Impact of doubled CO₂ on global-scale leaf area index and evapotranspiration: Conflicting stomatal conductance and LAI responses

Laurent Kergoat, Sébastien Lafont, Hervé Douville, Béatrice Berthelot, Gérard Dedieu, Serge Planton, and Jean-François Royer

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[1] Current increase in atmospheric CO₂ is expected to modify both climate and plant function, thereby impacting plant structure and gas exchange. We investigate the effects of doubled CO₂ on leaf area index (LAI) and evapotranspiration (ETR) using a global vegetation model for present-day and doubled-CO₂ conditions. The model assumes that adaptation of plants to the local climate leads to an equilibrium LAI, which depends on resource availability (minimizing water stress, canopy carbon cost and self-shading). The model compares reasonably well with remote sensing estimates of LAI. Four doubled-CO₂ simulations are designed to investigate the role of climate, CO₂-induced stomatal closure, enhanced photosynthesis, and a combination of these effects. These simulations show that plant physiological responses to doubled CO₂ are potentially more important than climate changes for LAI, and equally important for ETR. In addition, even the sign of the simulated changes in LAI and ETR varies with the assumptions on plant responsiveness to CO₂. A reduction of stomatal conductance moderates or cancels the water losses caused by a warmer and drier climate, but photosynthesis stimulation counteracts this stomatal effect, especially in the mid-to-high latitudes, because of enhanced LAI. Experimental evidence of LAI and ETR response to CO₂ has been reviewed and compared to the different simulations. On the basis of this confrontation we argue that plant response to CO₂ doubling may have a relatively small net impact on global ETR and may cause a moderate increase of LAI. Tree stomata may be less responsive to CO₂ than was previously assumed, and stimulated plant growth partly cancels the water savings caused by stomatal closure. Understanding the responses of plant canopies to CO₂ is therefore critical for land surface hydrology in a CO₂ rich world.

INDEX TERMS: 1818 Hydrology: Evapotranspiration; 1851 Hydrology: Plant ecology; 1655 Global Change: Water cycles (1836); 3322 Meteorology and Atmospheric Dynamics: Land/atmosphere interactions; KEYWORDS: LAI, CO₂, stomatal conductance, global, evapotranspiration


1. Introduction

[2] Early studies have long demonstrated the effects of carbon dioxide on plant physiology and gas exchange [e.g., Heath and Russell, 1954]. Numerous experiments with plants grown in elevated CO₂ have shown an increase in leaf photosynthesis rate and often, but not always, a decrease of leaf stomatal conductance; see reviews by Bazzaz [1990], Field et al. [1995], Körner [1996], Drake et al. [1997], Morison [1998], Medlyn et al. [2001], but see also Saxe et al. [1998], Curtis and Wang [1998]. Given the current rise of atmospheric CO₂, it becomes important to understand the consequences that these effects may have on ecosystem function and on the water cycle. Indeed, water vapor fluxes over the continents are largely controlled by plant canopies. Pollard and Thomson [1995], and Henderson-Sellers et al. [1995] (hereinafter referred to as HS95) have shown that a decrease in stomatal conductance significantly impacts 2xCO₂ climate simulations and thus has to be considered for the elevated CO₂ climate predictions. Sellers et al. [1996a] (hereinafter referred to as S96) further suggested that the biosphere physiological response to CO₂ might reinforce the climate warming. The stomatal closure induced by increased CO₂ reduces the latent heat flux and favors the sensible heat flux over the forested continents [see also Cox et al., 1999]. The possible impact of CO₂-
induced reduction in stomatal conductance on the water cycle and run-off has been highlighted by Idso and Brazel [1984], Ashton [1984], Wigley and Jones [1985], Neilson and Marks [1994] among others. However, large uncertainties remain. Different processes are expected to impact the ecosystem-scale water budget. The first process is a reduction of the leaf-scale transpiration due to a CO2-induced decrease in the leaf conductance for water vapor diffusion. Such a decrease was generally assumed in previous studies [e.g., HS95, S96], but recent works shed a different light on stomatal response, as will be detailed later. The second process concerns the response of canopy-scale latent fluxes. This response depends on the changes in ecosystem structure, and especially on the changes in canopy leaf area index (LAI, projected leaves area per ground area, m²/m²). Both enhanced plant growth and shifts in species composition within the ecosystem can provoke changes in LAI. These processes are particularly relevant to the decade-to-century timescale of the current CO2 increase. Such changes in ecosystem structure are particularly important for the water budget: if the plants benefit from better environmental conditions and greater resource availability, for example, water, CO2, LAI may increase significantly and this can enhance canopy conductance and canopy-scale ETR, in spite of a leaf-level stomatal closure. This balance between leaf-scale and canopy-scale effects is the so-called “compensatory response” to elevated CO2, highlighted by Field et al. [1995]. This effect is a potentially important, still largely uncertain, driver of surface climate and hydrology in a CO2 rich world.

At the global scale, Betts et al. [1997] (hereinafter referred to as B97) first demonstrated that ecosystem structural changes in a coupled climate-vegetation simulation could partly cancel the physiological effects on plants. They found that an increased LAI partially compensates the effect of stomatal closure on ETR. These results significantly differ from previous studies [HS95, S96]. Another simulation was carried out by Levis et al. [1999, 2000] (hereinafter referred to as L00). They also found a large impact of increased LAI on the energy and water budgets. Both B97 and L00 studies have convincingly highlighted the importance of LAI in vegetation-climate feedbacks, through changes in ETR, energy budget and precipitation recycling. However, they obtained drastically different simulations of global LAI changes. The lack of consensus between these studies [see also Pan et al., 1998] indicates that the mechanisms which cause changes in LAI and canopy evapotranspiration in global-scale 2xCO2 simulations, need to be discussed in detail and compared with experimental results.

In this study, we use a model, which simulates LAI [Kergoat, 1998], for present-day and doubled-CO2 climate conditions, along with different assumptions on plant canopy response to CO2. A dedicated simulation investigates the recent observations that tree stomata may be rather insensitive to CO2 doubling [Saxe et al., 1998; Curtis and Wang, 1998], as opposed to what was assumed in previous studies [HS95, S96, B97, L00]. Based on a series of simulations, we address the following questions: (1) How does the simulated LAI compare to satellite observations for present-day climate? (2) What is the relative importance of physiological versus climatic effect of CO2 on global-scale LAI and evapotranspiration? (3) Are there compensations between the physiological and structural changes in the response of evapotranspiration to elevated CO2? The recent CO2-enrichment literature, including Free-Air CO2 Enrichment (FACE), natural CO2 sources, whole-ecosystem enclosures, is then reviewed to address the following issues: (4) How do the mechanisms leading to changes in the 2xCO2 simulations of LAI and evapotranspiration compare to canopy-scale experimental data? (5) Is it possible to define the likely global-scale pattern of plant canopies response to increasing CO2?

2. Model and Data Description

2.1. Vegetation Model

The vegetation model aims at estimating LAI and vegetation carbon and water budgets, from prescribed climate and biome distribution. The basic underlying assumption is that, on the long term, plant canopies develop until they reach a quasi-equilibrium, which depends on local resource availability [Woodward, 1987; Woodward et al., 1995; Neilson, 1995; Kergoat, 1998]. This balanced functioning is characterized by 3 criteria: The average water stress must be sustainable (this criterion is referred to as the “water stress criterion”), the canopy lowest leaves must have a positive annual carbon balance (the “self-shading criterion”), and the annual photosynthesis must cover the canopy construction and maintenance costs (the “carbon-cost criterion”). In practice, for each gridcell, these three criteria are computed for increasing LAI values, and the model retains the highest LAI, which fulfills all of them. The first two criteria are described by Kergoat [1998] and are only briefly outlined below. Details on the carbon-cost criteria are given in Appendix A.

2.1.1. Water Stress Criterion

As evapotranspiration usually increases with LAI, the soil water deficit also increases with increasing LAI. By assumption, for a given climate, the LAI is limited to prevent critical soil water depletion [Grier and Running, 1977; Eagleson, 1982; Woodward, 1987]. The model takes into account the physiological and ecological adaptations of different plant functional types. It accounts for plant drought-avoidance and drought-resistance strategies, such as drought-deciduousness and deep rooting [Kergoat, 1998]. The water balance submodel is a two source PM equation. Soil evaporation, rainfall interception, transpiration, snowpack and freezing processes are simulated.

2.1.2. Self-Shading Criterion

Increasing canopy LAI attenuates the light, which is available at the bottom. As a result, the photosynthesis of the lowest leaf layer decreases, and may be exceeded by leaf respiration. This criterion is thought to limit LAI for dense canopies, for example, moist tropical forests [Alexandre, 1981]. The self-shading criterion uses a leaf photosynthesis and respiration submodel for the lowest leaf layer of the canopy [Kergoat, 1998].

2.1.3. Carbon-Cost Criterion

This criterion corresponds to an ‘energy’ limitation of vegetation growth [Grier and Running, 1977; Gholz, 1982; Neilson, 1995]. It is an addition to the model used by Kergoat [1998], stating that the annual canopy carbon gain must cover the canopy maintenance and construction cost.
Canopy photosynthesis and net primary productivity saturate with increasing LAI, whereas the carbon requirement is approximately proportional to LAI. As a result, there is a physical limit to LAI development, which is reached when carbon supply equals carbon demand (Appendix A). This equilibrium strongly depends on the environmental conditions. For example, a short and cold growing season, typical of high latitudes, will drastically reduce annual photosynthesis and net productivity. The carbon-cost criterion will then produce a low LAI. Such an energy limitation also coincides with a nutrient constraint on plant growth. Indeed, high latitude ecosystems are often nutrient limited, and low soil temperature reduces nitrogen mineralization. In the model, warming is expected to stimulate photosynthesis in a cold climate, which is what is expected from both a direct effect of temperature on photosynthesis and a nutrient-mediated effect on growth. Overall, the carbon-cost criterion captures the primary constraint of low temperature and solar radiation on LAI and productivity [Neilson, 1995; Haxeltine and Prentice, 1996].

In order to estimate the equilibrium LAI from these three criteria, the model is run for five years, at the daily time step, using climate data interpolated from monthly climate inputs. It requires the distribution of 7 vegetation types: tundra, evergreen needle-leaved forest, evergreen broad-leaved forest, dry-deciduous forest, cold-deciduous forest, grasslands and crops, and Mediterranean vegetation or shrubland. Parameters, ranging from physiological characteristics, like maximum stomatal conductance, to ecological adaptations like drought resistance, are taken from the literature [Kergoat, 1998]. For deciduous types, LAI is set to 0 during a dormancy period, which is prescribed from satellite data [Moulin et al., 1997]. Details of the gas exchange equations can be found by Cayrol et al. [2000] and in the Appendix A.

### 2.2. Satellite Derived LAI and fPAR Data Sets

Satellites provide unique data sets to check global models of terrestrial ecosystems. The reflectance factors in the visible and near-infrared domain and their combination (NDVI) have been related to the fraction of PAR (photosynthetically active radiation) absorbed by plant canopies (fPAR), and to other surface parameters, like LAI and vegetation cover. The AVHRR global archive has been processed to produce different estimates of fPAR and LAI [Sellers et al., 1996b; Myneni et al., 1997a; Tian et al., 2000]. Here, modeled LAI and fPAR are compared to their counterparts derived from the AVHRR-FASIR 1987 data set [Sellers et al., 1996b, ISLSCP CD-ROM] and from the MODIS-LASUR data set. This data set is based on the MODIS algorithm [Tian et al., 2000] prototyped with the LASUR surface reflectances [Berthelot et al., 1997, LASUR CD-ROM]. It benefits from atmospheric corrections [Ouaidrari et al., 1997] and state-of-the-art retrieval algorithm [Tian et al., 2000]. fPAR estimates are more accurate than satellite derived LAI [Myneni et al., 1997a], because of a reduced sensitivity to signal noises.

### 3. Simulation Design

[11] Given the variability of plant response to CO2, we use a number of different assumptions on leaf-level response to CO2. Besides a control simulation, four simulations investigate the model sensitivity, whereas two additional simulations address the impact of atmospheric feedback on global LAI (Table 1).

#### 3.1. Simulation CLIM: Control Simulation

[12] The CLIM simulation estimates the LAI in equilibrium with present-day climate (350 ppmv) using the standard input of the IGBP model intercomparison [Cramer et al., 1999]. It includes the 0.5° × 0.5° monthly climatology of Leemans and Cramer [1991] (updated, Cramer, personal communication, 1995), and the Zobler soil map. For consistency reasons, the biome distribution map is the one used by the ARPEGE climate model [Wilson and Henderson-Sellers, 1985].

#### 3.2. Simulation RAD: Climate Only Simulation

[13] The second simulation, RAD, uses a 2xCO2 climate (700 ppmv) that accounts solely for CO2 radiative effect. Monthly anomalies obtained from the ARPEGE climate simulation have been super-imposed to the climatology: additional biases for air temperature, proportional biases for precipitation, vapor pressure and incoming short-wave monthly fields. The doubled-CO2 climate simulations are performed with the ARPEGE-Climat model of Météo-France [Déqué et al., 1994; Douville et al., 2000] forced by sea surface temperature and sea-ice anomalies obtained from the “GHG” transient coupled experiment of the Hadley Centre [Mitchell and Johns, 1997]. With a 2°C global warming and a 6% precipitation increase, the ARPEGE model shows a moderate response to CO2 doubling, which is within the range of similar studies, but closer to the less responsive models [Houghton et al., 2001].

#### 3.3. Simulation STOM: Stomatal Response

[14] The third simulation, STOM, uses the same climate as RAD, but accounts for a decrease of stomatal conductance in response to elevated CO2. We choose to investigate leaf-level responses of stomata and photosynthesis to elevated CO2 independently. In fact, it is still unclear whether a single set of prognostic equations, like coupled photosynthesis-stomata models, is able to represent the variety of

### Table 1. Simulation Design

<table>
<thead>
<tr>
<th>Simulations</th>
<th>Climate</th>
<th>Leaf Level Assumption</th>
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<tbody>
<tr>
<td>CLIM</td>
<td>Present-day, Leemans and Cramer</td>
<td>-</td>
</tr>
<tr>
<td>RAD</td>
<td>ARPEGE:2xCO2</td>
<td>-</td>
</tr>
<tr>
<td>STOM</td>
<td>ARPEGE:2xCO2</td>
<td>Stomatal closure</td>
</tr>
<tr>
<td>FERT</td>
<td>ARPEGE:2xCO2</td>
<td>Enhanced photosynthesis</td>
</tr>
<tr>
<td>MAX</td>
<td>ARPEGE:2xCO2</td>
<td>Stomatal closure and enhanced photosynthesis</td>
</tr>
<tr>
<td>STOM2</td>
<td>ARPEGE:2xCO2+STOM iterated</td>
<td>Stomatal closure</td>
</tr>
<tr>
<td>MAX2</td>
<td>ARPEGE:2xCO2+MAX iterated</td>
<td>Stomatal closure and enhanced photosynthesis</td>
</tr>
</tbody>
</table>
contrasted experimental results. Calibration of key-parameter is often necessary (e.g., nitrogen content, Bunce [2000], Luo et al. [1999], Medlyn et al. [2001]). Here, a maximum CO₂ impact on plant stomata [Field et al., 1995; Drake et al., 1997; Morison, 1998] is obtained by increasing the leaf-level minimum stomatal resistance (Appendix A). Medlyn et al. [2001] have shown that such a framework successfully reproduces the CO₂ effect on stomatal conductance for a set of enrichment experiments. For consistency reasons, we apply the same resistance bias as Douville et al. [2000]. This bias is taken from a 2xCO₂ simulation with the Hadley Center GCM [Cox et al., 1999] (hereinafter referred to as C99). It averages +51%. Simulations using a uniform +50% response, (not shown) lead to similar results. Compared to the results of elevated CO₂ field experiments, this is a strong leaf-level physiological response. It is closer to the change prescribed by Sellers et al. [1996a] than to the +100% increase prescribed by Pollard and Thomson [1995] and Henderson-Sellers et al. [1995].

3.4. Simulation FERT: CO₂ Fertilization
[15] In contrast, the FERT simulation assumes unchanged stomatal conductance, but includes a CO₂ fertilization effect on photosynthesis. This simulation is motivated by some recent studies, which suggest that tree stomata do not close or close slightly in elevated CO₂ [Curtis and Wang, 1998; Saxe et al., 1998; Medlyn et al., 2001]. This possibility has been overlooked in previous global modeling studies. The CO₂ fertilization effect is applied to the leaf-level photosynthesis. Both the maximum photosynthesis rate and the quantum yield are increased by 25% (Appendix A). Such a leaf-level photosynthesis response is commonly observed, at least for short-term CO₂ enrichment [Drake et al., 1997]. Many experiments produce even larger stimulation of the assimilation rate (40% to 60%), but the biomass increases usually less and acclimation often reduces CO₂ fertilization.

In the model, carbon allocation and annual cost of leaves are not modified by elevated CO₂. As a result, changes in carbon available for leaf biomass parallel changes in photosynthesis. Therefore, a 25% increase is reasonable. Since phenological changes are also likely to occur, the growing season is shifted according to the climate: Temperature and rainfall thresholds associated with phenological changes are inferred by matching present-day phenology prescribed from satellite data and climate (CLIM). In simulation FERT, leaf emergence and leaf shedding are triggered by the same thresholds, and follow the temporal shifts in temperature seasonal course for cold-deciduous biomes, and the temporal shift in rainfall for dry-deciduous biomes.

3.5. Simulation MAX: Stomatal Response and Fertilization Effect

3.6. Feedback Simulations
[17] In addition, the importance of feedbacks between vegetation and the atmosphere is assessed with the STOM2 and MAX2 simulations. These simulations correspond to an asynchronous coupling between vegetation and the atmosphere, for the STOM and MAX scenarios. The stomatal resistance and LAI anomalies from simulations STOM and MAX are imposed to the ARPEGE climate model, through changes in the land surface scheme. This in turn provides new 2xCO₂ climates. These climatic scenarios are fully described by Douville et al. [2000]. They are used here as a forcing for the LAI model, which leads to the STOM2 and MAX2 simulations. The comparison with STOM and MAX provides insights on the feedback in the vegetation/climate loop.

4. Results

4.1. Control Simulation

4.1.1. Evaluation With AVHRR Satellite Data
[18] Figure 1 shows the fPAR obtained by the model and derived from the AVHRR for year 1987 (FASIR data set), along with the LAI from the model and MODIS-LASUR data set for July. Pixel-based scatterplots for fPAR and LAI are displayed on Figure 2.

[20] The agreement between modeled fPAR and remotely sensed fPAR is good (Figures 1a 1b, and Figure 2). This indicates that the model mechanisms capture the global patterns of vegetation development and light-harvest. For LAI, the agreement is not as good but still reasonable, the main discrepancies being over the Amazon Basin and the high latitude forests (Figures 1c, 1d and 2b, 2c). The LAI simulation successfully reproduces aridity gradients, e.g., East-West in North America, North-South in central Asia, and also temperature gradients (high latitudes, mountains).

The model provides reasonable LAI values for the moist tropical and temperate forests. The disagreement between modeled and satellite-derived LAI over the Amazon basin is likely to be caused by persistent cloud cover that lower the NDVI signal. The discrepancy for the high latitude forest may indicate a model bias. However, there is growing evidence that the FASIR satellite-derived LAI product may be overestimated for the high-latitude forests. Recent remotely sensed LAI maps for the Canada (Chen, unpublished data) show significantly lower values, which are closer to the modeled LAI in Figure 1c. The MODIS-LASUR data set also gives lower LAI values for both Canada and Eurasia, and the agreement is better for Figure 2c than Figure 2b. The same discrepancy between modeled and remotely sensed LAI was found by Dickinson et al. [1998] with a different LAI model. Besides, field measurements found LAI values of 1.5 and 2.5 for some Siberian mature pines and larches stands respectively [Kellieher et al., 1997, 1998]. We acknowledge, however, that our LAI model might be biased toward...
low values for high latitude forests. Since we are investigating the response of vegetation to a change in resource availability, it is important to note that the agreement for fPAR is good in the high latitudes. Indeed, fPAR represents the light resource. Model and observations agree that there is a potential for LAI development and increased light capture in the high latitudes. Considering the good agreement for fPAR and the caveat in remotely sensed LAI, we conclude that the model predicts a reasonably accurate global LAI. The level of agreement between the model and observations suggests that the model might have the same sensitivity to climate change as real vegetation.

4.2. Elevated CO₂

4.2.1. Response of LAI

[21] In experiment RAD, where only the CO₂ radiative effect is considered (Figure 3a), the patterns of LAI anomalies show both decreases and increases. As expected, there is an increase of LAI at high latitudes, on the order of 0.3 m²/m² (Table 2). This increase is related to the air warming, which favors photosynthesis and therefore enhances the annual productivity. As a result, LAI values that were limited by the carbon-cost criterion in CLIM reach larger values in RAD. A second point to note is the decrease of LAI over Southern Eurasia and the western continental US, which is caused by an alteration of the water balance. Indeed, the atmospheric demand for water vapor is larger in RAD, leading to high water losses and increased water stress. As a consequence, the equilibrium hypothesis adjusts LAI to lower values for these areas so that the water stress remains sustainable. The tropical zones display both positive and negative LAI anomalies, directly related to local changes in the precipitation field.

[22] When the stomatal closure is considered, experiment STOM (Figure 3b), most of the drought-induced LAI decrease is compensated for, and LAI is turned back to its CLIM values or above. This result means that stomatal closure induces a reduction of water losses, which is large enough to significantly improve the yearlong water availability, in contrast to the RAD scenario. This affects plant canopies that are limited by the water criterion, and, to a lesser extent, plant canopies that are limited by the carbon-cost criterion where water availability is not optimal.

[23] The FERT simulation (Figure 3c) is closer to RAD, with both increase and decrease of LAI, with the exception that high-latitude LAI increase is much stronger, commonly reaching +1 m²/m². Such stimulation is explained by an
enhanced carbon balance due to warmer temperature and increased photosynthesis, which alleviates the carbon-cost criterion. The shift in leaf phenology, corresponding to an earlier spring warming and a later fall cooling, also contributes to enhance the carbon budget. This shift averages 7 days both in spring and fall for the temperate and boreal deciduous ecosystems, and is nearly nonexistent for the tropical biomes. In addition, enhanced photosynthesis has an impact on canopies limited by the self-shading criterion (e.g., moist Tropics), because it decreases the light compensation point of the lowest leaves. A new equilibrium is reached for a slightly higher LAI value. As a result, even dense canopies display positive anomalies (e.g., Amazon basin). Conversely, the areas limited by the water criterion are almost identical in the RAD and FERT experiments.

When both photosynthesis enhancement and stomatal closure are considered, experiment MAX (Figure 3d), there is an overall increase of LAI. The LAI anomaly map approximates the sum of the STOM and FERT maps, but the processes are not strictly additive (Table 2). As in simulation FERT, there is a positive feedback between LAI and photosynthesis, in areas where the carbon-cost criterion is the limiting factor. Indeed, when photosynthesis is enhanced, the LAI also increases, which in turn allows additional photosynthesis. Table 2, for instance, shows that a 25% increase of the photosynthesis rate gives a LAI increase of 41%, from the STOM to the MAX simulations of tundra. This positive feedback, pointed out by Lloyd and Farquhar [1996], is important where the fPAR is low.

### 4.2.2. Response of Evapotranspiration and Soil Water

In response to the atmosphere warming (simulation RAD), there is a general increase of the latent heat flux wherever soil moisture is available (Figure 4a). This increase reaches 10 to 15% (∼9 mm/mo) of the CLIM evapotranspiration during the tropical rain season and the boreal summer. Some spatial variability in the Tropics is related to variations in the precipitation. As a result, the soil water in the root zone decreases significantly, mostly in the Tropics (Figure 5a). However, when a CO2-induced stomatal closure is taken into account, (simulation STOM Figure 4b), the latent heat flux anomaly is reversed, in spite of the higher atmospheric demand. This is especially true for fully developed canopies, with high LAI values and a small contribution of soil evaporation. Sellers et al. [1996a] and Betts et al. [1997] have underlined this feature. Compared to RAD, the soil water anomaly is reversed in STOM, and the difference with present-day climate becomes positive (Figure 5b). Such a pattern, however, is completely changed if CO2 is assumed to enhance photosynthesis without affecting stomatal conductance (simulation FERT). In this case, ETR is considerably enhanced compared to present-day simulation (Figure 4c). For the northern mid-to-high latitudes, ETR is significantly larger than in the climate-only RAD simulation, and the soil moisture is depleted in the summer (Figure 5c). This is a straightforward impact of increased LAI and longer growing season. In FERT, the water cycle in the Tropics is similar to the climate-only simulation RAD. When both photosynthesis and stomatal changes are considered (MAX), the Tropics behave like in the STOM simulation; Stomatal closure has a larger impact than LAI increase and this maintains ETR to present-day level, despite increased
The overall soil moisture is close to present-day values (Figure 5d). From Figures 4 and 5, it appears that even the sign of the effect of CO2 on ETR and soil moisture is uncertain and depends on plant response to CO2.

4.3. Atmospheric Feedback

[26] The RAD, STOM, FERT and MAX simulations are performed with the same climate forcing. Since these simulations lead to large differences in LAI and canopy gas exchange, feedbacks to the atmosphere may be expected. Douville et al. [2000] used the leaf conductance and LAI of the STOM and MAX simulations to perform 2xCO2 climate experiments with the ARPEGE model. They found that the climate response to CO2-induced changes in the vegetation was globally a second-order effect compared to the radiative effect, but regional impacts proved to be important. These “new” 2xCO2 climatic fields are used here to simulate equilibrium LAI and ETR. The resulting LAI simulations, referred to as STOM2 and MAX2, therefore represent the second iteration of an asynchronous coupling between the atmosphere and the vegetation systems. As shown in Table 3, biome-averaged LAI values in STOM and STOM2 are

Table 2. Biome-Averaged Leaf Area Index (L, m^2/m^2), Annual Evapotranspiration (E, mm/yr), and Available Water in the Root Zone (W, mm) for the CLIM, RAD, STOM, FERT, and MAX Simulations

<table>
<thead>
<tr>
<th>Biome</th>
<th>L</th>
<th>E</th>
<th>W</th>
<th>L</th>
<th>E</th>
<th>W</th>
<th>L</th>
<th>E</th>
<th>W</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tundra</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
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<tr>
<td>Needle-Leaved Forest</td>
<td>1.4</td>
<td>97</td>
<td>35</td>
<td>2.9</td>
<td>318</td>
<td>64</td>
<td>2.8</td>
<td>389</td>
<td>66</td>
</tr>
<tr>
<td>Evergreen Forest</td>
<td>1.6</td>
<td>121</td>
<td>34</td>
<td>3.2</td>
<td>381</td>
<td>63</td>
<td>2.9</td>
<td>429</td>
<td>66</td>
</tr>
<tr>
<td>Cold Deciduous Forest</td>
<td>1.7</td>
<td>106</td>
<td>35</td>
<td>3.6</td>
<td>319</td>
<td>68</td>
<td>3.0</td>
<td>372</td>
<td>69</td>
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<tr>
<td>Dry Deciduous Forest</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Broad-Leaved Evergreen Forest</td>
<td>1.4</td>
<td>87</td>
<td>31</td>
<td>2.9</td>
<td>427</td>
<td>66</td>
<td>3.1</td>
<td>476</td>
<td>70</td>
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<tr>
<td>Mediterranean Vegetation/ Shrubland</td>
<td>1.7</td>
<td>474</td>
<td>120</td>
<td>3.6</td>
<td>486</td>
<td>102</td>
<td>4.2</td>
<td>528</td>
<td>108</td>
</tr>
<tr>
<td>Grass/Crops</td>
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<td>229</td>
<td>84</td>
<td>3.1</td>
<td>469</td>
<td>98</td>
<td>4.2</td>
<td>510</td>
<td>104</td>
</tr>
</tbody>
</table>

Figure 3. Effect of a doubling of CO2 concentration on Leaf Area Index (m^2/m^2). (a) LAI anomaly between the RAD (climate only) and CLIM (present-day) simulations. (b) Anomaly between STOM (maximum stomatal response) and CLIM. (c) Anomaly between FERT (maximum photosynthesis response) and CLIM. (d) Anomaly between MAX (stomatal and photosynthesis response) and CLIM. See color version of this figure at back of this issue.
nearly the same. The reduction of latent heat flux in STOM produces a small additional warming \[\text{Douville et al.}, 2000\] which does not affect the equilibrium LAI so much, and the differences between STOM and STOM2 are small in comparison to the differences between the RAD, STOM, FERT, and MAX scenarios themselves. This is also true for the MAX and MAX2 simulations. Overall, at the biome level, the differences between the first and second steps of the coupling are smaller than 0.1 m²/m², with only the grass/crop biome showing a 0.2 m²/m² increase.

Figure 4. Latitude versus time maps of monthly evapotranspiration anomaly (mm/mo). (a) RAD-CLIM. (b) STOM-CLIM. (c) FERT-CLIM. (d) MAX-CLIM.

[27] Ecosystem averages (Table 3) tend to mask some regional patterns. Figure 6 displays the strongest regional feedbacks found over 10⁵ x 10⁵ areas - the Amazon basin, North-Western Eurasia - along with an example of a weak response over North-Eastern Eurasia.

[28] Over the Amazon basin, the STOM2 and MAX2 simulations show an enhancement of ETR and nearly no change in LAI (Figure 6a). This is due to the slightly enhanced air temperature and atmospheric water demand simulated by ARPEGE forced by the STOM and MAX.
Over North-Western Eurasia, the atmospheric feedback-loop stimulates LAI and ETR, as expected from a slightly warmer climate (Figure 6b). However, over North Eastern Eurasia, these effects are much smaller and even reversed (Figure 6c). Such a heterogeneous response contributes to make biome-averaged LAI very similar for the STOM/STOM2 and MAX/MAX2 simulations. In most regions, ETR is slightly increased in STOM2 and MAX2 compared to STOM and MAX respectively, and the feedbacks are therefore mostly negative. This suggests that results from STOM and MAX are robust and not underestimated. Atmospheric feedbacks, which may depend to some extent on the atmospheric model, proved to be second order effects, as far as plant structure is concerned. This study, as well as Levis et al. [2000], points out that the basic assumptions on plant response to CO2 are preeminent in biosphere/climate coupling [Foley et al., 1998].

5. Discussion

Given such a large uncertainty in LAI and ETR response to CO2, we have reviewed the literature of CO2 surface changes [Douville et al., 2000]. Over North-Western Eurasia, the atmospheric feedback-loop stimulates LAI and ETR, as expected from a slightly warmer climate (Figure 6b). However, over North Eastern Eurasia, these effects are much smaller and even reversed (Figure 6c). Such a heterogeneous response contributes to make biome-averaged LAI very similar for the STOM/STOM2 and MAX/MAX2 simulations. In most regions, ETR is slightly increased in STOM2 and MAX2 compared to STOM and MAX respectively, and the feedbacks are therefore mostly negative. This suggests that results from STOM and MAX are robust and not underestimated. Atmospheric feedbacks, which may depend to some extent on the atmospheric model, proved to be second order effects, as far as plant structure is concerned. This study, as well as Levis et al. [2000], points out that the basic assumptions on plant response to CO2 are preeminent in biosphere/climate coupling [Foley et al., 1998].
enrichment experiences, looking for effects of physiology and structure on plant canopies and ETR. This section presents a discussion of these experimental results, with a focus on the mechanisms that lead to changes in LAI and ETR in our global simulations. We also attempt to define a “likely” response for the different ecosystems.

5.1. Self Shading Criterion

[30] According to our simulations, CO₂ fertilization results in a lower light compensation point for the lowest leaf layer and therefore produces an increase in LAI, where this criterion is limiting. In line with this mechanism, several experiments report an increased growth in forest-floor plants in response to elevated CO₂, for both temperate and tropical forests [Osborne et al., 1997; Hättenschwiler and Körner, 1996; Würth et al., 1998; Naumburg and Ellsworth, 2000]. Close examinations have demonstrated that plant carbon balance was improved in typical understory light regimes [Naumburg and Ellsworth, 2000]. Fewer studies have considered a whole dense canopy growing in near natural conditions. So far, recent results from FACE facilities point toward an insignificant increase or an uncertain trend of LAI for dense forest canopies. Wullschleger and Norby [2001] did not measure any significant effect of CO₂ on LAI for mature sweetgum plantations (LAI = 6). The Duke forest FACE experiment led to uncertain changes in LAI (Lichter et al. [2000] do not discard a small increase), with understory saplings showing stimulated photosynthesis [DeLucia and Thomas, 2000]. Unfortunately, such tree plantations, where the dominant strata is monospecific, often even-aged, and species diversity is usually low, may overemphasize the individual response of the dominant trees. Multispecific and multistrata canopies have a greater plasticity [Reich et al., 2001] and might show a stronger LAI response. Overall, although experiments with mature and multispecies forest ecosystems are still scarce, a moderate increase of LAI is likely to affect dense canopies growing in favorable environments. This is compatible with the moderate increase in LAI (10%) simulated for tropical dense forests and some temperate closed canopies in the FERT and MAX simulations (Figures 3c, 3d, Table 2).

[31] As a consequence of such a weak LAI response, the impact of LAI on ETR is expected to be small for dense canopies limited by the self-shading criteria. Canopy conductance is not sensitive to changes in LAI for high LAI values [Schulze et al., 1994]. Therefore, ETR will mainly reflect the changes in leaf-level stomatal conductance. In contradiction with what was commonly assumed in several global-scale studies, there is growing evidence that tree stomatal conductance may not respond strongly to elevated CO₂. More precisely, recent experimental results suggest that needle-leaved trees are less responsive than broad-leaved deciduous trees, which are less responsive than grasses. Even more important, mature trees seem to be less responsive than saplings [Saxe et al., 1998; Medlyn et al., 2001]. Conductance decrease on the order of 0–10% is commonly found in conifers, whereas 5–25% and 20–40% are often reported for broad-leaved deciduous trees [Medlyn et al., 2001; Saxe et al., 1998] and herbaceous plants respectively. Therefore, there is growing suspicion that dense forests may exhibit a moderate or hardly significant decrease in canopy conductance in response to CO₂. Ellsworth [1999] found that elevated CO₂ had no significant impact on canopy evapotranspiration of the Duke forest loblolly pines FACE. Stomatal conductance and soil moisture were unchanged by CO₂ treatment. For the sweetgum FACE, Wullschleger and Norby [2001] estimated a 12% reduction in stand transpiration and did not notice any LAI compensation effect. These two experiments point toward a relatively small impact of CO₂ on dense temperate forests ETR. So far, there is no evidence that tropical trees stomatal response would differ from those of temperate broad-leaved deciduous and evergreen trees [Lovelock et al., 1999; Körner, 1998]. We therefore argue that dense forests response to CO₂ may consist of a moderate canopy conductance decrease, ranging from 0 to 15%, resulting from moderate stomatal responsiveness and minor increase in LAI.

5.2. Carbon-Cost Criterion

[32] In our simulations, boreal and arctic ecosystems are especially constrained by the carbon cost criterion, which also colimits some temperate ecosystems. Experiments on these systems have investigated the effects of both temperature and CO₂ increase. There is ample evidence that productivity is enhanced by experimental warming at ambient CO₂ (e.g., Chapin et al. [1995], ITEX experiment Henry and Molau [1997]). Such results are in line with the conclusions of many modeling studies, including this one (climate only simulation RAD, Figure 3a). As far as CO₂ is concerned, Oechel et al. [1994] have shown that warming was able to sustain CO₂ fertilization in tundra, which otherwise tends to decrease with time. They stated that warming stimulates nitrogen mineralization, allowing enhanced plant growth. Hoosbeek et al. [2001] found no significant effect of CO₂ on plant biomass for nutrient-poor bogs. Cook et al. [1998] found that grasses growing near CO₂ vents in Iceland show a significant, long-term down-regulation of photosynthesis and decreased LAI. According to Saxe et al. [1998] review, downregulation in trees is rarely large enough to offset the photosynthetic gains. The

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**Table 3. Biome-Averaged Leaf Area Index (L, m²/m²) for the STOM and MAX Simulations and Their Iterations STOM2 and MAX2**

<table>
<thead>
<tr>
<th>Biome</th>
<th>Needle-Leaved</th>
<th>Cold Deciduous</th>
<th>Dry Deciduous</th>
<th>Broad-Leaved</th>
<th>Mediterranean Vegetation / Shrubland</th>
<th>Grass/Crops</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Tundra</td>
<td>Forest</td>
<td>Forest</td>
<td>Forest</td>
<td>Vegetation / Shrubland</td>
<td>Grass/Crops</td>
</tr>
<tr>
<td>L</td>
<td>L</td>
<td>L</td>
<td>L</td>
<td>L</td>
<td>L</td>
<td>L</td>
</tr>
<tr>
<td>CLIM</td>
<td>1.4</td>
<td>2.9</td>
<td>2.8</td>
<td>3.5</td>
<td>4.9</td>
<td>0.8</td>
</tr>
<tr>
<td>STOM</td>
<td>1.7</td>
<td>3.6</td>
<td>3.0</td>
<td>4.2</td>
<td>5.2</td>
<td>1.2</td>
</tr>
<tr>
<td>STOM2</td>
<td>1.7</td>
<td>3.6</td>
<td>3.1</td>
<td>4.3</td>
<td>5.2</td>
<td>1.1</td>
</tr>
<tr>
<td>MAX</td>
<td>2.4</td>
<td>4.4</td>
<td>4.0</td>
<td>4.7</td>
<td>5.6</td>
<td>1.2</td>
</tr>
<tr>
<td>MAX2</td>
<td>2.4</td>
<td>4.5</td>
<td>4.0</td>
<td>4.7</td>
<td>5.6</td>
<td>1.2</td>
</tr>
</tbody>
</table>

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**Source:** ACL 30 - 10 Kergoat et al.: CO₂ Effects on Global LAI and Evapotranspiration.
CLIMEX experiment has exposed a small catchment of undisturbed boreal vegetation to CO2 enrichment and climate warming [Beerling, 1999]. No effect of CO2 on water runoff was noted, a fact attributed to a small LAI increase fully compensating the small reduction in stomatal conductance. Taken together, these results point toward a clear positive impact of temperature and a weak CO2 fertilization effect, reduced in nutrient-poor habitats. Synergy between warming and CO2 causes larger stimulation of plant productivity and LAI. Whether plant carbon budgets can improve and result in denser canopies seems to be closely related to the future of nutrient availability. Unfortunately, the potential role of nutrients in a CO2 rich world is still a matter of hot debate; see discussion by Gifford [1994], McGuire et al. [1995], Lloyd and Farquhar [1996], and Schimel [1998] among others. Nitrogen (N) use efficiency is sometimes considered to be an absolute constraint on growth, whereas others state that the nitrogen cycle could “follow” the carbon cycle on the long term. Biotic N fixation, atmospheric N deposition and temperature-stimulated decomposition rates [Rustad et al., 2001] favor N availability, but the low N content of plants grown in elevated CO2 may provide a negative feedback to N availability on the long term. Interestingly, several experiments have shown an increase of the fraction of N-fixing plants [e.g., Warwick et al., 1998, Zanetti et al., 1997]. Moreover, plant carbon balance, as well as the whole nutrient cycle, will benefit from a shift in phenology leading to earlier springs and delayed falls. Such a modification of plant phenology has already been recorded in the temperate and boreal zones, and attributed to the rise in temperature observed during the last decades [Menzel and Fabian, 1999; Myneni et al., 1997b]. For these reasons, we suggest that the likely response of LAI to warming and CO2 doubling is a moderate but significant increase at high latitudes and high elevations. Such a LAI response is consistent with, and possibly slightly weaker than our FERT and MAX simulations, which lead to an LAI increase on the order of 1 m2/m2 (Figures 3c, 3d, Table 2). Furthermore, given the current uncertainty on tree stomatal response to CO2 (especially for old conifers), it is well possible that the CO2 net effect at boreal latitudes will be an increase rather than a decrease in ETR, as illustrated by simulation FERT (Figure 4c).

5.3. Water Stress Criterion

Interactions between CO2, water and plant growth have been documented by a fair number of field experiments, dealing with different types of grasslands, rain-fed crops, and, marginally, with shrubland and dry woodland ecosystems. For herbaceous canopies, elevated CO2 is generally found to decrease evapotranspiration rate, to enhance soil moisture, and to increase plant growth and LAI. Elevated CO2 tends to promote a significant but incomplete LAI compensation effect, with either a larger maximum LAI or an increase in late-season LAI caused by the delay of soil

Figure 6. (opposite) Atmospheric feedbacks on regional LAI and ETR for 10 by 10 degrees areas located in (a) Amazonia, (b) North-West Eurasia, and (c) North-East Eurasia. Stomatal closure in STOM and MAX reduces ETR, increases atmospheric demand for water vapor, which in turn causes ETR to increase in simulation STOM2 and MAX2, for Amazonia and North-West Eurasia (maximum regional responses) but not for North-East Eurasia. LAI is slightly or not affected by atmospheric feedbacks.
moisture depletion (C3 annuals Field et al. [1997], C4/C3 tallgrass prairie Owensby et al. [1999], C4 shortgrass prairie Morgan et al. [2001], calcareous grassland Niklaus et al. [1998], Mediterranean community Nijs et al. [2000]). Site fertility may dampen these effects [Field et al., 1997], and there is a consensus that water relations drive plant growth more than CO2 fertilization per se. Experiments with crops usually follow this pattern, with a significant species-specific variability. Stomatal closure is usually strong (30–50% in doubled CO2), and the compensation by LAI growth varies from nonexistent to more than complete, depending on the crop. An increase in ETR, resulting from a strong LAI enhancement has been reported for sunflower canopies [Hui et al., 2001], an almost exact compensation effect has been noted for cotton in a FACE [Kimball et al., 1994], whereas partial compensation has often been found, for instance for wheat [Kimball et al., 1999]. Much less is known for shrublands and dry forests. Moderate stomatal conductance decrease (10% to 20%) has been reported (Nevada FACE facility Pataki et al. [2000] and Nowak et al. [2001], natural CO2 springs Bettarini et al. [1998]).

Overall, for water limited herbaceous systems, experimental results support the assumption of the STOM and MAX simulations, which suggest that plant water savings can alleviate the increased atmospheric demand for water vapor (climatic effect of CO2) and even slightly increase growth and LAI. For shrubland and dry woodlands, LAI response could fall between FERT (slight decrease, Figure 3c) and STOM (slight increase, Figure 3b). Most often, annual ETR does not change much, because of LAI partial compensation and delayed onset of drought. Changes in ETR seasonality are expected, though. According to our model, water limited LAI is rather insensitive to photosynthesis fertilization, as the MAX and STOM simulations are similar for these areas. This is consistent with the results of Häitenschwiler et al. [1997] (for Quercus ilex) and Morgan et al. [2001] (C3 grassland). Water limited ecosystems show a strong decoupling between leaf-level response (stomatal conductance and photosynthesis rate) and canopy scale response, caused by the dynamical adjustment of LAI to soil moisture.

5.4. Global-Scale Response

When the different plant types and climate zones are considered, this review points toward a moderate increase of global LAI and a relatively small decrease of global annual ETR caused by vegetation response to a doubling of CO2 concentration. The main causes are a moderate response of tree stomata to CO2 and a compensation by stimulated growth (grasslands, crops and boreal zones). Shifts in phenology and soil moisture seasonality also contribute to this result. A tentative global response of LAI and ETR is illustrated by the shaded area in Figure 7. As large areas may be closer to the FERT or CLIM simulations than to the

![Figure 7. Effect of doubled CO2 on LAI (m^2/m^2) and ETR (mm/day). Differences between global LAI and ETR from STOM, FERT, MAX simulations and from RAD (climate only) simulation are displayed, along with the results of some previous studies. HS95 is for Henderson-Sellers et al. [1995], S96a and S96b are for Sellers et al. [1996a], C99 is for Cox et al. [1999], L00a and L00b (B97a and B97b, respectively) are for simulations with fixed and dynamical canopies by Levis et al. [2000] and Betts et al. [1997], respectively. The shaded zone figures a tentative response of plant canopies to doubled CO2 accounting for a possibly low response of tree stomata (see text).](image-url)
STOM and MAX simulations (boreal zone, tropical forests), the STOM simulation has been replaced by the middle-point of STOM and CLIM, and the MAX simulation has been replaced by the middle-point of MAX and FERT. Other studies, with either fixed [HS95, S96, C99, B97a, L00a] or dynamical LAI [B97b, L00b], are also displayed for the purpose of comparison. Figure 7 clearly illustrates the impact of LAI adjustment on ETR, since studies allowing for LAI changes show a weak negative or even positive effect of plant response to CO₂ on ETR.

The compensating role of LAI found in this study is in line with the conclusion of Betts et al. [1997] and Levis et al. [2000], but it is much closer to the former than to the latter. In fact, our likely response of LAI and ETR agrees fairly well with Betts et al. [1997] estimates but differs noticeably from the strong LAI increase of Levis et al. [2000], especially in the tropics (+4.5 LAI averaged over 10S-10N). Whether this is a consequence of differences in modeling, or in the climate-coupling procedure is unclear [Levis et al., 2000]. Differences in LAI response to CO₂ are larger and more difficult to analyze than differences in stomatal response. One can note that Betts et al. [1997] vegetation model relies on “ecosystem-physics” rules to determine LAI [Woodward, 1987; Woodward et al., 1995], as does our model. Such an approach has the ability to decouple the leaf and canopy scale responses [Körner, 1996], which results in moderate response to elevated CO₂.

6. Concluding Remarks

In this study, we analyzed LAI and evapotranspiration response to a doubling of CO₂ concentration using a vegetation model. The respective roles of leaf-level stomatal conductance decrease and photosynthesis enhancement were investigated with the help of several simulations. We showed that evapotranspiration is intimately tied to plant response to elevated CO₂, and that uncertainty in plant response could either lead to a significant decrease or a small increase of evapotranspiration, compared to a situation where only the effect of CO₂ on climate is accounted for. However, after reviewing the literature on CO₂ enrichment experiments, we conclude that plant response to CO₂ doubling may have a relatively small net impact on global evapotranspiration, and may provoke a moderate, but locally more important, increase of LAI. This conclusion is mainly based on the fact that (1) tree stomata may be less responsive to CO₂ than was previously assumed, (2) stimulated plant growth and phenology adjustment have the potential to partly cancel the water savings caused by stomatal closure in elevated CO₂. Although plant types significantly differ in their response to CO₂, as do the mechanisms controlling LAI in different climatic conditions, moderate LAI increase and small or even negligible cumulative ETR decrease are remarkably common features of experimental studies. The amplitude of plant growth stimulation in the boreal zone, related in an uncertain manner to the nutrient cycle, and the stomatal response of mature trees in the moist Tropics are the main sources of uncertainties. Clearly, a number of other factors have the potential to impact biosphere-atmosphere interactions in a CO₂ rich world, the first of them being human-induced land-use change. Nevertheless, this work demonstrates the importance of plant response to CO₂ for land surface hydrology.

Appendix A: Description of the Vegetation Model

The vegetation model is extensively described in Kergoat [1998], the gas-exchange equations are detailed in Cayrol et al. [2000]. Additions to these papers are briefly listed here.

A1. Carbon Cost Criteria

The annual leaf carbon requirements depend on plant specific leaf area (SLA) and leaf lifetime (τ). The carbon cost criterion estimates SLA, τ according to Reich et al., [1992] relationships, following Haxeltine and Prentice [1996]. The LAI that optimizes the carbon-cost criterion is computed according to equation:

\[ \text{LAI}/\tau \times \text{SLA} = A_1 \times \text{Rc} \times \text{GPP}(\text{LAI}), \]

where \( \tau \times \text{SLA} = 0.02 \text{ m}^2 \text{ g}^{-1} \text{ °C yr}, \text{Rc} \) is the respiration fraction (set to 0.5 for grasses and 0.6 otherwise), \( A_1 \) is the fraction of carbon allocated to the leaves, set to 0.33 for all the vegetation types, GPP is the canopy photosynthesis.

A2. Photosynthesis and Conductance Submodels

For each grid cell, a leaf level photosynthesis model is integrated to the canopy level according to LAI. The daily rate of leaf photosynthesis, P, is given by

\[ P = \frac{\Delta D}{r_s + r_r}, \]

where \( \Delta D \) is the difference in CO₂ concentration between the chloroplast and the atmosphere, \( r_s \) and \( r_r \) are the stomatal and nonstomatal resistances to CO₂ transfer. DI is the day length. The stomatal resistance is a “Jarvis” type resistance [Jarvis, 1976], with a minimum resistance \( r_{s\text{min}} \) modulated by soil available water, vapor pressure deficit and incoming photosynthetically active radiation:

\[ r_s = r_{s\text{min}} \times f_1(W) \times f_2(VPD) \times f_3(I). \]

The residual resistance accounts for mesophyll diffusion and carboxylation processes and is controlled by PAR level and temperature:

\[ r_r = r_{r\text{min}} \times f_4(I) \times f_5(Ta). \]

Parameters for the residual resistance are derived from the maximum rate of photosynthesis, Pmax, the quantum yield, \( \alpha \) and the minimum stomatal resistance, \( r_{s\text{min}} \) [see Cayrol et al., 2000] taken from Körner [1994]. Integration to the canopy gives

\[ P_{\text{can}} = \int_{LAI} P_{\text{dL}} \]

\[ = D \Delta / \left[ k (r_s + r_r) \right] \times \log \left[ r_s I_s + r_r I_r + k I_o (r_s + r_r) \right] / \left[ r_s I_s + r_r I_r + (r_s + r_r) k I_o e^{-k LAI} \right]. \]
where Pean is the daily canopy photosynthesis, \( I_0 \) the surface incoming PAR, \( k \) the PAR extinction coefficient, LAI the canopy leaf area index. \( rs^\prime \) and \( rr^\prime \) are equal to \( rs/f_1 \) and \( rr/g_1 \), respectively. \( I_\text{s} \) and \( I_\text{r} \) are parameters of \( g_1 \) and \( f_3 \).

Similarly, the canopy conductance for water vapor diffusion, \( G_\text{can} \) is given by

\[
G_\text{can} = \int L_\text{ALI} \frac{1.6 \, \text{DL}/rs}{(k/\text{rs})' \log [(I_s + kI_0)/(I_s + kI_0e^{-kL_{\text{ALI}}})]}.
\]

### A3. Doubled CO₂ Parameterizations

[42] The CO₂ impact on stomatal resistance is

\[
r_{\text{min}}'' = \gamma r_{\text{min}}.
\]

The bias \( \gamma \) is prescribed on a pixel basis (see text).

[43] The CO₂ impact on photosynthesis is

\[
r_{\text{min}}'' = \gamma r_{\text{min}}(\text{MAX}) \quad \text{or} \quad r_{\text{min}}'' = r_{\text{min}}(\text{FERT})
\]

\[
P_{\text{max}}'' = 1.25 P_{\text{max}}
\]

\[
\alpha'' = 1.25 \alpha
\]

\[
\Delta'' = 2 \Delta.
\]

### Acknowledgments

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### References


Kergoat et al.: CO₂ Effects on Global LAI and Evapotranspiration


Figure 1. Comparison of the LAI model results with remote sensing estimates. Maximum fPAR (a) simulated for present-day climate and (b) retrieved from the FASIR/AVHRR data set. (c) July maximum LAI (projected, m²/m²) simulated for present-day climate and (d) retrieved from the LASUR/AVHRR data set processed with the MODIS prototype algorithm.
Figure 3. Effect of a doubling of CO₂ concentration on Leaf Area Index (m²/m²). (a) LAI anomaly between the RAD (climate only) and CLIM (present-day) simulations. (b) Anomaly between STOM (maximum stomatal response) and CLIM. (c) Anomaly between FERT (maximum photosynthesis response) and CLIM. (d) Anomaly between MAX (stomatal and photosynthesis response) and CLIM.