soil moisture and high CO₂–low soil moisture combinations led to large differences in the model results. The variability reduced with increasing CO₂ as the effects of other variable changes were damped. Overall, CO₂ changes appear to stimulate a larger response for the Vegetation Type 7 (C3 shrubs and bare ground) than for C4 grass or C3 woody trees. This feature of the model response is in agreement with the discussion presented in the meta-analysis for the CO₂ doubling effects presented in Curtis and Wang (1998).

The model results for mixed C3 dwarf trees and shrubs (Vegetation Type 8, not shown), were generally similar to those seen for Vegetation Type 3 (Broadleaf and Needleleaf

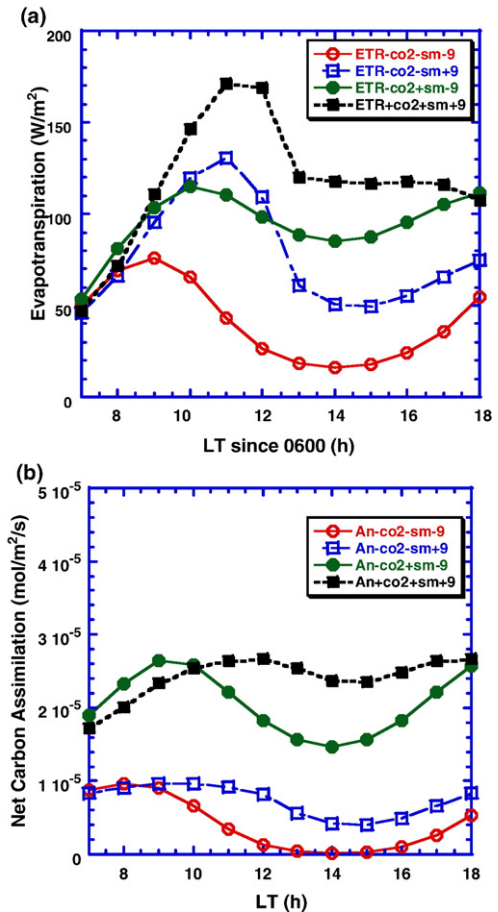


Fig. 10. Same as Fig. 2 except for Vegetation Type 9 (C3 agriculture or grassland).

mixed trees). The Etr response was soil moisture dominated, while A_n was responsive to both soil moisture and CO_2 changes. Considering that these two vegetation types have biophysical characteristics that are for somewhat similar geographical regions in the SiB2 global landuse characteristics database (Sellers et al., 1996b), this similarity is not surprising. Typically, higher soil moisture and higher CO_2 conditions resulted in higher Etr values. The factor separation results for Etr and A_n indicate that a CO_2 increase affects both the variables. The soil moisture and the interaction term are almost similar and synergistic. Thus, the increase of CO_2 could have a stronger influence on the model results under high soil moisture conditions.

The Etr and A_n results for C3 agricultural crops (Vegetation Type 9) are shown in Fig. 10a–b. Similar to Vegetation Type 7, these results are somewhat opposite to the C4 grassland case and generally similar to the woody C3 Vegetation Types discussed earlier. Both soil moisture and CO_2 changes control evapotranspiration, and higher evapotranspiration rates were obtained for higher soil moisture and CO_2 scenarios. A_n was dominated by and proportional to CO_2 values. The A_n response increased with higher soil moisture availability.

The factor-separated interactions between soil moisture and CO_2 are shown in Fig. 11a–b. For Etr, both CO_2 and

soil moisture increase showed a positive response. The interaction term, on the other hand, is antagonistic, and its impact on the combined model result would be to reduce the effect by about 25% (as also discussed in Dugas et al., 1997). For A_n , both CO_2 and soil moisture show a positive correlation and the interaction term could introduce a larger variability. In general, the effect of CO_2 doubling was about four times as effective in enhancing A_n than increasing soil moisture from near-wilting to near-field capacity.

Thus, the effect of simultaneous CO_2 and soil moisture change is significantly uncertain (variable) and will affect the model response for C3 agricultural grasslands depending on ambient CO_2 levels. Also, because of the opposite signs of the direct and the indirect effect, the response will be buffered and not as dramatic as expected through the one-at-a-time sensitivity analysis cited in studies such as Martin et al. (1989).

4. Discussion

In this study, we tested whether model response for the biological effect of CO_2 change in different biomes is interactively linked with soil moisture availability. The results for all the nine global biomes, as defined through the SiB2 land cover classification (Sellers et al., 1996b), were analyzed for terrestrial responses such as evapotranspiration, and net carbon assimilation rates.

The model results were compared with findings reported in field studies to assist in developing better assessment of the biological impacts of CO_2 changes that can be obtained in the coupled model response. Indeed, these results should be tested and analyzed using a detailed regional scale ensemble modeling analysis that considers a number of soil moisture stress settings and landscape heterogeneities. Some broad results that should be tested further are discussed below.

For the model Broadleaf tree group (SiB2 Vegetation Types 1, 2, and 3), doubling of CO_2 increased A_n . This is generally consistent with the findings of Ceulemans and Mousseau (1994) and Carswell et al. (2000). Similarly, the numerical results for the Needleleaf trees (SiB2 Vegetation Types 4 and 5) are consistent with the observations of Murthy et al. (1996), Idso and Idso (1994), and Clark et al. (1999). Our results suggest a strong interaction between CO_2 and soil moisture changes that can generally act to modulate the changes due to the lesser dominant CO_2 or soil moisture direct effect. The magnitude of the indirect effect term was typically similar to the magnitude of the lesser dominant term. The results indicate that, for soil moisture limiting conditions, Etr would decrease (as a response to the increase in stomatal resistance), irrespective

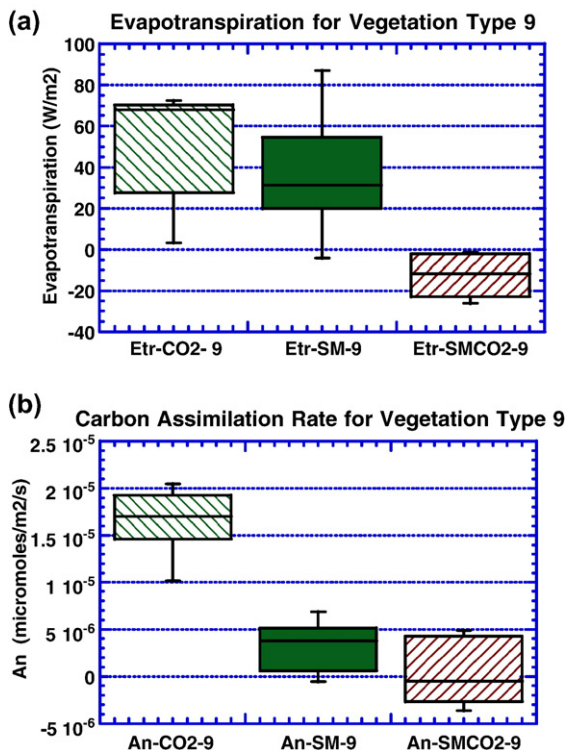


Fig. 11. Same as Fig. 3 except for Vegetation Type 9 (C3 agriculture or

of the CO₂ levels. The higher soil moisture availability could assist A_n , but the CO₂ effect appears to be dominant. Generally, as the model vegetation characteristics changed from Broadleaf to Narrowleaf, the interaction term between soil moisture and CO₂ became larger.

Despite the generalities, each vegetation type showed a unique response to the doubling of CO₂ (Lovelock et al., 1998). For example, Etr changes for Broadleaf–evergreen trees were dominated by soil moisture availability, while CO₂ changes controlled A_n with no significant feedback from soil moisture change (also see Ward et al., 2000).

For the Needleleaf trees, the model response reaffirmed the previous results where low CO₂ availability led to lower stomatal response and a lowered carbon assimilation value (Woodward, 1997). For Etr, the results suggest a high correlation with CO₂. The factor separation results suggest increasing CO₂ enhanced A_n as a direct effect (cf. Clark et al., 1999, for C3 trees). In the model response, the interaction effect was of smaller magnitude, but of a positive nature. Overall, the results indicate that the soil moisture effect might assist carbon loss due to respiration (Jackson et al., 1998). In summary, for the coupled biospheric/land surface model, many of the general features of Broadleaf and Needleleaf trees, with simultaneous changes in soil moisture and CO₂, appear to be similar.

In general, the model results for the C3 and C4 vegetation were opposite for similar changes in soil moisture and CO₂ levels. For C4 vegetation, soil moisture availability could be a critical factor affecting plant assimilative capacity, and respiration losses were high under high soil moisture conditions (Ham et al., 1995; Nie et al., 1992; Amthor, 2000). In the modeling framework, the C4 vegetation could be unique in its association with regards to the soil moisture and CO₂ doubling scenario (Collatz et al., 1992). In our model results, the WUE increase appears to be due to CO₂ enhancement rather than soil moisture changes. Yet, consistent with the results for the C3 trees, due to an increase in ambient CO₂ levels, the C4 vegetation also exhibited a strong coupling between CO₂ and soil moisture interactions. The interpretation of model representations regarding biological changes and scaling should consider hydrological status in their results.

As reviewed by Mayeux et al. (1991), and discussed in Polley et al. (1997), C3 shrubs have shown a dominant increase globally in areas that were predominantly C4 grasslands. Everything else being constant, for CO₂ doubling, C3 shrubs can show more biological assimilative capacity over C4 grass (cf. Ehleringer et al., 1997) with high soil moisture availability. However, this advantage could decrease with increased drought-like conditions (lower soil moisture availability; cf. Clark et al., 1999). Since the major drying and wetting cycles

are a conspicuous feature of pasturelands (Greer et al., 1995; Clark et al., 1999), the interaction and the competition between C3 and C4 vegetation, particularly with increased CO₂ levels, could be uncertain and depend on the soil moisture status in coupled models (Owensby et al., 1993, 1997). Thus, surface hydrology and carbon assimilation as well as competitive ecology appear to be coupled. Therefore, future studies that consider a longer time period of model simulations (e.g., seasonal to years) should assess the role of soil moisture on CO₂ doubling impacts.

Thus, our findings highlight the potential importance of soil moisture and the role of land–atmosphere interactions in modulating the biological effects of CO₂ changes. Several of the variable changes simulated in the biospheric models appear to be consistent with the CO₂ doubling based experimental results presented in the literature. For instance, Kimball et al. (1999) suggested that the effects of CO₂ changes on evapotranspiration seem to be uncertain, which they attributed to the partial stomatal closure that reduces the water vapor exchange. Our results indicated that this uncertainty is also largely due to the active interaction effect between soil moisture availability and CO₂ changes and should be studied further, with particular reference to stomatal resistance (cf. Curtis and Wang, 1998).

5. Study limitations

This is an initial study to provide an additional perspective on the response of the biological impact of CO₂ changes in a coupled biosphere–atmosphere model. As such, the model setup is designed to help integrate the results where land use change (vegetation type) experiments are performed for a similar synoptic setup. The model has a single climate (meteorological) forcing, representing a single region (Southern Great Plains). The different biomes considered are represented by coefficients in a simple biosphere model and do not account for intra-specie heterogeneities or soil heterogeneity. The model results can be considered valid for summertime mid-latitude conditions, and the feedback will change depending on the model used, the period to be simulated, and the study domain. The model was run for a two week period to avoid seasonality and to retain soil moisture memory. The radiative effects of CO₂ changes are relatively minor, and in a more comprehensive long term future assessment, they could also become significant. The study results cannot be linearly applied to assess the implications of global or regional landuse change, and the impact of land surface heterogeneities will be an important consideration for future studies. Yet, the central conclusions that the effects

of CO₂ changes within the model are significantly dependent and coupled to the surface hydrology and more specifically, soil moisture in this study, are valid. The biological effects of CO₂ changes are often the same order of magnitude as soil moisture effects, and this forcing causes important feedbacks in the coupled system. The soil moisture–CO₂ interactions stressed in this study do not implicate causality; rather, they suggest possible empirical mechanisms that the models may be adopting (e.g., by modifying the carboxylation rate estimates, Wilson et al., 2000). Future studies should review this question using detailed regional and global models to study the interaction between the CO₂ biological and radiative effects and the soil moisture feedbacks and their combined impact on transpiration and coupled land–atmosphere processes. This study lays the framework for interpreting the one-at-a-time response due to land use change, a framework which can be used to design and clarify the complex responses in regional and global-scale models. Future studies can also attempt to identify specific feedbacks associated with both biological and radiative changes due to CO₂ doubling experiments in climate change studies.

6. Conclusion

We hypothesized that the biological effect of CO₂ changes simulated by a coupled atmosphere biospheric land surface model is intrinsically linked with soil moisture-based surface forcing and resulting land–atmosphere interactions. This hypothesis was reviewed using a photosynthesis-based land surface modeling system coupled to an atmospheric boundary layer model and tested for different SiB2-based landuse/vegetation types. Our analysis suggests, resolving the interactions explicitly, that both the C3 and the C4 vegetation responses are affected by the biological effects of CO₂ changes in the models. The study highlights the role of the interaction effect between soil moisture and CO₂ as a potentially significant term for understanding the trajectory of the response. Overall, the response of the changes in CO₂ concentrations under high and low soil moisture availability varied for the biome type and the effect under study. The effects analyzed in this study, evapotranspiration and net carbon assimilation, are generally coupled with each other, yet they showed significant variations in their individual responses. Thus, a major conclusion from the study is that biological impacts associated with CO₂ changes in a coupled biospheric model should be interpreted in consideration of the soil moisture status. It is possible that the model results for drought or high soil moisture availability can enhance, completely balance, or even reverse the effects associated with CO₂ changes and need to be explicitly considered in

climate change assessments. When applying the biospheric models for regional or global terrestrial carbon cycle studies, the effects of land surface processes, particularly those of soil moisture, need to be explicitly considered for interpreting and scaling the results. Such studies also need to recognize that the effects of CO₂ changes are highly correlated to soil moisture changes. This can cause confounding in interpreting the results in the coupled studies. The CO₂ doubling impacts should explicitly consider soil moisture status in interpreting and attributing the effects due to CO₂ changes and soil moisture changes.

Acknowledgements

The study benefited through support from NASA-THP (Dr. J. Entin), NSF-ATM (Dr. S. Nelson), NASA-IDS (Drs. G. Gutman and J. Entin), NASA-Radiation Sciences (Drs. T. Lee and D. Anderson), USDA, and Purdue University. It is our pleasure to acknowledge discussions with Drs. Roger Pielke, Sr. at Colorado State University, Kell Wilson at ATDD/NOAA, Oak Ridge, John Norman, University of Wisconsin at Madison, and Richard Norby from Oak Ridge National Laboratory. The paper also benefited from discussions with participants at a 2001 workshop hosted by the Aspen Global Change Institute in Aspen, CO by Drs. Gregg Marland and Roger Pielke Sr. Thanks also to Drs. Noah Diffenbaugh and Matt Huber at Purdue University for the suggestions on the title, and to the three anonymous reviewers, and to Dr. Rezaul Mahmmud from the University of Western Kentucky for their comments and suggestions on the earlier version of this paper.

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