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# Modeling Global and Regional Net Primary Production under Elevated Atmospheric CO<sub>2</sub>: On a Potential Source of Uncertainty

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**ABSTRACT:** Terrestrial ecosystem models are built, among several reasons, to explore how the Earth's biosphere responds to climate change and to the projected continual

increase of atmospheric CO<sub>2</sub> concentration. Many of these models adopt the Farquhar et al. approach, in which leaf carbon assimilation of C<sub>3</sub> plants is regulated by two limitations depending on the rate of Rubisco activity and ribulose-1, 5-bisphosphate regeneration (RuBP). This approach was expanded upon by others to include a third limitation that expresses the occurrence, in some plant species, of a photosynthetic downregulation under high concentrations of ambient CO<sub>2</sub>. Several ecosystem models, however, constrain leaf photosynthesis using only two limitations according to the original formulation of Farquhar et al. and thus neglect the limitation that represents the downregulation of photosynthesis under elevated atmospheric CO<sub>2</sub>. In this study, the authors first reviewed the effect of elevated CO<sub>2</sub> on photosynthesis of C<sub>3</sub> plants, which illustrated that short-term observations are likely to considerably underestimate the number of plant species that exhibit a photosynthetic downregulation. Several recent long-term field observations have shown that such downregulation starts to be effective only after several seasons/years of plant exposure to elevated CO<sub>2</sub>. Second, an ecosystem model was used to illustrate that neglecting the photosynthetic downregulation may significantly bias predictions of net primary production of the middle and high latitudes under high atmospheric CO<sub>2</sub> concentrations. Based on both review of field observations and results of simulations, the authors conclude that a more appropriate representation of plant physiology and choice of plant functional types may be required in ecosystem models in order to accurately simulate plant responses to changing environmental conditions.

**KEYWORDS:** Atmospheric CO<sub>2</sub>; Photosynthetic downregulation; Net primary production; Plant functional types; Ecosystem models.

## 1. Background [Return to TOC](#)

Atmospheric CO<sub>2</sub> concentration ( $C_a$ ) has increased by more than 30% since the preindustrial era, from 280 to about 370 ppm, and is expected to reach about 540–970 ppm by the end of the twenty-first century (Houghton et al. 2001). Both laboratory and field observations indicate that a doubling of  $C_a$  would enhance photosynthesis of C<sub>3</sub> plants by about 50%, although the response varies considerably among species (e.g., Curtis and Wang 1998; Lüscher et al. 1998; Norby et al. 1999; Kimball et al. 2002). Some observations also show that an enhancement of plant photosynthesis does not necessarily lead to an enhancement of terrestrial carbon storage (Norby et al. 2002) and that the highly variable responses to increased  $C_a$  among plant types could alter the process of competition among plant species (e.g., Derner et al. 2003), which ultimately may lead to changes in terrestrial ecosystem composition. An additional effect of  $C_a$  increase is the alteration of Earth's climate and its variability through effects of CO<sub>2</sub> on the Earth's radiative budget (Houghton et al. 2001). Consequently, current scientific knowledge suggests that evaluating the implications of the continual  $C_a$  increase requires very sophisticated parameterizations to help understand the complex interactions between the different components of the Earth system.

It is now well recognized that terrestrial ecosystems play a key role in fashioning the Earth's climate and atmospheric chemistry, through its exchanges of energy, momentum, water vapor, and various trace gases such as CO<sub>2</sub> and CH<sub>4</sub> with the atmosphere (Schlesinger 1991; Pielke et al. 1998). For that reason, considerable efforts have been made over the last three decades to develop terrestrial ecosystem

models that describe the multiple interactions that occur at the land surface, and between the surface and the atmosphere at varying spatiotemporal scales (Foley 1995; Hurtt et al. 1998). For instance, some models are now able to integrate a detailed description of land surface physics, vegetation physiology, biogeochemistry, and vegetation dynamics [e.g., IBIS (Foley et al. 1996); MOSES-TRIFFID (Cox 2001); LSM-DGVM (Bonan et al. 2003)].

The representation of processes that occur at the leaf level is a critical aspect of current biospheric models, because of the control that stomatal conductance exerts on water and carbon budgets of the plant (e.g., Woodward 2002) and ultimately on the whole ecosystem (e.g., Pollard and Thompson 1995). To represent the assimilation of carbon at the leaf level, most current models of the terrestrial biosphere adopt the widely accepted photosynthesis model of Farquhar et al. (Farquhar et al. 1980, hereafter referred to as FM), as expanded upon by others to incorporate the coupled carbon-water exchanges at the leaf-atmosphere interface (Collatz et al. 1991; Leuning et al. 1995). Originally, FM stipulated that leaf assimilation is regulated by two limitations, namely, low activity of the carboxylase-oxygenase enzyme (Rubisco) under low intercellular concentration of CO<sub>2</sub> ( $C_i$ ), and by the rate of regeneration of the ribulose-1, 5-bisphosphate (RuBP) under low irradiance level. This formulation was expanded thereafter by Sharkey (Sharkey 1985) to include a third limitation that represents a reduction of the rate of leaf photosynthesis (or photosynthetic downregulation), related to the inadequate rate of utilization of triose-phosphate (TPU) on carboxylation under high irradiance and  $C_i$  levels. This limitation takes effect when, under high  $C_a$ , the accumulation of sugars in the leaf is sufficiently high to cause an inadequate release of inorganic phosphorus to sustain photosynthesis (Harley and Sharkey 1991; Krapp et al. 1993; Socias et al. 1993; Van Oosten and Besford 1995; Paul and Driscoll 1997).

More than 10 years ago, Wullschleger (Wullschleger 1993) analyzed the response of 109 C<sub>3</sub> species to elevated  $C_a$  and found that one-fourth of them were TPU limited. The latter analyses were based, however, on short-term observations only. Several recent field experiments have shown that the photosynthetic downregulation process becomes evident only after long-term plant exposure to elevated CO<sub>2</sub>, and its occurrence may be caused either by an inadequate use of triose-phosphate, as suggested by Sharkey (Sharkey 1985), or by other mechanisms depending on the plant species. For instance, Lewis et al. (Lewis et al. 1996) who observed the response of loblolly pine (*Pinus taeda* L.) to elevated CO<sub>2</sub> over three growing seasons reported a reduction in photosynthetic capacity that started only in the third season. Similarly, Griffin et al. (Griffin et al. 2000) observed that the same phenomenon was triggered only after 4 years of *Pinus radiata* D.'s exposure to elevated CO<sub>2</sub>. Besford et al. (Besford et al. 1998) also reported a downregulation of photosynthesis that started only during the third year of exposure of three tree species. Furthermore, while Curtis and Wang (Curtis and Wang 1998) reported that photosynthetic downregulation under high  $C_a$  did not occur in many short-term experiments made in indoor pots, Medlyn et al. (Medlyn et al. 1999) reported an 18% downregulation resulting from long-term field observations of 10 different tree species. Lee et al. (Lee et al. 2001) also found that a short-term exposure of C<sub>3</sub> prairie grasses to an elevated rate of ambient CO<sub>2</sub> caused an increase of photosynthetic rate by about 55%. This enhancement of photosynthesis dropped to about 13% and 8% after one and two complete years of exposure, respectively. Additionally, while most of the observations used in Curtis and Wang (Curtis and Wang 1998) were related to indoor pot experiments, Gunderson and Wullschleger's (Gunderson and Wullschleger 1994) analysis of field observations of 39 C<sub>3</sub> tree species exposed to high  $C_a$  exhibited an average of 21% photosynthetic downregulation. Moreover, Rey and Jarvis (Rey and Jarvis 1998) and Tissue et al. (Tissue et al. 1999) observed that the downregulation of photosynthesis of young birch (broadleaf deciduous species) and ponderosa pine (coniferous species) trees was maintained over the 4 years and the 3 last years, respectively, of their exposure to elevated  $C_a$ .

Several hypotheses have been suggested to explain the processes underlying the photosynthetic downregulation of C<sub>3</sub> plants that occurs under high C<sub>a</sub> (also termed acclimation and photosynthetic adjustment; see the review of Gunderson and Wullschleger 1994; Tissue et al. 1999). In addition to the already mentioned inadequate TPU (Sharkey 1985), these processes include a decrease in maximum Rubisco activity and electron transport in relation to leaf nitrogen content (Medlyn et al. 1999); the occurrence of physical damage to the thylakoidal membrane (DeLucia et al. 1985; Sage 1994); possible effects of some environmental factors such as photoperiod and light, and nutrient availability (El Kohen and Mousseau 1994; Lewis et al. 1996; Kubiske et al. 2002); soil nitrogen and phosphorus status (e.g., Oren et al. 2001; Winkler and Herbst 2004); an unclear phloem loading mechanism (Körner et al. 1995); and a possible combination of several mechanisms (Lee et al. 2001). Furthermore, a recent review of the mechanisms involved in the response of C<sub>3</sub> plant photosynthesis to elevated CO<sub>2</sub> suggested the existence of a complex system in which several feedbacks occur permanently to regulate photosynthesis (Paul and Foyer 2001). Moreover, some long-term observations show a strong seasonal variability of photosynthetic downregulation (e.g., Lewis et al. 1996; Besford et al. 1998; Rey and Jarvis 1998; Medlyn et al. 1999), though the environmental conditions that control that seasonal variability are unclear (Gunderson and Wullschleger 1994; Lee et al. 2001). In summary, in spite of the significant advances in recent years, the mechanisms responsible for photosynthetic downregulation are still poorly understood and more research is needed (e.g., Rey and Jarvis 1998; Saxe et al. 1998; Lee et al. 2001; Loreti et al. 2001; Paul and Foyer 2001; Ainsworth and Long 2005).

The fact that photosynthetic downregulation in C<sub>3</sub> plants under elevated C<sub>a</sub> has been observed in some species, but not in others, has led some biosphere modelers to consider a third photosynthetic limitation in their models, while others have not. A literature survey shows that several ecosystem models, including equilibrium models of the terrestrial biosphere [e.g., DOLY (Woodward et al. 1995); BIOME3 (Haxeltine and Prentice 1996); BIOME-BGC (Hunt et al. 1996); remote sensing-based models (e.g., BEPS of Liu et al. 1999); InTEC (Chen et al. 2000); Soil-Vegetation-Atmosphere-Transfer (SVAT) models (e.g., LSM of Bonan 1995); CLASS as modified by Araïn et al. (2002) and dynamic global vegetation models (DGVM) (IBIS2.0 of Kucharik et al. 2000); HYBRID3.0 (Friend et al. 1997); LPJ (Sitch et al. 2003)] do not include a third limitation on simulated leaf assimilation, while other models such as CARAIB (Warnant et al. 1994), IBIS1.1 (Foley et al. 1996), and TRIFFID (Cox 2001) include the limitation. In this study, we are not trying to prove that ecosystem models must incorporate such a limitation to account for the photosynthetic downregulation at high C<sub>a</sub>. Additional long-term field observations of the response of C<sub>3</sub> plants to elevated CO<sub>2</sub> are needed to further demonstrate the need for inclusion in ecosystem models (e.g., see Besford et al. 1998; Rey and Jarvis 1998; Medlyn et al. 1999; Jurola 2003; Nowak et al. 2004). However, we think that the role of this limitation within these models deserves more attention for the following two main reasons.

- First, several models among those cited above use the concept of plant functional types (PFTs) to represent the Earth's major biomes based on a combination of climatic criteria (e.g., tropical versus temperate) and some key ecological characteristics (broadleaf versus needleleaf, and deciduous versus evergreen) (e.g., Foley et al. 1996; Bonan et al. 2003). This concept groups an ensemble of species together within a single PFT (e.g., temperate broadleaf deciduous trees), and assumes a common physiology for all species that belong to that PFT. However, under high concentrations of CO<sub>2</sub>, photosynthetic downregulation may occur in some species and not in others, even though they belong to the same PFT. As an illustration, El Kohen et al. (El Kohen et al. 1993) observed that sweet chestnut (*Castanea sativa*), a temperate broadleaf deciduous tree, exhibited photosynthetic downregulation under elevated C<sub>a</sub>, while beech (*Fagus sylvatica*), which is also a temperate broadleaf deciduous tree, did not. Li et al. (Li et al. 1999) also reported that

when exposed to high  $C_a$ , *Quercus geminata*, an scrub-oak species grown in Florida downregulated its photosynthesis while *Quercus myrtifolia*, another scrub-oak species grown in the same region, did not. Consequently, ecosystem models that incorporate a third limitation (but assume that all species within a PFT downregulate) may systematically underestimate net primary production (NPP), while models that ignore downregulation may systematically overestimate NPP.

- Second, leaf photosynthetic downregulation is likely to have some ramifications at the canopy scale (e.g., [Marek et al. 2001](#) ; [Kubiske et al. 2002](#) ) and at the ecosystem scale. For instance, a reduction in NPP of some PFTs is likely to affect their ability to capture environmental resources, such as water and light, which may alter their competitive ability and ultimately lead to changes in ecosystem composition. Subsequently, changes in ecosystem composition may lead to changes in ecosystem energy and water budgets (e.g., [Aguiar et al. 1996](#) ; [Cramer et al. 2001](#) ; [Twine et al. 2004](#) ), which may in turn affect NPP. Such complex interactive processes, especially long-term feedbacks, can be investigated effectively only through modeling studies or long-term observational studies.

Thus, we used an ecosystem model to examine the sensitivity of the simulated NPP and other components of the carbon cycle of the Earth's major biomes to leaf photosynthetic downregulation that occurs under high  $C_a$  (700 ppm), by comparing results of a simulation where the FM is used in its original form (i.e., leaf photosynthesis is constrained by only two limitations; see above) and results of a second simulation in which we incorporate downregulation by adding a third limitation to photosynthesis. Our results will illustrate the influence of photosynthesis downregulation on the predictions of ecosystem models and highlight a possible source of error that may affect projections of regional and global carbon budgets under elevated  $C_a$ .

## 2. Method [Return to TOC](#)

We used version 2.6 of the Integrated Biosphere Simulator (IBIS) ([Kucharik et al. 2000](#) ). This DGVM simulates the presence/absence of 12 PFTs, where each PFT represents a group of plants with similar ecological and physiological characteristics (e.g., temperate deciduous forest, boreal conifer forest, grasses, and shrubs). Plant competition for light and water, which is influenced by interannual climatic variations, leads to changes in vegetation structure and distribution. Trees (which form the simulated upper canopy vegetation) compete with grasses and shrubs (lower canopy) for water and light. Within each vegetation canopy, competition is driven by differences in the annual carbon balance resulting from different ecological strategies, including differences in phenology (evergreen versus deciduous), leaf form (needle versus broadleaf), and photosynthetic pathway ( $C_3$  versus  $C_4$ ).

The model simulates processes at multiple time scales. Fluxes of energy, water, and carbon between the vegetation and atmosphere are simulated on an hourly time step using the land-surface-transfer scheme (LSX) of [Pollard and Thompson \(Pollard and Thompson 1995\)](#) , modified to account for the simultaneous transfer of carbon and water based on the leaf physiology models of [Farquhar et al. \(Farquhar et al. 1980\)](#) and [Collatz et al. \(Collatz et al. 1991, 1992\)](#) . Leaf-level photosynthesis is further scaled to the canopy level by assuming that photosynthesis is proportional to the absorbed photosynthetically active radiation (APAR) within the canopy, and stomatal conductance is scaled using a big-leaf assumption ([Amthor 1994](#) ). Leaf biomass accumulation and leaf area index are computed daily in the phenology module. The remaining model processes are computed using an annual time step and include estimation of annual carbon balance; spatial changes in vegetation biomass and species

composition; and flows of carbon between vegetation, detritus, and soil organic matter (Kucharik et al. 2000).

The model was forced with observed, gridded climate data (New et al. 1999), consisting of monthly normals (1961–90) of mean temperature and diurnal temperature range, total precipitation, relative humidity, cloud cover fraction, wind speed, and number of wet days. The International Geosphere Biosphere Program global soil database (IGBP-DIS 1999) was used to represent soil texture conditions in terms of fraction of sand, silt, and clay. The simulation was made at 2° × 2° spatial resolution. Moreover, to ensure that all ecosystem carbon pools had equilibrated, the simulation was performed for a 300-yr period. Results reported here represent the state of the simulated carbon pools at year 300. It should be noted that in reality, the soil carbon pool takes thousands of years to equilibrate; IBIS therefore uses a numerical acceleration technique that allows for the simulation of about 5000 yr of soil carbon dynamics in only 150 yr (Kucharik et al. 2000).

In version 2.0 of IBIS described in Kucharik et al. (Kucharik et al. 2000), the leaf photosynthesis of C<sub>3</sub> plants is constrained by only two limitations. Here, in simulations where we introduced a third limitation to account for the photosynthetic downregulation under high C<sub>a</sub>, we simply expressed it as half of the maximum catalytic capacity of Rubisco ( $V_{max}$ ), according to Collatz et al. (Collatz et al. 1991). This formulation ( $V_{max}/2$ ) is a general expression of the effect of the photosynthetic downregulation under elevated C<sub>a</sub>, in contrast to other formulations that express the downregulation due to one particular mechanism, such as the inadequate use of triose-phosphate (Sharkey 1985). In this paper, we are interested in exploring how a third limitation might affect global terrestrial carbon budgets, rather than finding the best formulation for simulating the third limitation.

### 3. Results [Return to TOC](#)

We first briefly examined the leaf-level simulations of gross assimilation of temperate/boreal (Figures 1a,b) and tropical (Figures 1c,d) trees using the coupled leaf photosynthesis (FM) stomatal conductance model (Collatz et al. 1991), as described in Kucharik et al. (Kucharik et al. 2000). The leaf photosynthesis model equations are presented in the appendix while its parameter values are shown in Table 1. The simulations were performed under unstressed water conditions in order to verify that the leaf model used in IBIS reproduces the ratio (0.7) of intercellular to ambient CO<sub>2</sub>, in agreement with reported experimental observations (Poorter and Farquhar 1994; Ehleringer and Cerling 1995; Kull and Niinemets 1998). At 350 ppm, the simulated leaf assimilation remained almost unchanged for both tree categories, regardless of whether a third limitation was considered or not (Figures 1a–d). At 700 ppm, however, the effect of this limitation became substantial. Furthermore, for tropical trees that have a higher photosynthetic capacity than temperate trees, as parameterized in IBIS (Kucharik et al. 2000), the third limitation became effective under a much higher irradiation level than temperate trees (Figures 1b,d).

Ecosystem-level simulations show that while the photosynthetic downregulation caused only a small reduction (6%) in the predicted global NPP, its effect varies largely across the different biomes, particularly along the north–south latitudinal transect (Figures 2a–c; Table 2). The simulated NPP was reduced, for example, by more than 0.2 kg C m<sup>-2</sup> yr<sup>-1</sup> (~15%) in central Europe (Figures 2b,c), which is more than the observed annual average NPP of boreal deciduous forests and about one-third of the observed annual average NPP of temperate deciduous forests (see Kucharik et al. 2000). However, downregulation caused only a very slight effect on NPP of tropical forests (Figures 2b,c). Moreover,

it is known that on an annual time scale, the amount of solar radiation received at low and high latitudes is approximately the same. Only about  $50 \text{ W m}^{-2}$  more is received at latitude  $0^\circ$  than at latitude  $45^\circ$  (Hartmann 1994). Ecosystem-level results are therefore in agreement with those of leaf-level simulations, in which it is illustrated that for similar irradiance levels, the effect of downregulation decreases with the increase of the photosynthetic capacity of the leaf (Figures 1b,d). Ecosystem-level simulations made at 350 ppm indicate that the difference between NPP as obtained with and without downregulation is very small (Figures 3a–c), which is also in good agreement with leaf-level simulations. Additionally, we should note that under current  $C_a$  conditions, IBIS predictions of NPP compare favorably with observations (Kucharik et al. 2000), and with predictions of models of similar degree of complexity [e.g., the LSM-DGVM (Bonan et al. 2003)]. Results of our simulations as performed with and without downregulation are thus being gauged against reasonable baseline simulations.

Some potential feedback effects that resulted from the inclusion of the photosynthetic downregulation on individual biomes are also illustrated in Table 2. NPP of tundra and boreal evergreen forest (BEF) decreased for example by 21% and 16%, respectively. At the same time, interestingly, the area of tundra decreased by 5% while area of BEF increased by 15%. Photosynthetic downregulation decreased the capacity of tundra vegetation to assimilate carbon and to grow further. This reduced this vegetation's capacity to utilize available environmental resources for maintenance. Consequently, a portion of this vegetation, which was able to grow under some extreme climatic conditions in the polar region when photosynthetic downregulation is not applied, was not able to do so when photosynthetic downregulation is applied. Thus, a part of the tundra is replaced by the polar desert biome, which explains the southern shift of the polar desert biome and the increase in its area (Table 2; Figures 4a–c). The case of BEF is different from the case of tundra because trees of the BEF are in ecophysiological competition with trees of the boreal deciduous forest (BDF). Although NPP of both BEF and BDF decreased in response to photosynthetic downregulation, area of BEF increased while area of BDF decreased. The increase in BEF area is due to an enhancement of the competitive ability of BEF trees over BDF trees, which resulted from an increase in the amounts of canopy light penetration and photosynthetically active radiation (PAR) that reach BEF trees. The increase of light penetration within the mixed BEF–BDF canopies resulted from a decrease in leaf area index (LAI) (Table 2). The overall increase in BEF area did not, however, totally compensate for the important decrease in its total NPP. This is because NPP per unit area is lower in the simulation with downregulation than in the simulation without downregulation. Another interesting case is the small increase in NPP of grasses though their area increased considerably (Table 2). In fact, area of grasses increased substantially (36%) at the expense of shrubs following the inclusion of the photosynthetic downregulation (Table 2; Figures 4a–c). That increase in area contributed only to a minor increase in total NPP (3%). Similar to the BEF case, the NPP per unit area is lower in the simulation with downregulation than in the simulation without downregulation. For all biomes, soil carbon changes were fairly similar to NPP changes (Table 2).

#### 4. Discussion and conclusions [Return to TOC](#)

Our main objective was to highlight a potential source of uncertainty related to ecosystem model representation of photosynthesis downregulation in  $C_3$  plants under elevated  $C_a$ . The study was stimulated by recent long-term field observations that revealed that photosynthetic downregulation occurs in a much higher number of  $C_3$  plant species compared to earlier knowledge based on indoor short-term experiments. Because such downregulation does not occur in all  $C_3$  plants, predictions of ecosystem models that both include photosynthetic downregulation for all PFTs or ignore it completely



2002). Currently, the plant C–N cycle is not simulated in IBIS, and a constant fraction of the assimilated carbon is allocated to the different plant pools (stem, root, leaf), independent of environmental conditions and plant age. Inhibitory effects of pollutants, such as ozone (O<sub>3</sub>) (e.g., Fowler et al. 1999; Fumagalli et al. 2001), and their interactions with atmospheric CO<sub>2</sub> on photosynthesis are additional processes that are not simulated in IBIS (as in most current global ecosystem models). Our results are likely to be different if O<sub>3</sub> effects on plant growth were simulated, especially in regions where O<sub>3</sub> concentrations are high, such as the northeastern United States.

In spite of the various uncertainties in scientific understanding of photosynthetic downregulation, we hope this study has sufficiently highlighted an important issue related to ecosystem model parameterizations of plant physiology. We hope these results will stimulate the emergence of new insights toward improving model simulations of carbon cycle under changing atmospheric CO<sub>2</sub> conditions. Finally, based on both recent long-term field observations and results of our simulations, we concur with Smith et al. (Smith et al. 1993) that a more adequate parameterization of PFTs in ecosystem models must necessarily take into account the physiological characteristics that govern their response to environmental conditions.

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### Description of the C<sub>3</sub> Plants Leaf Photosynthesis Model Used in IBIS, as Described in Kucharik et al. (Kucharik et al. 2000)

Following Farquhar et al. (Farquhar et al. 1980) and Farquhar and Sharkey (Farquhar and Sharkey 1982), gross assimilation of C<sub>3</sub> plants,  $A_g$  (mol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>), is expressed as the minimum of two potential capacities to fix carbon as follows:

$$A_g = \min(J_e, J_c), \tag{A1}$$

where  $J_e$  and  $J_c$  are light and Rubisco limited rates of photosynthesis, respectively.

The rate  $J_e$  is given as

$$J_e = \alpha Q_p \frac{C_i - \Gamma^*}{C_i + 2\Gamma^*}, \tag{A2}$$

where  $\alpha$  is the intrinsic quantum efficiency for CO<sub>2</sub> uptake (mol CO<sub>2</sub> Einstein<sup>-1</sup>),  $Q_p$  is the flux density of photosynthetically active radiation absorbed by the leaf (Einstein m<sup>-2</sup> s<sup>-1</sup>),  $C_i$  is the concentration of CO<sub>2</sub> in leaf's intercellular air spaces (mol mol<sup>-1</sup>), and  $\Gamma^*$  is the compensation point for gross photosynthesis (mol mol<sup>-1</sup>), given as

$$\Gamma^* = \frac{O_2}{2\tau}, \quad (\text{A3})$$

where  $O_2$  is the atmospheric oxygen concentration (0.209 mol mol<sup>-1</sup>), and  $\tau$  is the ratio of kinetic parameters describing the partitioning of enzyme activity to carboxylase or oxygenase function.

The rate  $J_c$  is given as

$$J_c = \frac{V_{\max}(C_i - \Gamma^*)}{C_i + K_c \left(1 + \frac{O_2}{K_o}\right)}, \quad (\text{A4})$$

where  $V_{\max}$  is the maximum catalytic capacity of Rubisco per unit leaf area (mol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>), and  $K_c$  and  $K_o$  are the Michaelis–Menten coefficients (mol mol<sup>-1</sup>) for CO<sub>2</sub> and O<sub>2</sub>, respectively.

The temperature dependence of  $V_{\max}$ ,  $K_c$ ,  $K_o$ , and  $\tau$  is described using a modified Arrhenius function of Lloyd and Taylor (Lloyd and Taylor 1994):

$$f(T) = e^{E_0 \left( \frac{1}{15-T_0} - \frac{1}{T-T_0} \right)}, \quad (\text{A5})$$

where  $T_0$  is the absolute zero temperature (-273.16°C), while  $E_0$  is the temperature sensitivity factor set to 3000, 1400, 6000, and -5000 for  $V_{\max}$ ,  $K_c$ ,  $K_o$ , and  $\tau$ , respectively.

Stomatal conductance,  $g_{s,h_2o}$  (mol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup>), is simulated according to Collatz et al. (Collatz et al. 1991) as follows:

$$g_s = \frac{mA_n}{C_s} h_s + b, \quad (\text{A6})$$

where  $A_n$ ,  $h_s$ , and  $C_s$  are net assimilation (mol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>), air relative humidity (fraction), and CO<sub>2</sub> concentration at the leaf surface (mol mol<sup>-1</sup>), respectively, and  $m$  and  $b$  are the slope and the intercept of the equation.

To account for the gradual transition between  $J_e$  and  $J_c$ , the quadratic equation of Collatz et al. (Collatz et al. 1991) is solved for. Leaf net assimilation,  $A_n$  ( $\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), is thereafter obtained as

$$A_n = A_g - \gamma V_{\max}, \quad (\text{A7})$$

where  $\gamma$  is the leaf respiration cost of Rubisco activity.

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