An interactive vegetation SVAT model tested against data from six contrasting sites

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Abstract

The interactions between soil, biosphere, and atmosphere scheme (ISBA) is modified in order to account for the atmospheric carbon dioxide concentration on the stomatal aperture. The physiological stomatal resistance scheme proposed by Jacobs (1994) is employed to describe photosynthesis and its coupling with stomatal resistance at leaf level. In addition, the plant response to soil water stress is driven by a normalized soil moisture factor applied to the mesophyll conductance. The computed vegetation net assimilation can be used to feed a simple growth submodel, and to predict the density of vegetation cover. Only two parameters are needed to calibrate the growth model: the leaf life expectancy and the effective biomass per unit leaf area. The new soil–vegetation–atmosphere transfer (SVAT) scheme, called ISBA–A–gs, is tested against data from six micrometeorological databases for vegetation ranging from temperate grassland to tropical forest. It is shown that ISBA–A–gs is able to simulate the water budget and the CO2 flux correctly. Also, the leaf area index predicted by the calibrated model agrees well with observations over canopy types ranging from shortcycled crops to evergreen grasslands or forests. Once calibrated, the model is able to adapt the vegetation density in response to changes in the precipitation distribution. © 1998 Elsevier Science B.V. All rights reserved.

1. Introduction

The soil–vegetation–atmosphere transfer (SVAT) schemes now employed in meteorology are designed to describe the basic evaporation processes at the surface together with the water partitioning between vegetation transpiration, drainage, surface runoff and soil moisture change. For example, the ISBA SVAT-model (Noilhan and Planton, 1989; Noilhan and Mahfouf, 1996) is used in the operational simulations of the French weather forecast and climate model ARPEGE (Action de Recherche Petite Echelle – Grande Echelle). In this meteorological SVAT model like in many others (see for example, Niyogi and Raman, 1997, for a review), the description of the biological control of transpiration is made through a simple empirical parameterization of the leaf stomatal conductance gs by adapting the approach proposed by Jarvis, 1976. The scaling up from the leaf to the canopy is made by multiplying gs by the leaf area index (LAI). The value of LAI must be prescribed from ancillary information (e.g. satellite data). The ISBA scheme, once calibrated, is able to describe the effect of the
atmospheric and radiation forcing on \( g_s \). Air temperature and humidity at reference level, global radiation, and the estimated soil moisture are used to compute \( g_s \). In general, the Jarvis-type parameterization used in ISBA provides good quantitative estimates of transpiration. However, the stomatal response to air humidity is simulated with difficulty and often requires a thorough analysis of in situ flux and stomatal conductance measurements to calibrate the model. Indeed, it is assumed that the various environmental factors act independently on \( g_s \), whereas measurements suggest that strong interactions may occur (Collatz et al., 1991; Jacobs, 1994). Also, the value of the prescribed LAI is often a crude estimate, which does not account for rapid changes in the vegetation cover associated with climatic events (droughts in particular). Another limitation of such a parameterization is the lack of feedback with the atmospheric concentration of CO\(_2\), especially in climate studies. Indeed, a CO\(_2\) concentration increase induces a physiological response of the plants through a reduction of \( g_s \). This effect may influence the surface energy and water balance at the various time scales of changes in CO\(_2\) concentration: diurnal, seasonal and, especially, secular. This is why physiological parameterizations of CO\(_2\), accounting for the CO\(_2\) effect, now seem more appropriate than Jarvis-type parameterizations. This is particularly true for climate change simulations (Betts et al., 1997), where vegetation–climate–CO\(_2\) feedbacks need to be described. In such studies, the fertilizing impact of the increase in CO\(_2\) concentration (i.e. a rise of LAI) and the effect of climate in general (rainfall, air temperature and humidity, solar radiation) must be included in the chosen modelling approach (Monteith, 1995; Sellers et al., 1996; Carlson and Bunce, 1996).

In summary, the objectives of the present work are: (1) to describe, in a more realistic way, the canopy stomatal conductance by considering the functional relationship between stomatal aperture and photosynthesis (Wong et al., 1979; Jarvis and Morison, 1981); (2) to make the ISBA SVAT-model more general in order to properly simulate the surface processes in contrasting CO\(_2\) concentration, air temperature, and air humidity conditions, with the same calibrated model; (3) to use the estimated assimilation rate to simulate the plant growth and mortality, and diagnose the leaf area index (LAI) consistently with the prescribed climate and CO\(_2\) concentration.

The approach we propose in this study consists in using the physiological parameterization of \( g_s \), presented by Jacobs (1994); Jacobs et al. (1996) slightly modified to account for soil water stress effects in the ISBA SVAT-model, instead of the Jarvis-type parameterization employed in the standard version. The resulting new version of ISBA is called ISBA–A–\( g_s \). The Jacobs’ model (or \( A–g_s \) model) is a semi-empirical physiological model of the leaf photosynthesis rate and net assimilation (\( A_n \)) of CO\(_2\), and of the leaf conductance \( g_s \). The \( A–g_s \) approach can be considered more physical than the Jarvis one because both physiological responses to external parameters and non-linear interactions between the various factors are handled, based on rather general relationships. For example, \( g_s \) is calculated according to \( g_s \), consistent with observations showing the strong correlation between water use and CO\(_2\) assimilation (Cowan, 1982). The net assimilation computed by the coupled physiology-SVAT model ISBA–A–\( g_s \) can be used to estimate LAI through simple parameterizations according to the prescribed climate and CO\(_2\) concentration. This approach seems more pragmatic than coupling a SVAT scheme with very complex crop or ecosystem models for use in atmospheric models (Ji, 1995). Alternatively, ISBA–A–\( g_s \) may work with a prescribed value of LAI, like the standard version of ISBA. Indeed, the ISBA–A–\( g_s \) approach is similar to the atmosphere–vegetation interaction model (AVIM) proposed by Ji (1995). However, ISBA–A–\( g_s \) differs from AVIM in the degree of complexity assigned to some biophysical processes: the scaling up from the leaf to the canopy is more complex in ISBA–A–\( g_s \), and the photosynthate allocation between the plant bioelements is simpler. The number of tunable parameters is lower in ISBA–A–\( g_s \), thanks to the simplified treatment of the photosynthate allocation and of the plant senescence.

The work presented in this paper was carried out in four phases: (1) adding the algorithm of the \( A–g_s \) model proposed by Jacobs (1994); Jacobs et al. (1996) to ISBA, together with an adapted representation of the soil water stress; (2) performing the scaling up from the leaf to the canopy through a simple description of the radiative transfer within the canopy (uniformly distributed LAI and integration by a three-point Gauss quadrature) according to the method proposed by Jacobs (1994) and using the work of
Roujean (1996); (3) using the net assimilation produced by the \(A-g_s\) model to estimate the produced biomass (through a very simple parameterization of growth, mortality, and nutrient redistribution in the plant) and convert it into LAI; (4) calibration and validation of the coupled model ISBA–A–\(g_s\) over contrasted surface types.

The datasets used to calibrate the model are presented in Section 2. They were all used and described in previous papers: MUREX (Bessemoulin et al., 1996; Calvet et al., 1998) is an agricultural fallow in southwestern France, PILPS/Cabauw (Chen et al., 1997) is a grassland in The Netherlands, HAPEx-MOBILHY/Caumont, INRA/Avignon, INRA/Castanet, and ARME. The canopies range from C\(_3\) to C\(_4\) plants (maize of Castanet in the latter case), herbaceous to woody (Amazon forest of ARME), natural to agricultural (MUREX fallow, maize of Castanet, soybean of Avignon and Caumont). For all the sites, continuous meteorological data (air temperature and humidity at screen level, atmospheric pressure, precipitation, wind speed, and solar and atmospheric radiation) are available over periods ranging from 2 months to 3 years (Table 1). Such data constitute the atmospheric forcing employed to run the SVAT models. However, the CO\(_2\) concentration was not measured in any of these experiments. In this study, a value of 340 ppm at screen level was assumed. In general, the external forcing data were registered on a 15, 30 or 60 min basis, according to the dataset. In the case of INRA/Castanet, the weather information was recorded daily. In order to run SVAT models with a suitable temporal resolution, standard diurnal cycles were reconstructed from the daily data.

Since the purpose of this study is to validate models of both hydrological and physiological processes, most appropriate datasets should comprise measurements or estimates of soil moisture in the root-zone \((w_2)\), evapotranspiration (LE) and heat surface fluxes, net assimilation of CO\(_2\) \((A_n)\), and LAI. As shown in Table 1, only one dataset provides observations of the

### 2. Datasets

The calibration and validation of the coupled model ISBA–A–\(g_s\), presented in the next section was performed in the case of six contrasted surface-types for which micrometeorological measurements were available over one annual cycle or more. The studied sites are presented in Table 1. The datasets were all employed and described in the framework of several field experiments: MUREX, PILPS/Cabauw, HAPEx-MOBILHY/Caumont, INRA/Avignon, INRA/Castanet, and ARME. The canopies range from C\(_3\) to C\(_4\) plants (maize of Castanet in the latter case), herbaceous to woody (Amazon forest of ARME), natural to agricultural (MUREX fallow, maize of Castanet, soybean of Avignon and Caumont). For all the sites, continuous meteorological data (air temperature and humidity at screen level, atmospheric pressure, precipitation, wind speed, and solar and atmospheric radiation) are available over periods ranging from 2 months to 3 years (Table 1). Such data constitute the atmospheric forcing employed to run the SVAT models. However, the CO\(_2\) concentration was not measured in any of these experiments. In this study, a value of 340 ppm at screen level was assumed. In general, the external forcing data were registered on a 15, 30 or 60 min basis, according to the dataset. In the case of INRA/Castanet, the weather information was recorded daily. In order to run SVAT models with a suitable temporal resolution, standard diurnal cycles were reconstructed from the daily data.

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### Table 1

<table>
<thead>
<tr>
<th>Dataset</th>
<th>Plants</th>
<th>Coordinates</th>
<th>Authors</th>
<th>Duration (month)</th>
<th>Years</th>
<th>(w_2)</th>
<th>LE</th>
<th>(A_n)</th>
<th>LAI</th>
</tr>
</thead>
<tbody>
<tr>
<td>MUREX</td>
<td>Fallow</td>
<td>43°24'N 1°10'E</td>
<td>Bessemoulin et al. (1996)</td>
<td>24</td>
<td>1995–96</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
<td>Measured</td>
</tr>
<tr>
<td>PILPS Cabauw</td>
<td>Grassland</td>
<td>51°58'N 4°56'E</td>
<td>Chen et al. (1997)</td>
<td>12</td>
<td>1987</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
<td>Estimated</td>
</tr>
<tr>
<td>HAPEx Mobily</td>
<td>Soybean</td>
<td>43°41'N 0°6'W</td>
<td>Goutorbe (1991)</td>
<td>12</td>
<td>1986</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
<td>Estimated</td>
</tr>
<tr>
<td>INRA Avignon</td>
<td>Soybean (late)</td>
<td>43°55'N 4°53'E</td>
<td>Olioso et al. (1996)</td>
<td>2</td>
<td>1990</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Measured</td>
</tr>
<tr>
<td>INRA Castanet</td>
<td>Maize</td>
<td>43°31'N 1°28'E</td>
<td>Cabelguenne et al. (1990)</td>
<td>2×12</td>
<td>1986</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
<td>Measured</td>
</tr>
<tr>
<td>ARME</td>
<td>Amazon forest</td>
<td>2°57'S 59°57'W</td>
<td>Shuttleworth et al. (1984)</td>
<td>25</td>
<td>1983–85</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
<td>Estimated</td>
</tr>
</tbody>
</table>

The availability of measurements of the output variables of ISBA–A–\(g_s\), is indicated: \(w_2\) is soil moisture in the root-zone, LE is latent heat flux, \(A_n\) is net assimilation of CO\(_2\), and LAI is leaf area index.

The duration of the period during which observations of all or part of these variables are available is given.

The leaf area index may be either thoroughly measured or estimated.
four model output variables: INRA/Avignon (Olioso et al., 1996). In particular, CO₂ assimilation is available only over the Avignon soybean (open chamber measurements). Evapotranspiration could be estimated in all the datasets, except over the maize of Castanet. The LE flux was not measured directly. Instead, it was derived as a residual of the surface energy balance (net radiation—sensible heat flux and ground heat flux). Root-zone soil moisture was not fully characterized during PILPS/Cabauw and ARME. But in both cases, severe soil water stress are not likely to occur, because of the rather large amount of precipitation and also, as far as the Amazon forest is concerned, because of the deep root-zone (deeper than 8 m as explained in Delire et al., 1997). The LAI was directly measured, on a 3–15 day basis, over the fallow of MUREX, the Avignon soybean, and the Castanet maize. Over the Cabauw grassland and the Caumont soybean, monthly estimates of LAI were proposed. Over the Ducke reserve forest of ARME, a single measurement was performed: LAI=5.7 (MacWilliam et al., 1993). The LAI of the Amazon forest is expected to vary little.

The MUREX fallow was cut in 1995 at the end of the spring growth. The resulting reduction of LAI was prescribed in ISBA—A—gs. The other agricultural canopies were grown in optimal conditions by providing the required tillage, irrigation water amount, nitrogen fertilization, and pesticide application. The irrigation amount was included in the precipitation of the SVAT forcing file. One of the two studied maize fields of Castanet was not irrigated in order to validate crop models. This is the one employed for the calibration of ISBA and ISBA—A—gs over maize (Section 4.2).

3. Coupled model

In this study, the ISBA SVAT-model is coupled with the Jacobs’ photosynthesis model. A simple, original method to drive plant growth and senescence from the modelled photosynthesis is proposed. As explained below in Sections 3.1 and 3.3, only one parameter is needed to calibrate the SVAT part of the model (the mesophyll conductance) and two parameters for the growth submodel (a maximum turnover time of leaves and an effective biomass per unit leaf area ratio). Soil respiration is not accounted for in the coupled model. However, this effect is discussed in Section 5.2. The major strength of the coupled model is that it uses a limited number of parameters.

3.1. ISBA and the Jacobs’ model

ISBA was developed at Météo-France by Noilhan and Planton (1989) in order to describe the surface processes in weather forecast and climate models. The ISBA scheme simulates surface fluxes—evapotranspiration, heat flux, and ground heat flux (LE, H, G)—and predicts the evolution of surface state variables using the equations of the force–restore method of Deardorff (1977, 1978). Five variables (surface temperature \( T_s \), mean surface temperature \( T_2 \), surface soil volumetric moisture \( w_g \), total soil volumetric moisture \( w_2 \), and the canopy interception reservoir \( W_r \) ) are obtained through prognostic equations. It must be noted that ISBA does not need information about root distribution: \( w_2 \) is the volumetric soil moisture associated to a bulk layer of thickness \( d_2 \) including the root zone. When used in stand-alone simulations, the ISBA model is driven by measurements of incoming radiation, precipitation, atmospheric pressure, air temperature and humidity, and wind speed at a reference level. Also, vegetation characteristics such as LAI and canopy height must be prescribed. These parameters may change with time. The model has prognostic equations for surface soil moisture, soil moisture in the root zone, and surface temperature, but initial values of these variables are required. The biological control of transpiration is made through a Jarvis-like parameterization of the canopy stomatal resistance (the inverse of stomatal conductance). In this kind of parameterization, the physiological processes involving both stomatal aperture and photosynthesis are not described. Instead, simple empirical response functions to external factors (air temperature and humidity, incoming solar radiation, and soil moisture) are employed to estimate the stomatal resistance. The parameter to be tuned is the minimum stomatal resistance \( r_{smin} \). Also, the function describing the air humidity effect should be adapted to each plant species (whereas in practice, a single function type is assumed). This is one limitation of the scheme, together with the lack of response to changes in CO₂ concentration.

As opposed to Jarvis-like parameterizations, the A—gs model proposed by Jacobs (1994); Jacobs et al.
(1996) describes the physiological phenomena occurring at the leaf scale, including CO$_2$ assimilation. It is a simple, semi-empirical scheme designed to mimic observed phenomena or simulations made by more complex biochemical models. The equations given in Appendix A correspond to the detailed algorithm proposed by Jacobs (1994) without soil water stress. In Jacobs (1994), the $A-g_s$ model’s simulations are compared with the measurements of $A_n$ and $g_s$ performed on unstressed grapevine. In this study, we propose a slight modification of the Jacobs’ model allowing the representation of the soil water stress effect. The scaling up to the canopy scale, together with the coupling to ISBA are described in the next section.

The purpose of the Jacobs’ model is to simulate the leaf net assimilation of CO$_2$ ($A_n$, expressed in units of mg of CO$_2$ per m$^2$ of leaf per second) and the associated leaf conductance to water vapour ($g_s$, in mm s$^{-1}$) as a function of air density $\rho_a$ (kg m$^{-3}$), concentration of CO$_2$ at the leaf surface $C_s$ (in parts per million, ppm), leaf temperature $T_s$ ($^\circ$C), saturation deficit at the leaf surface $D_s$ (g kg$^{-1}$), global radiation $R_g$ (W m$^{-2}$), and plant type (C$_3$ or C$_4$). The saturation deficit $D_s$ represents the difference between the saturation specific humidity at leaf temperature and the air specific humidity close to the leaf surface. Along with $A_n$ and $g_s$, the Jacobs’ model computes the leaf internal CO$_2$ concentration ($C_i$, in ppm) and the leaf transpiration $E$ (mg m$^{-2}$ s$^{-1}$). The $C_i$ and $E$ variables are calculated within the $A-g_s$ model and are not used further in the coupled model. The $A-g_s$ model employed in this study is presented in the Appendix A.

Net assimilation is calculated first (Eqs. (A1), (A2),(A3),(A4),(A5),(A6),(A7),(A8) and (A9)). The basic physiological and biochemical processes associated with CO$_2$ assimilation, such as photorespiration, and temperature or saturation responses are accounted for through simple empirical equations. The model parameters defining the response of the leaf assimilation rate to the external factors are presented in Table 2: $\varepsilon_0$ is the maximum quantum use efficiency, $I^*$ is the CO$_2$ compensation concentration (i.e. the value of $C_i$ below which the leaf is unable to assimilate CO$_2$, because of photorespiration), $f_0$ is the ideal value of the $C_i/C_s$ ratio (i.e. without photorespiration and saturation deficit), $g_m$ is the mesophyll conductance, and $A_{m,\max}$ is the maximum value of the photosynthetic rate. The calibration of the $A-g_s$ model in the case of unstressed grapevine (Jacobs, 1994) produces values similar to those presented in Table 2 for C$_3$ plants, except for the mesophyll conductance $g_m$ at 25$^\circ$C (the fitted value is 2 mm s$^{-1}$ against a ‘standard’ value of 7 mm s$^{-1}$). A priori, these parameters together with the temperature response specification ($T_1$, $T_2$, and $X(\@25)$), may vary from one species to another. In this study, in order to reduce the number of tunable parameters, it is assumed that the plant type (C$_3$ or C$_4$) is the only factor explaining changes in the specification of assimilation, as in Table 2, except for mesophyll conductance. Therefore, $g_m$ is the parameter permitting the calibration of the physiological part of ISBA–$A-g_s$ (Section 4). Its

### Table 2

<table>
<thead>
<tr>
<th>Parameter ($X$)</th>
<th>$X(@25)$</th>
<th>$Q_{10}$</th>
<th>$T_1$ ($^\circ$C)</th>
<th>$T_2$ ($^\circ$C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>C$_3$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\varepsilon_0$ (mg J$^{-1}$)</td>
<td>0.017</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>$f_0$ (ppm)</td>
<td>0.85</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>$I^*$ (ppm)</td>
<td>45</td>
<td>1.5</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>$g_m$ (mm s$^{-1}$)</td>
<td>7.0</td>
<td>2.0</td>
<td>5</td>
<td>28</td>
</tr>
<tr>
<td>$A_{m,\max}$ (mg m$^{-2}$ s$^{-1}$)</td>
<td>2.2</td>
<td>2.0</td>
<td>8</td>
<td>38</td>
</tr>
<tr>
<td>C$_4$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\varepsilon_0$ (mg J$^{-1}$)</td>
<td>0.014</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>$f_0$ (ppm)</td>
<td>0.50</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>$I^*$ (ppm)</td>
<td>2.8</td>
<td>1.5</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>$g_m$ (mm s$^{-1}$)</td>
<td>17.5</td>
<td>2.0</td>
<td>13</td>
<td>36</td>
</tr>
<tr>
<td>$A_{m,\max}$ (mg m$^{-2}$ s$^{-1}$)</td>
<td>1.7</td>
<td>2.0</td>
<td>13</td>
<td>38</td>
</tr>
</tbody>
</table>

The $Q_{10}$, $T_1$ and $T_2$ values modulate the sensitivity of each parameter to temperature. $X(\@25)$ is the value of the parameter at 25$^\circ$C.
tuning role is equivalent to $r_{min}$ in the Jarvis-type parameterization of stomatal aperture of the standard version of ISBA (Noilhan and Planton, 1989). The leaf conductance is deduced from the net assimilation (Eqs. (A10), (A11), (A12), (A13), (A14) and (A15)). The cuticular diffusion, parallel to the main stomatal diffusion processes, is accounted for. The value of the cuticular conductance is generally weak. It is assumed the leaf mesophyll conductance (the only tunable parameter of the physiological model in order to introduce a response to soil water stress. The soil water stress effect was applied to the diffusion processes, is accounted for. The value of the leaf conductance is deduced from the net assimilation $g_s$, that is multiplied by the normalized soil moisture $\theta_2$, also employed in the standard version of ISBA to represent the soil water stress

$$\theta_2 = \frac{w_2 - w_{\text{wilt}}}{w_{fc} - w_{\text{wilt}}} \quad (1)$$

where $w_2$ is the soil volumetric moisture in the root-zone, and $w_{fc}$ and $w_{\text{wilt}}$ are the root-zone moisture content at field capacity and wilting point, respectively. In seasonal simulations, $w_2$ is a value predicted by ISBA. In Eqs. (A5), (A7), (A11) and (A12), $g_m$ is replaced by $\theta_2 \times g_m$. Fig. 1 displays the predicted values of the leaf conductance $g_s$, as a function of saturation deficit $D_s$ and relative soil moisture $\theta_2$. Both variables contribute to reduce the predicted $g_s$. Without soil water stress ($\theta_2 = 1$), even low values of $D_s$ lead to a steep decrease in leaf conductance. When soil water stress is prescribed, $g_s$ is lower but the relative (modelled) effect of $D_s$ at low values is attenuated. On the other hand, $g_s$ quickly reaches its residual (cuticular) value at high values of $D_s$, even for moderate soil water stress.

3.2. From the leaf to the canopy

The $A-g_s$ model described in the previous section simulates the net assimilation and the stomatal conductance at the leaf scale. In particular, one important aspect of the coupling between the $A-g_s$ model and ISBA consists in computing input variables of the $A-g_s$ model ($T_s$, $C_s$, and $D_s$) representative of the whole canopy, and to calculate the attenuation of the incident solar radiation in the canopy. The extension of the model to the canopy scale was performed according to the method proposed by Jacobs (1994).

The intensity of leaf conductance and CO$_2$ assimilation processes is not homogeneous within the canopy because of the factors acting on photosynthesis: the photosynthetically active radiation (PAR) is attenuated by the vegetation; also, the leaf temperature and the air CO$_2$ concentration and saturation deficit (i.e. $T_s$, $C_s$, and $D_s$ in the Jacobs’ model) may vary within the canopy. Since the purpose of this study is to obtain a simple and tractable coupled model, several approximations must be made. The radiation attenuation is simulated by a very simple submodel presented in the Appendix B, and it is assumed that the input variables of the physiological model $T_s$, $C_s$, and $D_s$ do not vary in the vegetation canopy layer together with the parameters of the $A-g_s$ model. In the coupled model, $T_s$ is the surface temperature calculated from the resolution of the surface energy balance, similar to the standard version of ISBA. The $C_s$ and $D_s$ variables at canopy level are obtained from their values at reference level from a simple flux-gradient relationship by using the aerodynamic resistance $r_a$ computed by ISBA and the CO$_2$ and water vapour fluxes ($A_{nc}$ and LE, respectively), of the previous time step. This assumption implies that the model time step does not exceed a few minutes. The net CO$_2$ above-canopy-flux...
\( A_{\text{nC}} \) is the difference between vegetation net assimilation \( A_{\text{nI}} \) and soil and root respiration \( R_{\text{Soil}} \). The \( R_{\text{Soil}} \) term is estimated with difficulty because its dependence on the soil moisture, LAI and surface temperature may vary from one site to another. Since soil respiration was not measured over the studied sites, this term is neglected in the calculations presented below. The effect of this assumption is discussed in Section 5.

The PAR extinction by the canopy must be described in the model: the leaves on top of the canopy intercept a large fraction of the incoming solar radiation, thus reducing the photosynthetic activity of lower layers. Assuming an homogeneous leaf vertical distribution, the integrated canopy net assimilation \( A_{\text{nI}} \) and conductance \( g_{\text{sI}} \) can be written as

\[
A_{\text{nI}} \hat{=} \int_{0}^{1} A_{\text{n}} \, d(z/h) \quad (2)
\]

and

\[
g_{\text{sI}} \hat{=} \int_{0}^{1} g_{\text{s}} \, d(z/h) \quad (3)
\]

where \( h \) is canopy height and \( z \) is the distance to the ground. The way \( A_{\text{nI}} \) and \( g_{\text{sI}} \) are estimated is detailed in Appendix B: note that variability in Eqs. (2) and (3) is assumed to be due to the light levels only. Possible air temperature and humidity differences within the canopy are not accounted for. Finally, the canopy conductance \( g_{\text{s}} \) (the driving factor of transpiration), is employed in the standard algorithm of ISBA to compute the heat and water vapour surface fluxes.

In Sections 3.1 and 3.2, the coupling between the standard version of ISBA and the \( A-g_{\text{s}} \) model was presented. In the coupled model ISBA–\( A-g_{\text{s}} \), the vegetation density, represented by the LAI value, may be either prescribed from ancillary information or estimated from the cumulated value of \( A_{\text{nI}} \). The LAI estimation is detailed below.

### 3.3. Growth and mortality

The most obvious way to predict LAI is to use the computed net assimilation \( A_{\text{nI}} \) (kg CO\textsubscript{2} m\textsuperscript{-2} s\textsuperscript{-1}): growth may be described as the accumulation of carbon obtained from the atmospheric CO\textsubscript{2} assimilation, and senescence as the result of a deficit of photosynthesis (due to external factors). In this study, the bulk biomass \( B \) (kg m\textsuperscript{-2}) is obtained from a differential equation as in Mougin et al. (1995) ; Ji (1995)

\[
\frac{dB}{dt} = \frac{M_{\text{C}}}{P_{\text{C}}M_{\text{CO}_2}} \times A_{\text{nI}} - BD(t)/\tau \quad (4)
\]

In the growth increment term of Eq. (4), \( P_{\text{C}} \) is the proportion of carbon in the dry plant biomass and \( M_{\text{C}} \) and \( M_{\text{CO}_2} \) are the molecular weights of carbon and CO\textsubscript{2} (12 and 44 g mol\textsuperscript{-1}), respectively. Typical values of \( P_{\text{C}} \) can be found in Scholes and Walker (1993), Table 10.1. Here, a constant value of 40% is assumed. The plant biomass \( B \) related to photosynthesis (and concerned by the instantaneous biomass increase due to photosynthesis) includes the leaves and a proportion of stems and roots: stems and roots contribute to provide the water required for the transpiration associated with the photosynthesis process.

The mortality increment term of Eq. (4) represents an exponential extinction of \( B \) characterized by a time-dependent effective life expectancy

\[
\tau(t) = \frac{\tau_{\text{M}}}{A_{\text{nI}}}(t) A_{\text{nI, max}}\quad (5)
\]

where \( \tau_{\text{M}} \) is the maximum effective life expectancy, \( A_{\text{nI}}(t) \) the maximum leaf net assimilation reached on the day before time \( t \) and \( A_{\text{nI, max}} \) the optimum leaf net assimilation. The value of \( A_{\text{nI}} \) corresponds to the highest average leaf net assimilation computed on the considered day

\[
A_{\text{nI}} = \text{Max} \left[ \int_{0}^{1} A_{\text{n}} \, d(z/h) \right] \quad (6)
\]

Indeed, the active biomass may decrease in three manners: (1) a part of the bioelements may wilt as a consequence of a soil water stress or other factors acting on photosynthesis (e.g. too low or too high temperatures); (2) organic molecules may be transferred from the leaves into stocking or structural organs (fruits, tubercles, stems and trunks), where biomass is no longer ‘active’ in our model; (3) plant diseases and the plant biomass taken by animals contribute to decrease \( B \). Each day, a fraction of the active biomass is removed due to these three factors. For sake of simplicity, any active biomass removal is
called mortality in this study. This implies that the nutrient redistribution in the plant bioelements is not explicitly described by the model, as well as the maintenance respiration of non-photosynthetic tissues (contrary to Mougin et al., 1995; Ji, 1995). Based on this assumption, a simple way to describe the mortality factors 2 and 3 is to prescribe a relevant value of $\tau_M$. For example, the leaves of a given ungrazed grass species maintained in optimum conditions of light, temperature, and water supply, would be characterized by a higher $\tau_M$ value than the same continuously grazed grass grown in ideal conditions. Factor 1 is related to the same external factors acting on photosynthesis. Therefore, it may be assumed that the leaf turnover is enhanced by suboptimal assimilation (as in Mougin et al., 1995). Here, the mortality due to unfavourable meteorological factors is estimated daily, according to the ratio between the maximum leaf net assimilation $A_{\text{nf}}$ (computed on the day before) and the optimum leaf net assimilation $A_{\text{nf,max}}$ (Eq. (5)): following Eq. (4), the active biomass $B$ is multiplied (each day) by the factor $\exp(-1/\tau)$, where $\tau$ (expressed in units of days) is the effective life expectancy on the considered day. The optimum leaf net assimilation $A_{\text{nf,max}}$ is a constant. It corresponds to the leaf net assimilation given by the Jacobs’ model with optimal input values $D_a=0$ g kg$^{-1}$, $I_a$ (h)=$500$ W m$^{-2}$, $T_s=25^\circ$C for C$_3$ plants and $T_s=35^\circ$C for C$_4$ plants. The effective maximum life expectancy of the leaves $\tau_M$ represents the period after which 37% of the initial biomass would remain (e-folding), in optimal conditions (i.e. if the maximum leaf net assimilation $A_{\text{nf}}$ would equal $A_{\text{nf,max}}$ at least once every day).

As in Mougin et al. (1995); Ji (1995), the value of LAI is obtained from $B$ by assuming that for a given vegetation canopy, the ratio between $B$ and LAI is a constant $\alpha$. Therefore, LAI is given by

$$\text{LAI} = \frac{B}{\alpha}$$

The computed value of LAI is related to the integrated net assimilation through the growth model represented by Eqs. (4),(5),(6) and (7). Only two parameters, the $\alpha$ ratio and $\tau_M$ have to be determined for each canopy type from LAI measurements or estimations. These vegetation parameters have to be retrieved during the model calibration, together with the mesophyll conductance $g_m$. Also note that an initial prescribed value of LAI is required.

The coupled ISBA–$A_{s}$ model may be employed in two configurations: (1) estimation of LE, H, G, $T_s$, $w_2$ and $A_{\text{nt}}$ in relation to the prescribed LAI and meteorological forcing; (2) estimation of LE, H, G, $T_s$, $w_2$, $A_{\text{nt}}$ and LAI in relation to the prescribed meteorological forcing. In other words describing LAI by using the equations presented in this section is optional. Configuration 1 may be used for short term simulations, for which LAI is not expected to depart from the initial estimated value. On the other hand, configuration 2 should be employed for seasonal simulations or in climate studies in order to account for associated changes in LAI.

4. Calibration and validation of ISBA–$A_{s}$

The interactive vegetation SVAT model presented in Section 3 is configured such that few parameter estimates are required. In this section, it is investigated whether the simple chosen parameterizations enable one to simulate surface fluxes and plant growth in very distinct situations. The model calibration was performed using a two-step procedure: the plant mesophyll conductance is estimated first and then the growth parameters. The two configurations of ISBA–$A_{s}$ were used: configuration 1 for the first step of the model calibration (the estimation of the mesophyll conductance $g_m$), and configuration 2 for the calibration of the growth and mortality submodel, i.e. the estimation of the $\alpha$ ratio and $\tau_M$. In this section, the calibration method and the model output comparison with the standard version of ISBA and in situ measurements are presented.

4.1. Calibration method

The calibration and validation of the standard version of ISBA was described in the previous studies in the case of MUREX (Calvet et al., 1998), PILPS/Cabauw (Chen et al., 1997), HAPEx-Mobilhy/Cabauw (Mahfouf and Noilhan, 1996), and ARME (Noilhan et al., 1995). The INRA datasets (Avignon and Castanet) were previously analyzed by Olioso et al. (1996); Cabelguenne et al. (1990) using physiological and agricultural-crop models, respectively. In this study, both ISBA and ISBA–$A_{s}$ are calibrated for these datasets. In the case of MUREX and INRA/Castanet, the dataset cover two growing cycles. Therefore, one growing cycle was used to calibrate the
model, and the other one allowed the model validation (Section 4.3). The calibration datasets consist of 1995-data over the MUREX fallow and an unirrigated maize field in 1986.

The estimation of either \( r_{\text{sm}} \) for ISBA or \( g_{m} \) for ISBA–A–\( g_{s} \) is performed by minimizing the rms difference between the simulated and measured surface fluxes (as in Calvet et al., 1998). In the case of the maize of INRA/Castanet (for which the surface fluxes were not measured) the function to be minimized, instead, is the rms error on soil moisture in the root-zone \( w_{2} \). In the first step of the calibration, only the SVAT part of ISBA–\( g_{s} \) is concerned, and the model is run in configuration 1 (LAI is prescribed). The ISBA–A–\( g_{s} \) model requires a second calibration step to determine the growth and mortality parameters (\( \alpha \) and \( \tau_{M} \)). Once \( g_{m} \) is known, configuration-2 simulations are performed in order to estimate the values of \( \alpha \) and \( \tau_{M} \) by minimizing the difference between simulated and measured LAI.

In the case of the Amazon forest, the reference LAI was assumed constant (LAI=5.7 after MacWilliam et al., 1993) since continuous measurements of LAI were not available. The 1995 MUREX fallow was cut on 1 June. In order to account for the reduction of LAI caused by the cutting, a LAI value of 0.3 was imposed in the model on 1 June. Furthermore, an additional parameter is required in the case of MUREX and Cabauw grassland. Indeed, the modelled LAI corresponds to the ‘active’ biomass as explained in Section 3.3, and in the model green leaves may disappear in a short period after a severe stress (e.g. soil moisture at wilting point). This may happen for crops and individual short-cycled plants. On the other hand, natural grasslands, for example, consist of many herbaceous plant species whose growing cycles overlap, contributing to maintain an evergreen canopy, even during unfavourable conditions. Furthermore, ISBA–A–\( g_{s} \) cannot make LAI increase from a zero initial value. Therefore, in this case a minimum value of LAI is needed, and prescribed in the model (LAI\(_{\text{min}}\)) in order to allow regrowth. In the case of crops an initial (low) value of LAI is prescribed at the beginning of the growing cycle.

Along with the stomatal and growth parameters, the model requires estimates of the canopy albedo and soil parameters (soil depth, texture, and water retention capacity). Such values are obtained from in situ measurements or ancillary information. Table 3 presents the values employed in the simulations performed in this study (6 sites) for both ISBA and ISBA–A–\( g_{s} \). Note that in the case of ARME, the soil properties defined in ISBA are adapted to Amazonian soils (Delire et al., 1997).

### 4.2. Calibration results

Simulations were performed by using either ISBA or ISBA–A–\( g_{s} \) over each dataset in order to estimate leaf conductance parameters (\( r_{\text{sm}} \) and \( g_{m} \) for ISBA and ISBA–A–\( g_{s} \), respectively), and growth parameters for ISBA–A–\( g_{s} \) (\( \alpha, \tau_{M} \) and LAI\(_{\text{min}}\)). All the simulations were executed with a time step of 300 s. In the case of the Amazon forest (ARME) the \( \tau_{M} \) parameter (12 months) was prescribed according to the estimation of the average leaf life span given by Medina and Klinge (1983).

The estimated values of the plant parameters are presented in Table 4. The obtained values are rather disparate, and correspond to different plant-develop-

<table>
<thead>
<tr>
<th>Dataset</th>
<th>Plants</th>
<th>Albedo</th>
<th>( d_{2} ) (m)</th>
<th>Sand (%)</th>
<th>Clay (%)</th>
<th>( w_{fc} ) (m(^{3}) m(^{-3}))</th>
<th>( w_{wilt} ) (m(^{3}) m(^{-3}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>MUREX</td>
<td>Fallow</td>
<td>0.20</td>
<td>1.3</td>
<td>14</td>
<td>28</td>
<td>0.34</td>
<td>0.20</td>
</tr>
<tr>
<td>PILPS</td>
<td>Cabauw Grassland</td>
<td>0.25</td>
<td>1.0</td>
<td>6</td>
<td>49</td>
<td>0.37</td>
<td>0.28</td>
</tr>
<tr>
<td>HAPEX-Mobilhy</td>
<td>Soybean</td>
<td>0.20</td>
<td>1.6</td>
<td>43</td>
<td>19</td>
<td>0.32</td>
<td>0.20</td>
</tr>
<tr>
<td>INRA Avignon</td>
<td>Soybean (late)</td>
<td>0.22</td>
<td>1.6</td>
<td>11</td>
<td>27</td>
<td>0.33</td>
<td>0.17</td>
</tr>
<tr>
<td>INRA Castanet</td>
<td>Maize</td>
<td>0.20</td>
<td>1.6–1.7</td>
<td>35–47</td>
<td>26–28</td>
<td>0.34–0.36</td>
<td>0.15–0.17</td>
</tr>
<tr>
<td>ARME</td>
<td>Amazon forest</td>
<td>0.13</td>
<td>8.0</td>
<td>6</td>
<td>85</td>
<td>0.43</td>
<td>0.34</td>
</tr>
</tbody>
</table>

The soil parameters are: soil root-zone depth (\( d_{2} \)), proportion of sand and clay, soil moisture at field capacity (\( w_{fc} \)), and soil moisture at wilting point (\( w_{wilt} \)).
ment strategies. The estimated LAI-related biomass $\alpha$ for example varies over one order of magnitude from 25 g m$^{-2}$ for the late soybean of INRA/Avignon, to 365 g m$^{-2}$ for the PILPS/Cabauw grassland. In the studied datasets, the highest obtained values of $\alpha$ correspond to evergreen, strongly rooted canopies (fallow, grassland, Amazon forest). Also, the Amazon forest exhibits the lowest value of $g_m$ (0.8 mm s$^{-1}$), associated with the highest value of $M$: the high leaf life span compensates for the low biomass production per leaf area unit, and contributes to maintain a stable, nearly constant value of LAI (see Fig. 2). Unlike the plants considered before, both soybean crops (late and precocious cultivars of INRA/Avignon and HAPEX-Mobilhy/Caumont, respectively), show low $\alpha$-values. This characteristic corresponds to their rapid life cycle (2 and 5 months, respectively): the production of leaves is favoured, and the growing cycle can be completed rapidly in spite of low values of $g_m$. The late cultivar presents a lower value of $\alpha$ and (especially) of $\tau_M$ than the precocious one, consistent with its shorter growing cycle.

The ISBA–$A-g_s$ scheme’s rms error and mean bias over evapotranspiration (LE), soil moisture in the root-zone ($w_2$), and leaf area index (LAI) are shown in Table 5. They were obtained from the comparison between the model simulations and the available in-situ measurements during the calibration period. For datasets lacking measurements of LAI, the error over LAI indicated in Table 5 is calculated according to the prescribed estimates in the standard version of ISBA. The calculated and prescribed values of LAI are shown in Fig. 2, together with the available observations. In the same way, Fig. 3 presents the root-zone soil moisture computed by both schemes, and the validation measurements.

The comparison of the modelled $w_2$ obtained by either ISBA or ISBA–$A-g_s$ (Fig. 3 and Table 5) shows that ISBA–$A-g_s$ is able to reproduce the standard simulations of the water budget very well, even in configuration 2 (predicted LAI). On the other hand, the simulated LAI is rather different from the measured or estimated LAI, especially over the irrigated soybean of HAPEX-Mobilhy/Caumont, and the un-

### Table 4

Estimation of the mesophyll conductance $g_m$ and of the plant growth parameters for the six studied surface types

<table>
<thead>
<tr>
<th>Dataset</th>
<th>Plants</th>
<th>Type</th>
<th>$g_m$ (mm s$^{-1}$)</th>
<th>$\alpha$ (g m$^{-2}$)</th>
<th>$\tau_M$ (d)</th>
<th>LAI$_{min}$ (m$^2$ m$^{-2}$)</th>
<th>$r_{s\min}$ (s m$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>MUREX</td>
<td>Fallow</td>
<td>C$_3$</td>
<td>20.0</td>
<td>365</td>
<td>90</td>
<td>0.3</td>
<td>47</td>
</tr>
<tr>
<td>PILPS Cabauw</td>
<td>Grassland</td>
<td>C$_3$</td>
<td>7.2</td>
<td>365</td>
<td>90</td>
<td>0.9</td>
<td>40</td>
</tr>
<tr>
<td>HAPEX-Mobilhy</td>
<td>Soybean</td>
<td>C$_3$</td>
<td>1.0</td>
<td>63</td>
<td>250</td>
<td>–</td>
<td>150</td>
</tr>
<tr>
<td>INRA Avignon</td>
<td>Soybean (late)</td>
<td>C$_3$</td>
<td>2.6</td>
<td>25</td>
<td>15</td>
<td>–</td>
<td>70</td>
</tr>
<tr>
<td>INRA Castanet</td>
<td>Maize</td>
<td>C$_4$</td>
<td>5.7</td>
<td>100</td>
<td>30</td>
<td>–</td>
<td>130</td>
</tr>
<tr>
<td>ARME</td>
<td>Amazon forest</td>
<td>C$_3$</td>
<td>0.8</td>
<td>250</td>
<td>365</td>
<td>–</td>
<td>272</td>
</tr>
</tbody>
</table>

The minimal stomatal resistance ($r_{s\min}$) of the standard version of ISBA is also indicated.

### Table 5

Comparison of modelled and observed evapotranspiration (LE), soil moisture in the root-zone ($w_2$), and leaf area index (LAI) with ISBA–$A-g_s$ in configuration 2, over the calibration datasets

<table>
<thead>
<tr>
<th>Dataset</th>
<th>Plants</th>
<th>LE rmsd ($W \text{ m}^{-2}$)</th>
<th>LE mean bias ($W \text{ m}^{-2}$)</th>
<th>$w_2$ rmsd (mm)</th>
<th>$w_2$ mean bias (mm)</th>
<th>LAI rmsd (m$^2$ m$^{-2}$)</th>
<th>LAI mean bias (m$^2$ m$^{-2}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>MUREX</td>
<td>Fallow</td>
<td>45.9 (42.2)</td>
<td>0.6 (3.4)</td>
<td>22.6 (21.1)</td>
<td>16.9 (16.5)</td>
<td>0.50</td>
<td>−0.15</td>
</tr>
<tr>
<td>PILPS Cabauw</td>
<td>Grassland</td>
<td>13.7 (13.4)</td>
<td>−1.6 (1.1)</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>0.31</td>
</tr>
<tr>
<td>HAPEX-Mobilhy</td>
<td>Soybean</td>
<td>71.4 (66.8)</td>
<td>0.6 (1.2)</td>
<td>32.2 (34.1)</td>
<td>−2.8 (−5.8)</td>
<td>1.16</td>
<td>−0.52</td>
</tr>
<tr>
<td>INRA Avignon</td>
<td>Soybean (late)</td>
<td>65.6 (52.9)</td>
<td>−13.0 (−9.9)</td>
<td>25.6 (17.0)</td>
<td>24.8 (16.4)</td>
<td>0.57</td>
<td>−0.14</td>
</tr>
<tr>
<td>INRA Castanet</td>
<td>Maize</td>
<td>−</td>
<td>−</td>
<td>14.5 (14.2)</td>
<td>2.1 (3.5)</td>
<td>1.02</td>
<td>−0.32</td>
</tr>
<tr>
<td>ARME</td>
<td>Amazon forest</td>
<td>69.8 (62.8)</td>
<td>20.8 (14.7)</td>
<td>−</td>
<td>−</td>
<td>0.21</td>
<td>0.04</td>
</tr>
</tbody>
</table>

The root mean square difference (rmsd) and the mean bias (modelled−observed) are indicated. The corresponding results using the standard version of ISBA are shown (in brackets) for LE and $w_2$. In the case of PILPS/Cabauw, the error on LE is based on daily averages (instead of hourly measurements).
irrigated maize of INRA/Castanet. In both cases, it was not possible to find suitable $\alpha-\tau_M$ parameters fitting the prescribed LAI over the entire growing cycle. Instead, the $\alpha-\tau_M$ parameters were chosen in order to simulate the initial growing phase correctly, regardless of the senescence period. Inspite of the large bias between simulated and prescribed values of LAI (Table 5), the simulated soil moisture is not fundamentally different (Fig. 3). Also, the difference in daily evapotranspiration from one scheme to the other (presented in Fig. 4) is not very high. More often than not, the evapotranspiration difference is less than 20%, and seldom exceeds 50% of the value obtained from the standard version of ISBA. In fact, the discrepancy between the modelled and prescribed LAI observed in the case of HAPEX-Mobilhy/Caumont and INRA/Castanet occurs when the soil moisture in the root-zone $w_2$ is close to the wilting point $w_{\text{wilt}}$, i.e. when transpiration is very low, whatever be the LAI value. When this happens, the model leaf conductance and net assimilation are close to zero. As a consequence of Eqs. (5) and (6), the mortality rate becomes large enough to make the active biomass (and LAI) disappear rapidly. One may wonder why this is not observed, particularly in the case of INRA/Castanet where LAI was thoroughly measured. An explanation may be that in stressed conditions, water is extracted from below the root-zone through capillarity rises. Indeed the root-zone depth $d_2$ of 1.7 m for INRA/Castanet was imposed by the maximum depth of the

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**Fig. 2.** Leaf area index over the six studied sites: observed (squares), prescribed in ISBA (dashed line) and computed by ISBA–A–$g_s$ (solid line).
soil moisture measurements. A higher value of $d_2$ would have probably been more appropriate: simulations performed using the parameters of Tables 3 and 4, except for $d_2=2.3$ m, show that LAI values after July are much better estimated. Another explanation may be the difficulty to measure green LAI in wilting conditions because the death of the plant tissues may be distributed over all the leaves: the entire surface of a given leaf is included in the observed LAI whereas this leaf is partly dead or inactive. In the case of HAPEX-Mobilhy/Caumont, the prescribed LAI may simply be erroneous, because it was estimated from the vegetation height rather than actually measured.

Despite the above mentioned limitations, ISBA–A–$g_s$ is able to represent very distinct situations by adapting only three tunable parameters ($\alpha$, $\tau_M$ and, possibly, $\text{LAI}_{\text{min}}$). For example, the stable LAI value of the Amazon forest is simulated as satisfactorily as the plant regrowth of the MUREX fallow (after the cutting of 1 June 1995 or after the autumn water refilling of the soil), as shown in Fig. 2.

4.3. Model validation

The ISBA–A–$g_s$ model computes the surface fluxes, including net assimilation, and the leaf area index...
LAI. Once calibrated over a given canopy, it may be assumed that the plant growth parameters ($\alpha$ and $\tau_M$) and mesophyll conductance $g_m$ at 25°C are intrinsic plant characteristics, which remain unaffected by changes in the climatic forcing. This hypothesis is tested in this section by running ISBA–$A_g$ over the 1996 growing cycle of the MUREX fallow, and over 1 year of irrigated maize of INRA/Castanet. Another way to validate the model consists in comparing the computed net assimilation with the in situ measurements of INRA/Avignon. Both validation approaches are presented below.

4.3.1. Net assimilation and evapotranspiration

The INRA/Avignon soybean dataset comprises observations of the net assimilation of CO$_2$. The measurements were performed by using two open chambers of 1.2 m $\times$ 1.5 m (Olioso et al., 1996). Contrary to heat and water atmospheric fluxes, these measurements do not integrate what occurs over the whole crop field. Therefore, they should be interpreted qualitatively, rather than quantitatively. The comparison between in situ measurements of net assimilation and evapotranspiration and the values simulated by ISBA–$A_g$ are presented in Fig. 5 over five clear-sky
Fig. 5. Water upward- and CO$_2$ downward-flux (right and left side of the Figure, respectively), as measured (dashed line) and simulated (solid line) by ISBA-A$_2$-$g_s$ during the senescence period of the INRA/Avignon late soybean. The two chamber measurements of net assimilation are plotted. The computed relative soil moisture ($\theta_2$) and LAI are indicated.
days (2, 3, 5, 8, and 12 September 1990), during the drying period accompanying the senescence. The modelled LAI and relative soil moisture \( \theta_2 \) are indicated. Both values decrease during the senescence. The LE diurnal cycle, and the transpiration decrease during the senescence period are satisfactorily simulated. On the other hand, the observed net assimilation is much higher than the simulated one at the beginning of the period. However, the observed midday photosynthesis depression, more pronounced at the end of the period, is relatively well simulated. As explained in Olioso et al. (1996), the dissymmetric evolution of net assimilation is due to a peak of saturation deficit in the early afternoon. This process is also at work in ISBA–A–\( g_s \), but the simulated effect is less marked than the observed one. The model difficulties to simulate all the combined air humidity and soil moisture stress effects suggests that the relationship between soil moisture and leaf functioning might be bettered. In particular, the stress function (reproduced from the standard version of ISBA) represented by Eq. (1) is somewhat arbitrary. It might be refined (empirically) by analysing a large range of datasets, under soil moisture stressed and unstressed conditions. However, the present version of ISBA–A–\( g_s \), is able to simulate the main physiological phenomena induced by air humidity and soil water stress.

### 4.3.2. Changes in the atmospheric forcing

In the calibration Section 4.2, 1995 and 1986 data from MUREX (fallow) and INRA/Castanet (unirrigated maize) were employed, respectively. In this section, 1996 data of MUREX and the 1986 irrigated maize of INRA/Castanet are considered in order to validate the calibrated ISBA–A–\( g_s \). Both datasets contrast sharply with those employed for the model calibration: (1) in 1996, the MUREX vegetation was not cut, and the precipitation regime was more favourable to plant growth (a precipitation total of 860 mm was registered in 1996, against 770 mm in 1995); (2) the 1986 INRA/Castanet maize field considered in this section, was irrigated (contrary to the calibration field); the precipitation and irrigation total is 400 mm during the growing cycle (12 May–29 September 1986), compared with 85 mm in the unirrigated crop development period (12 May–9 September 1986).

In the validation simulations, the values of the plant parameters (\( \alpha \), \( \tau_M \), and \( g_m \)) are those obtained from the calibration (Table 4). The simulated LAI and \( w_2 \) are presented in Fig. 6, together with the available observations. Both variables are properly simulated over the fallow, and over the irrigated maize. Table 6 presents the ISBA–A–\( g_s \) scheme’s rms error and mean bias over LE, \( w_2 \), and LAI over the two validation datasets. The error magnitude is the same as that observed during the calibration (Table 5). Over the irrigated maize, a significant bias is still observed for LAI, especially at the beginning of the senescence period (from the end of July onward). Again, the LAI underestimation might be caused by the difficulty to distinguish between the photosynthetic and the senescent parts of the maize leaves during the LAI measurements or to changes in the value of the \( \alpha \) ratio. However, the obtained result confirms that once calibrated, the ISBA–A–\( g_s \) model is able to simulate the main vegetation response to changes in the atmospheric conditions, and that it represents a rather robust approach.

### 5. Sensitivity to CO2 concentration

Once the ISBA A–\( g_s \) model is calibrated for given conditions of climatic and atmospheric CO2 concentration ([CO2]), one may try to use the model to simulate the vegetation behaviour in a different situation. Such simulations imply many hypotheses and

<table>
<thead>
<tr>
<th>Dataset</th>
<th>Plants</th>
<th>Plants</th>
<th>LE rmsd (W m(^{-2}))</th>
<th>LE mean bias (W m(^{-2}))</th>
<th>( w_2 ) rmsd (mm)</th>
<th>( w_2 ) mean bias (mm)</th>
<th>LAI rmsd (m(^2) m(^{-2}))</th>
<th>LAI mean bias (m(^2) m(^{-2}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>MUREX Fallow</td>
<td>Fallow</td>
<td>45.0 (43.3)</td>
<td>0.4 (1.3)</td>
<td>26.2 (23.9)</td>
<td>0.8 (2.1)</td>
<td>0.58</td>
<td>0.07</td>
<td></td>
</tr>
<tr>
<td>INRA Castanet</td>
<td>Maize</td>
<td>–</td>
<td>–</td>
<td>25.7 (20.0)</td>
<td>16.1 (10.6)</td>
<td>0.79</td>
<td>–0.49</td>
<td></td>
</tr>
</tbody>
</table>
approximations, as discussed before. In spite of this difficulty, it was shown in Section 4.3 that one may assume a constant value of the structure parameters of the soil–plant system, even in contrasting climatic conditions. In climate studies, the effect of increasing \([\text{CO}_2]\) on LAI and leaf conductance is another factor to be accounted for. In this section, a sensitivity study is presented concerning the impact of a large increase in \([\text{CO}_2]\), for fixed atmospheric and radiative conditions. Also, the impact of soil and root respiration (through the \(\text{CO}_2\) concentration inside the canopy) is discussed.

5.1. Impact of increased \([\text{CO}_2]\)

From the water balance viewpoint, an increase in \([\text{CO}_2]\) has two immediate conflicting effects: (1) LAI may increase because of the photosynthesis enhancement (at least for \(\text{C}_3\) plants); (2) the leaf conductance decreases. The first effect tends to increase transpiration, and the second effect tends to decrease transpiration. Therefore, the resulting change in evapotranspiration and soil moisture may be totally different from one plant type to another, for given climate conditions. Also, there is a third effect related to the feedback between transpiration and \(w_2\): changes in transpiration affect soil moisture availability and thereby also change leaf conductance (by Eq. (1)). This latter effect occurs over longer periods of time and may trigger seasonal differences in the resulting water balance change. Such a feedback is accounted for in ISBA–\(A_g\). The root-zone soil moisture \(w_2\) is obtained through a prognostic equation using the force–restore method of Deardorff (1977, 1978). The time evolution of \(w_2\) is driven by the difference between the non-intercepted precipitation and the plant transpiration and bare soil evaporation. Runoff occurs at values of \(w_2\) exceeding the saturation point (Mahfouf and Noilhan, 1996).

In this study, the impact of increased \([\text{CO}_2]\) was investigated over the considered six datasets using ISBA–\(A_g\). Whereas \([\text{CO}_2]\) was set at 340 ppm in the previous simulations, new model runs were performed with values of \([\text{CO}_2]\) corresponding to \(2 \times 340\) and \(3 \times 340\) ppm (680 and 1020 ppm, respectively). The \(\text{CO}_2\) concentration is the only variable varied in the forcing datasets (i.e. planetary boundary layer feedbacks are not accounted for, contrary to Jacobs (1994)). It must be noted that in this study the para-

![Fig. 6. Leaf area index (up) and root-zone soil moisture (down) over the MUREX fallow (left) and INRA/Castanet irrigated maize (right): observed (boxes and +, respectively) and calculated by ISBA–\(A_g\), (line) during the validation period.](image-url)
Fig. 7. Leaf area index (left) and root-zone soil moisture (right) simulated by ISBA–A–g, over the six studied sites for different prescribed values of the CO₂ atmospheric concentration at reference level: 340 ppm (fine line), 680 ppm (dashed fine line) and 1020 ppm (dashed thick line).
meterization of the plant mortality is affected by the changes in [CO2]: the optimum leaf net assimilation $A_{\text{max}}$ depends on [CO2], and presents higher values in increased-[CO2] conditions.

Fig. 7 presents a comparison between LAI and $w_2$ computed by ISBA–$A_g$ (using the parameter values indicated in Table 4) under different prescribed values of [CO2]. The corresponding average differences are written in Table 7. It can be observed that despite rather strong LAI responses to CO2 enrichment the simulated soil moisture seldom departs from its reference value, because stomatal closure limits the LAI increase effect on transpiration. For four datasets (the Cabauw grassland, the MUREX fallow, the irrigated maize and the Amazon forest), the values of the $w_2$ difference are positive, i.e. less evapotranspiration is produced in doubled [CO2] conditions. In general, such values of the $w_2$ difference are associated with a relative increase of maximum LAI less than 50% in doubled [CO2] conditions —Table 7—, consistent with many CO2-enrichment field or laboratory experiments (see Cure and Acock, 1986 for a review and, more recently, Rujet et al., 1996 for maize and Cassella et al., 1996 for grassland). In this case, the increased leaf surface does not totally compensate for the stomatal closure predicted by the Jacobs’ model, and less water is extracted from the soil root-zone. The low biomass response of the irrigated maize was expected, because maize is a C₄ plant (CO₂ is not or little fertilizing for C₄ plants). On the other hand, the [CO2] increase boosts the net assimilation of irrigated soybean, and the net assimilation increase strongly affects LAI because of the low value of the $\alpha$ ratio (only 25 g m⁻² for the late soybean). In this case, the $w_2$ difference is negative. It is interesting to note that the magnitude of CO2 effect depends on the other external factors. For example, the unirrigated maize presents a significant biomass response (and finally a negative $w_2$ difference), because the stomatal closure permits the plant to limit the effect of the soil water stress and the wilting point is reached later. This response is not at stake if the plant is well watered. Also, the evapotranspiration response may vary from one season (or one year) to another because of the LAI–$w_2$ feedback, as illustrated in Fig. 7 in the case of MUREX (1995). In this case, the average $w_2$ difference in 2×[CO2] conditions is positive with the 1995 atmospheric forcing and becomes negative in 1996.

In this study, the soil and root respiration effect was neglected. In order to assess to what extent this hypothesis acts upon the simulations and on the [CO2] sensitivity study presented in this section, a simple parameterization of $R_{\text{Soil}}$ was applied to the MUREX fallow.

### 5.2. Soil respiration effect

Norman et al. (1992) proposed a parameterization of $R_{\text{Soil}}$ based on chamber measurements performed during the FIFE experiment (Sellers et al., 1992) over
The effect on the model soil moisture effect of soil respiration on LAI occurs at the end of July, after the growing period following the cutting. More than one annual cycles are available (MUREX, INRA/Avignon). According to the empirical results of Norman et al. (1992), the estimated \( R_{\text{Soil}} \) (expressed in units of mg CO\(_2\) m\(^{-2}\) s\(^{-1}\)) is given by the \( Q_{10} \) temperature function Eq. (A1), with \( Q_{10}=2 \) and a value of \( R_{\text{Soil}} \) at 25°C given by

\[
R_{\text{Soil}}(0.25) = (0.5940 + 0.2376 \times \text{LAI}) \times w_g \quad (8)
\]

where \( w_g \) is top soil moisture (m\(^3\) m\(^{-3}\)). Over MUREX, the average computed \( R_{\text{Soil}} \) (through the parameterization proposed by Norman et al., 1992) is about 0.15 mg CO\(_2\) m\(^{-2}\) s\(^{-1}\) in 1995. It represents a significant source of CO\(_2\) since the simulated CO\(_2\)-uptake by the vegetation averages to 0.55 mg CO\(_2\) m\(^{-2}\) s\(^{-1}\) at daytime. However, the impact of \( R_{\text{Soil}} \) on the simulations is weak: the maximum difference in simulated LAI is 0.15 m\(^2\) m\(^{-2}\) (soil respiration tends to increase CO\(_2\) concentration in the canopy and favours photosynthesis). The maximum simulated effect of soil respiration on LAI occurs at the end of July, after the growing period following the cutting. The effect on the model soil moisture \( w_2 \) is maximum at the end of July, also, and does not exceed 3 mm. The impact of \( R_{\text{Soil}} \) on the sensitivity of the model to [CO\(_2\)] enrichment is relatively weak: the maximum-LAI increase is slightly reduced (41% and 62% for 2× and 3×[CO\(_2\)] conditions, respectively, against 43% and 66% without soil respiration), and the \( w_2 \) mean difference is virtually unchanged (+7.6 and +6.7 mm for 2× and 3×[CO\(_2\)] conditions, respectively, against +7.7 and +6.5 mm without soil and root respiration).

6. Conclusion

The ISBA–\( A-g_s \) model presented in this study seems to be a good tool to analyze the plant response to climate change. Although the model uses a limited number of parameters, it is shown that ISBA–\( A-g_s \) is able to depict very distinct situations. The calibration and the validation of the new scheme over six intensively observed sites is satisfactory: from the in situ measurements it is shown that ISBA–\( A-g_s \) can be employed to model the surface fluxes (including net assimilation in the case of INRA/Avignon) and to simulate the seasonal evolution of LAI over the whole range of the studied vegetation types. The model is validated well over the surface types for which more than one annual cycles are available (MUREX, INRA/Avignon). The main advances of ISBA–\( A-g_s \) in relation to the standard version of ISBA are: (1) a more realistic representation of the leaf conductance, because the functional link between photosynthesis and stomatal aperture is represented; (2) a better integration to the canopy scale by using a (simple) radiative transfer parameterization; (3) a climate-derived LAI may now contribute to better account for the biological control of evapotranspiration; (4) the new scheme may be validated through the computed net assimilation by using in situ measurements of the CO\(_2\) flux; (5) the complex phenomena associated with an increase of the atmospheric concentration of CO\(_2\) may possibly be accounted for. Concerning this latter issue, it must be noted that the sensitivity study performed in the last part of this study is about CO\(_2\) concentration and that other significant driving variables are assumed invariant between the different climate scenarios of enhanced CO\(_2\). Should this model be placed in a climate model, then boundary layer and rainfall feedbacks may force different conclusions from those drawn in Fig. 7.

A limitation of ISBA–\( A-g_s \) is the increased computing time. Compared to the standard version of ISBA, the computing time is increased by 45%. However, the surface scheme module in an atmospheric model is far from being the most time consuming, and such a rise would be rather negligible in the mass calculations performed in either a mesoscale or climate model. As far as soil respiration is concerned, the lack of a CO\(_2\) source below the vegetation seems to have little influence on the simulated net assimilation and water budget. However, it may hamper quantitative comparisons between simulations and in situ CO\(_2\)-flux measurements, in most cases. Simple parameterizations of soil respiration may be easily included in the algorithm.

The ISBA–\( A-g_s \) scheme presented in this study is designed to be employed in atmospheric models. Also, ISBA–\( A-g_s \) may represent the soil–vegetation–atmosphere interface in hydrological models. The calibration of ISBA–\( A-g_s \) over six surface-types performed in this study needs to be extended to other sites from either in situ micrometeorological measurements or synoptic and satellite observations. Furthermore, the model sensitivity to changes in the atmospheric concentration of CO\(_2\) needs to be compared with the results of CO\(_2\)-enrichment experiments.
Acknowledgements

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Appendix A

The Jacobs’ A–gs model at leaf scale

The algorithm presented below is fully described and discussed by Jacobs (1994); Jacobs et al. (1996). In the version of the Jacob’s model employed in this study, the coupled leaf net assimilation–conductance is obtained in five steps: (1) estimation of the ratio between the leaf internal concentration of CO₂ (Cᵢ) and the concentration at the leaf surface (Cₛ); (2) leaf net assimilation; (3) first guess of the stomatal conductance to CO₂ (gₛ); (4) first guess of leaf transpiration and conductance to water vapour (gₛ); (5) final estimation of the stomatal conductance to CO₂ (gₛc) and of leaf conductance to water vapour (gₛ).

A.1 Estimation of the Cᵢ/Cₛ ratio

First, the compensation point Γ (ppm) and the mesophyll conductance gₘ (mm s⁻¹) are estimated according to the leaf temperature (Tₛ) by the Q₁₀ functions Eqs. (A1) and (A2), respectively

\[
X(Tₘ) = X(0) \times Q₁₀(Tₘ/25) / 10 \quad (A1)
\]

\[
X(Tₛ) = \frac{X(0) \times Q₁₀(Tₛ/25) / 10}{1 + \exp\{0.3(Tᵢₘ - Tₛ\)}[1 + \exp\{0.3(Tₛ - T₁)\}]] (A2)
\]

where X (Tₛ) and X (0) are the values of these variables corresponding to the leaf temperatures Tₛ and 25°C, respectively. In Eq. (A1), an increase of 10°C in temperature triggers a Q₁₀ factor increase of X. In Eq. (A2), X is reduced to zero for either low or high values of Tₛ, according to the reference temperatures T₁ and T₂. Standard values of X (0), Q₁₀, T₁ and T₂ are indicated in Table 2.

The Cᵢ/Cₛ ratio is written as

\[
\frac{Cᵢ}{Cₛ} = f + (1 - f) \frac{Γ}{Cₛ} \quad (A3)
\]

with

\[
f = f₀ \left(1 - \frac{Dₛ}{Dₘ₃ₜₕ} \right) + fₘₚ₉ \left(\frac{Dₛ}{Dₘ₃ₜₕ} \right) \quad (A4)
\]

where f₀ is the value of f for Dₛ=0 g kg⁻¹ (Table 2), Dₘ₃ₜₕ=45 g kg⁻¹ is the maximum value of the saturation deficit and

\[
fₘₚ₉ = \frac{gₘ}{gₘ + gₘ₃} \quad (A5)
\]

where gₘ is the cuticular conductance, allowing diffusion of water vapour and CO₂ through the leaf cuticle, differently from the main stomatal mechanism.

A.2 Leaf net assimilation Aₙ

This part of the Jacobs’ model is based on the approach proposed by Goudriaan et al. (1985). The maximum net assimilation Aₘ₃ₜₕ is calculated first, as a function of temperature (as gₘ), according to Eq. (A2). Also, the initial quantum use efficiency is given by

\[
ε = ε₀ \frac{Cᵢ - Γ}{Cᵢ + 2Γ} \quad (A6)
\]

where ε₀ is the maximum quantum use efficiency (Table 2).

The net assimilation is limited by a deficit of CO₂ through the following saturation equation

\[
Aₙ = \frac{Aₘ₃ₜₕ}{1 - \exp\{-gₘ(Cᵢ - Γ)/Aₘ₃ₜₕ\}} \quad (A7)
\]

The leaf respiration Rₜ, which represents a CO₂ emission (the only component of net assimilation without light) is parameterized very simply as (Van Heemst, 1986)

\[
Rₜ = \frac{Aₘ₃ₜₕ}{9} \quad (A8)
\]

Finally, the net assimilation is limited by a light deficit according to a saturation equation similar to Eq. (A7)

\[
Aₙ = (Aₘ₃ₜₕ + Rₜ)[1 - \exp\{-εₐ/(Aₘ₃ₜₕ + Rₜ)\}] - Rₜ \quad (A9)
\]

where Iₐ is the PAR reaching the leaf.
A.3 First guess of the stomatal conductance to CO2, g^sc

The stomatal conductance to CO2 is estimated using a flux–gradient relationship, modified to account for the effect of a water vapour deficit on stomatal aperture.

\[
g^*_{sc} = \frac{A_n - A_{min}}{C_s - C_i} \left( \frac{D_s \times A_n + R_d}{A_{max} + R_d} + R_d \left( 1 - \frac{A_n + R_d}{A_{max} + R_d} \right) \right)
\]

(A10)

In Eq. (A10), \( A_{min} \) represents the residual photosynthesis rate (at full light intensity) associated with cuticular transfers when the stomata are closed because of a high saturation deficit (\( D_s = D_{max} \)).

\[
A_{min} = g_m (C_{min} - \Gamma)
\]

(A11)

where \( C_{min} \) is the value of \( C_i \) corresponding to \( D_s = D_{max} \) (from Eqs. (A3),(A4) and (A5))

\[
C_{min} = \frac{g_c C_s + g_m \Gamma}{g_c + g_m}
\]

(A12)

A.4 First guess of leaf transpiration and conductance to water vapour, \( g^*_s \)

Assuming that the ratio of stomatal conductances to water vapor and CO2 equals the ratio of diffusivities (1.6), the leaf conductance can be written

\[
g^*_{s} = 1.6g^*_{sc} + g_c
\]

(A13)

and the leaf transpiration

\[
E = \rho_s g_s D_s
\]

(A14)

The latter variable is computed only to refine the estimation of the leaf conductance, as explained below.

A.5 Final estimates

The diffusion of CO2 interacts with the diffusion of water vapour. This effect is accounted for in Eq. (A15)

\[
g_{sc} = g^*_{sc} + E \frac{M_a}{\rho_s M_v} \times \frac{C_s + C_i}{2(C_s - C_i)}
\]

(A15)

where \( M_a \) and \( M_v \) are molecular masses of air and water (28.9 et 18 g mol \(^{-1}\), respectively).

Then, Eq. (A13) is applied with the new value of stomatal conductance to CO2. A few iterations between Eqs. (A13) and (A15) enable one to refine the estimation of \( g_{sc} \) and \( g_s \).

Appendix B

Simplified radiative transfer scheme within the canopy, and integration

In Eqs. (2) and (3), \( A_n \) and \( g_s \) are calculated by the A–g, model at level \( z \) above the soil surface, within the canopy, consistent with the PAR available at level \( z \): \( I_a \) (\( z \)). The dimed radiation is calculated by taking into account its reference value at the top of the canopy \( I_a (h) = 0.48R_e \) and the extinction coefficient \( K (z) \) between the top of the canopy and the level \( z \).

\[
I_a (z) = (1 - K(z)) \times I_a (h)
\]

(B1)

with

\[
K(z) = f(\theta_s) \times K_{dt}(z) + (1 - f(\theta_s)) \times K_{dr}(z)
\]

(B2)

where \( K_{dt} (z) \) and \( K_{dr} (z) \) are the extinction of diffuse and direct light, respectively:

\[
K_{dt}(z) = 1 - \exp\left(-0.8bLAI(h-z)/h\right)
\]

(B3)

\[
K_{dr}(z) = 1 - \exp\left(-\frac{G}{\cos \theta_s} bLAI(h-z)/h\right)
\]

(B4)

Here, \( \theta_s \) is the solar zenith angle (\( \theta_s = 0 \) at the zenith), and a spherical angular distribution of leaves is assumed, i.e. \( G = 0.5 \). The ratio \( f \) is the ratio of diffuse to total solar radiation at the top of the canopy, and \( b \) is the foliage scattering coefficient (Roujean, 1996)

\[
f(\theta_s) = \frac{0.25}{0.25 + \cos \theta_s}
\]

(B5)

\[
b = 1 - \frac{1 - \sqrt{1 - \omega}}{1 + \sqrt{1 - \omega}}
\]

(B6)

In Eq. (B6), \( \omega = 0.2 \) is the leaf single scattering albedo in the part of the solar spectrum corresponding to the PAR.

The integration of Eqs. (2) and (3) is performed through a three-point Gauss quadrature method, following Jacobs (1994).
\[ A_{nl} = \text{LAI} \times \sum_{i=1}^{3} W_i A_n(z_i) \]  
\[ g_d = \text{LAI} \times \sum_{i=1}^{3} W_i g_s(z_i) \]

where \( z_i \) and \( W_i \) are the Gauss levels and weights, respectively.

References


