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Discussions**

**Effect of carbon
dioxide on plant
growth and
transpiration**

J.-C. Calvet et al.

Title Page	
Abstract	Introduction
Conclusions	References
Tables	Figures

◄◄	►►
◄	►
Back	Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Past and future scenarios of the effect of carbon dioxide on plant growth and transpiration for three vegetation types of southwestern France

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EGU

Abstract

The sensitivity of an operational CO_2-responsive land surface model (the ISBA-A-gs model of Météo-France) to the atmospheric CO_2 concentration, $[CO_2]$, is investigated for 3 vegetation types (winter wheat, irrigated corn, coniferous forest). Past (1960) and future (2050) scenarios of $[CO_2]$ corresponding to 320 ppm and 550 ppm, respectively, are explored. The sensitivity study is performed for 4 annual cycles presenting contrasting conditions of precipitation regime and air temperature, based on continuous measurements performed on the SMOSREX site near Toulouse, in southwestern France. A significant CO_2-driven reduction of canopy conductance is simulated for the irrigated corn and the coniferous forest. The reduction is particularly large for corn, from 2000 to 2050 (–18%), and triggers a drop in optimum irrigation (–30 mm y^{-1}). In the case of wheat, the response is more complex, with an equal occurrence of enhanced or reduced canopy conductance.

1 Introduction

Carbon dioxide (CO_2) has a direct effect on plant transpiration. On one hand, the carbon fertilization yields an increase of the vegetation biomass and, to a lesser extent, of the leaf area index (LAI). On the other hand, the antitranspirant action of CO_2 infers a reduction of the leaf stomatal conductance to water vapour regulating the latent heat flux. The competition between the two phenomena may either result in an increase or a decrease of canopy conductance (g_c), this depending on plant characteristics, climatic conditions, and nutrient availability (Field et al., 1995; Douville et al., 2000). A recent study (Gedney et al., 2006) has led to the conclusion that direct effect of CO_2 on plant stands may have been a contributor to an enhancement of river flows during the 20th century. However, they did not consider the impact of increasing biomass and LAI due to increased atmospheric CO_2 concentration ($[CO_2]$).

In numerical weather prediction (NWP) models, hourly fields of the surface temper-

ature, the water and heat fluxes, are produced through dedicated module interfaces. Météo-France is developing SURFEX (SURFace EXternalisée) to be used in operational NWP models, and offline for applications in hydrology and vegetation monitoring (Martin et al., 2007). SURFEX serves the merging of a number of land and ocean surface models. Over land, SURFEX includes ISBA-A-gs, a CO_2 responsive land surface model able to simulate the diurnal cycle of carbon and water vapor fluxes (Calvet et al., 1998; Calvet et al., 2004; Gibelin et al., 2006). This latter model accounts for different feedbacks in response to changes in [CO_2], photosynthesis enhancement and transpiration reduction. Daily values of LAI and biomass can be produced by ISBA-A-gs. A previous study showed that ISBA-A-gs is able to represent CO_2-enrichment effects (Calvet and Soussana, 2001) on plant transpiration and plant growth.

In this study, the impact of the rapid increase in [CO_2] on land surface processes, that is photosynthesis and transpiration, is investigated by simulating LAI with ISBA-A-gs offline. The objective is to assess to what extent the use of a CO_2-responsive land surface model is needed in current and future operational NWP simulations. The model is run offline over the experimental Surface Monitoring Of the Soil Reservoir Experiment (SMOSREX, De Rosnay et al., 2006) site and we take benefit of having a period of 4 contrasted years. The fallow site of SMOSREX is chosen because long-term continuous observations of atmospheric variables are available, together with vegetation biomass and soil moisture content measurements. These data were used in another study to validate the control simulations of ISBA-A-gs and test different methods of data assimilation in the model (Muñoz Sabater et al., 2007).

Emphasis is given on the net [CO_2] effect on g_c for past (from 1960 to 2000) and future scenarios (from 2000 to 2050). Three vegetation types found in southwestern France are considered: winter wheat (WTW), irrigated corn (IRC), and coniferous forest (CNF). A method to account for nitrogen dilution and the implementation of a sensitivity study are described in Sect. 2. The results are presented in Sect. 3 and the model's response to [CO_2] is analysed and discussed in Sect. 4.

2 Material and methods

2.1 Forcing atmospheric data

Atmospheric and radiation variables were continuously measured at the weather station of the SMOSREX research site located near Toulouse (43°23′ N, 1°17′ E, at 188 m altitude), in southwestern France. SMOSREX is a long-term experiment devoted to land surface monitoring studies, which started in 2001 (De Rosnay et al., 2006). In this study, we take advantage of having four contrasting annual cycles during the period 2001–2004 (Table 1), where continuous half-hourly time series of air temperature and humidity, wind speed, precipitation, shortwave and longwave down-welling radiation observations were acquired.

2.2 Parameters of ISBA-A-gs

In this study, we use the same model and the same model parameters obtained at a global scale by Gibelin et al. (2006) (Gi06). However, we must prescribe specific values of the leaf nitrogen concentration, N_L because this parameter depends on the environmental conditions, and particularly in nutrient availability (Table 2). Another difference with the Gi06 simulation is that, for corn, a sowing date is prescribed (15 May) and the irrigation is simulated: (1) From 1 January to the sowing date, LAI is forced below a minimum value of $0.3 \, m^2 \, m^{-2}$; (2) An irrigation amount of 30 mm is added to the precipitation forcing each time the simulated extractable soil moisture content (dimensionless) reaches a predefined threshold. This threshold decreases from 0.70 for the first irrigation, to 0.55 for the second, 0.40 for the third, and 0.25 for the following ones.

The ecosystem respiration R_e is represented by a Q_{10} temperature-response func-

tion (Rivalland et al., 2005):

$$R_e = R_{e25} \cdot Q_{10}^{(T_2-25)/10} \tag{1}$$

where R_{e25} is the baseline ecosystem respiration at a near-surface soil temperature (T_2) of 25 degree C. T_2 is a variable simulated by the model, and in this study a Q_{10} value of 2 is used. Similarly to Gi06, simulations are performed offline, that is no coupling with the atmospheric boundary layer is performed, and a constant value of $[CO_2]$ is prescribed.

2.3 Scenarios for a sensitivity test

Contrasting $[CO_2]$ situations are considered for past and future decades: (1) 320 ppm is representative of the early 1960s (Keeling et al. 1996), (2) 550 ppm is projected for the year 2050 (Long et al., 2006). The reference situation is 371 ppm, corresponding to 2000 (Fung et al., 2005). Changes in the precipitation regime and the mean air temperature are not directly represented. However, four contrasting years are considered: 2001 is rather representative of the present climatology; 2002 was a wet and cool year; 2003 and 2004 were dry and warm years; 2003 was especially hot, with a monthly average maximum air temperature 3.6 to 5.7 degree C higher than the same period in 2001, from June to August. These latter two are expected to represent future climates scenarios (Table 1).

2.4 Representation of nitrogen dilution

The CO_2 fertilization effect tends to increase the vegetation biomass but this effect is limited by nitrogen dilution. In this study, nitrogen dilution is accounted for by parameterizing the change in leaf nitrogen mass-based concentration N_L in response to $[CO_2]$ rise. The sensitivity of leaf nitrogen concentration versus $[CO_2]$ is accounted for by

EGU

using the meta-analysis of the literature carried out by Yin 2002 (Yi02). The meta-analysis of Yi02 indicates that, on average, a CO_2-doubling causes a 18% decrease in N_L, but that the N_L response to CO_2 is influenced by a number of factors. A change in $[CO_2]$, from $[CO_2] = C_1$ to $[CO_2] = C_2$, produces a change in N_L from N_{L1} to N_{L2} following:

$$\ln\left(\frac{N_{L2}}{N_{L1}}\right) = -a \, \exp\left[b - \frac{N_{L1}}{N_{L\,\max}}\right] \, \ln\left(\frac{C_2}{C_1}\right) \tag{2}$$

with $a=0.048$ and $N_{L\,\max}=6.3$ %. In the Yi02 study, C_2/C_1 ranges from 0.53 to 3.2. The b parameter may vary significantly from one vegetation type to another. For example, in median radiation and air temperature (T_a) conditions, $b = 1.48$ for a fertilised crop, $b = 2.56$ for a deciduous forest, $b = 1.81$ for a coniferous forest or natural grasslands. The values of b are given by:

$$b = 0.75 DF - 0.33 FERT + 1.1 PPFD + \frac{T_a}{23} \tag{3}$$

with $DF=1$ for deciduous forests (0 for other biomes), and $FERT=1$ for fertilized ecosystems like crops (0 for other biomes). $PPFD$ is the average photosynthetically active solar radiation reaching the leaf within the vegetation canopy (median value of 0.74 mmol m^{-2} s^{-1}, equivalent to a total solar radiation of 335 W m^{-2}). In this study, no solar radiation or temperature effect is associated with a change in $[CO_2]$ and the median $PPFD$ and T_a values of Yi02 are used in Eq. (3).

2.5   Analysis of the $[CO_2]$ impact

The scenario impacts were analysed in respect to five hourly variables (canopy conductance g_c, mean leaf temperature T_s, water vapour and heat fluxes, net ecosystem exchange of carbon NEE) and one daily variable (LAI). Only the situations favourable to significant land-atmosphere exchanges controlled by the vegetation were considered. The time periods were chosen by applying the following criteria to the 2000 reference

simulation: (1) a significant amount of green biomass: LAI $>1\,\mathrm{m^2\,m^{-2}}$, (2) medium to high levels of available energy for turbulent fluxes of sensible and latent heat flux (H and LE, respectively): H+LE $> 200\,\mathrm{Wm^{-2}}$, (3) moderate to high leaf temperature: $T_s >$ 15 degree C. These thresholds act at filtering out nocturnal and wintertime situations mainly. As for crops, the threshold fixed on LAI values serves to segregate the growing period (March-June for WTW, June-September for IRC) as well as a possible regrowth (from August to October in the case of WTW). This corresponds from 10% to 15% of the 4-year hourly simulations, that is about 4200 h for WTW, 3500 h for IRC, and 5300 h for CNF.

3 Results

3.1 The reference simulation (year 2000)

Table 3 presents a yearly summary of the current climate simulations (for year 2000), for winter wheat, irrigated corn, and coniferous forest (WTW, IRC and CNF, respectively). The dry/warm years Y3 and Y4 contrast sharply with the Y1 and Y2 annual cycles. For IRC, much higher irrigation amounts are simulated in Y3 and Y4 (up to 270 $\mathrm{mm\,y^{-1}}$) and higher evapotranspiration (more than 560 $\mathrm{mm\,y^{-1}}$) and gross primary production (GPP). However, the rainfed WTW presents lower values of evapotranspiration and GPP in Y3 and Y4.

3.2 Past and future scenarios of [CO_2] impact

The fertilization effect of [CO_2] is responsible for an increase of the maximum LAI for all vegetation types between 1960 and 2000, also between 2000 and 2050 (Table 4). The trend is particularly noticeable for WTW (about 0.6 $\mathrm{m^2\,m^{-2}}$ from 2000 to 2050) and is less marked for C4 plant like IRC, as it could be expected, with only changes in LAI less than 0.1 $\mathrm{m^2\,m^{-2}}$.

For IRC and CNF, in spite of a rise in LAI, the evapotranspiration is reduced. This is due to the reduction of g_c and to the increase in water use efficiency in response to the [CO_2] rise. This effect is particularly significant for C4 plants (IRC). In the case of IRC, the optimum irrigation decreases in 2050 while the simulated maximum biomass increases. In the case of WTW, median changes in g_c and evapotranspiration are small, and the two quantities tend to increase between 1960 and 2050. In this case, the fertilization effect and the LAI increase prevail (CO_2 is a strong limiting factor for C3 plants) and tend to mask the decrease in leaf stomatal conductance.

The median change in T_s is small, except for IRC in 2050 (+0.42 degree C, Table 4, and more than +0.86 degree C for 10% of the distribution, not shown).

Since the median values in Table 4 may hide more complex features, the median difference is presented together with 6 percentiles (5, 10, 20, 80, 90, and 95%) in Fig. 1, for LAI and g_c, for each annual cycle. Most often than not, larger differences are simulated from 2000 to 2050 than from 1960 to 2000. In general, the distribution of the difference in g_c is bimodal. In particular, large changes in g_c, either positive or negative, are simulated for WTW, from 2000 to 2050. The diurnal cycle of the 10 and 90% percentiles changes in g_c are presented in Fig. 2, along with the corresponding changes in leaf temperature.

3.3   A bimodal response of g_c: the WTW case

The analysis of the WTW simulations shows that in the case of WTW, the simulated net effect of CO_2 on canopy conductance may be either positive or negative (Fig. 2) and this is a seasonal variation (Fig. 3).

Figure 2 shows that (1) the highest increase of g_c (up to +540%) and the concomitant decrease of T_s (down to –4.4 degree C) are observed, mainly, around noon (from 1200 to 1400 LST) ; (2) the highest decrease of g_c (down to –80%) and the concomitant increase of T_s (up to +1.9 degree C) are observed, mainly, in the afternoon (from 15:00 to 17:00 LST).

Figure 3 shows that the g_c increase is often observed at the start of the growing sea-

EGU

son (March) and during the regrowth (September). Indeed, the relative LAI increase of WTW presents a maximum value (25% or more) in March, and a second maximum is simulated in September for the dry annual cycles Y3 and Y4. When the LAI enhancement prevails over the antitranspirant effect of CO_2, the increase in g_c and the decrease in T_s are particularly significant from 12:00 to 14:00 LST. This latter is the consequence of a radiative effect, accounted for in ISBA-A-gs. The influence of LAI on g_c is enhanced along daytime, in particularly thanks to a better penetration the solar radiation within the vegetation canopy around noon. The variable g_c is all the more increased since the decrease of T_s tends to reduce the leaf-to-air saturation deficit (in general, the saturation deficit presents maximum values between 12:00 and 14:00 LST).

The antitranspirant effect of CO_2 prevails over the LAI enhancement in springtime (April to June), during the most active period of carbon uptake by the wheat crop. At that time, LAI peak is reached with values ranging from 3 to $4\,m^2\,m^{-2}$ in April–May, and from 4 to $5\,m^2\,m^{-2}$ in June (except for 2003 with less than $1\,m^2\,m^{-2}$ in June). It yields a decrease in g_c particularly significant from 15:00 to 17:00 LST. Indeed, LAI increase does not necessarily trigger a rise in g_c, due again to a radiative effect: increasing high LAI values have an adverse effect on the penetration of light into the canopy, which tends to increase the proportion of shaded leaves, especially as the sun moves away from the zenith direction.

In the case of CNF, the antitranspirant effect is more significant than for WTW. However, in this modeling study, the CO_2 effect is considered, only. In the case of forests, other factors may influence the forest's growth and LAI, such as long term nitrogen deposition or changes in forest management. These additional factors may amplify the CO_2 effects on LAI (Cannell, 1999) and bring the CNF response closer to the WTW one.

3.4 Biomass

As far as biomass is concerned, 2050 results can be compared with those of Long et al. (2006), based on enclosure and FACE studies at 550 ppm. They show that

enclosure studies give an average yield increase of 31 and 18% for wheat and C4 crops, respectively. They also show that the Free Air CO_2 Enrichment (FACE) studies give much lower values: 13 and 0%. Our 2050 WTR and IRC results (Table 4) are consistent with the enclosure estimates (we obtain 32 and 15%, respectively), not with the FACE ones. Note that the FACE results are based on a very small number of experiments (4 annual cycles for wheat at the same site, only one annual cycle for corn).

3.5   Irrigation

The IRC simulations show that, for a given annual cycle, the 2050 scenario tends to reduce the required amount of irrigation (Table 4), while increasing the biomass production. However, in the future, Y3 and Y4 years may be more common than now and the irrigation demand (Table 3) will increase: there is a factor 2 or more from the optimal irrigation of Y1 to Y3 and Y4.

4   Conclusions

An operational land surface model was used in order to perform a sensitivity study to [CO_2]. This modelling study was conducted for climatic conditions found in southwestern France. Our simulations show that:

– In general, changes in LAI and canopy conductance are more significant from 2000 to 2050 than from 1960 to 2000, showing that although the need for using of a CO_2-responsive land surface model in operational NWP simulations was not expressed so far, the CO_2 effect on vegetation may have to be accounted for in the future in order to avoid seasonal and diurnal biases in the simulations.

– The impact of increasing biomass and LAI due to increased [CO_2] must be accounted for since it tends to compensate for the antitranspirant effect. It is likely that adding the CO_2 fertilisation mechanism would change the conclusions that Gedney et al. (2006) derived from their simulations.

Effect of carbon dioxide on plant growth and transpiration

J.-C. Calvet et al.

EGU

- The net effect of CO_2 on canopy conductance, leaf temperature, and latent and sensible heat fluxes may be either positive or negative (especially for C3 plants) and may affect the seasonal variability.

- For C3 plants, the simulated net CO_2 effect on canopy conductance may depend, to a large extent, on the way light interception within the canopy is simulated.

- An extensive CO_2-driven reduction of canopy conductance is simulated for the irrigated corn and the coniferous forest. The reduction is particularly large for corn, from 2000 to 2050 (−18%), and triggers a drop in optimum irrigation (−30 mm y^{-1}).

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Table 1. Four contrasting annual cycles (Y1, Y2 ,Y3, Y4), derived from the SMOSREX data set: average maximum air temperature (degree C), Tx, for quarters 2 and 3 (AMJ and JAS, respectively), cumulated annual and quarterly precipitation, RR (mm).

Annual cycle	Year	AMJ r Tx	JAS Tx	Annual RR	AMJ RR	JAS RR	Characteristics
Y1	2001	20.7	26.1	621	179	173	Normal year
Y2	2002	20.5	25.0	677	228	137	Wet year; cool summer
Y3	2003	23.4	30.0	574	80	144	Dry Spring ; hot
Y4	2004	21.0	27.3	677	196	100	Dry Summer; warm

Table 2. Standard values of ISBA-A-gs parameters (Gibelin et al., 2006) for 3 vegetation types (Winter wheat –WTW-, irrigated corn –IRC-, coniferous forest –CNF-) and specific values of leaf nitrogen concentration N_L and ecosystem respiration at 25 degree C R_{e25}, for southwestern France (SWF). N_L in % of dry mass. g_m^* is the mesophyll conductance in well-watered conditions, in mm s^{-1}, τ_M is the maximum leaf span time, in days, LAI_{min} is the minimum leaf area index, in m^2 m^{-2}, g_c is the cuticular conductance, in mm s^{-1}, θ_C is the critical extractable soil moisture content, dimensionless, e is the SLA (specific leaf area) sensitivity to N_L, in m^2 kg^{-1}%$^{-1}$, f is SLA at $N_L = 0$%, in m^2 kg^{-1}, R_{e25} is in mgCO$_2$m^{-2}s^{-1}.

Vegetation Type	Photo-synthesis type	SWF N_L	N_L	g_m^*	τ_M	LAI_{min}	g_c	θ_C	e	f	R_{e25}	Response to drought
WTW	C3	1.1	1.3	1	150	0.3	0.25	0.3	3.79	9.84	0.27	avoiding
IRC	C4	2.2	1.9	9	150	0.3	0.15	0.3	7.68	−4.33	0.53	tolerant
CNF	C3	2.3	2.8	2	365	1	0	0.3	4.85	−0.24	0.56	avoiding

Table 3. Flux and biomass annual production for the 2000 reference simulation, for 3 vegetation types: winter wheat (WTW), irrigated corn (IRC), and coniferous forest (CNF). The results are presented for four contrasting annual cycles (Y1 to Y4, Table 1). GPP is gross primary production (i.e. raw carbon uptake by photosynthesis).

Variable	Type	Y1	Y2	Y3	Y4
Evapotranspiration (mm y^{-1})	WTW	570	561	444	469
GPP (gC m^{-2} y^{-1})	WTW	1419	1480	1150	1181
Maximum LAI (m^2 m^{-2})	WTW	5.7	5.7	4.7	5.4
Maximum leaf biomass (kg m^{-2})	WTW	0.38	0.37	0.32	0.36
Maximum aboveground biomass (kg m^{-2})	WTW	1.36	1.32	1.04	1.26
Optimum irrigation (mm y^{-1})	IRC	120	60	270	240
Evapotranspiration (mm y^{-1})	IRC	526	483	616	563
GPP (gC m^{-2} y^{-1})	IRC	2567	2394	2658	2396
Maximum LAI (m^2 m^{-2})	IRC	6.25	5.97	6.14	6.07
Maximum leaf biomass (kg m^{-2})	IRC	0.47	0.45	0.46	0.45
Maximum aboveground biomass (kg m^{-2})	IRC	1.92	1.78	1.84	1.80
Evapotranspiration (mm y^{-1})	CNF	544	520	528	519
GPP (gC m^{-2} y^{-1})	CNF	2614	2621	2316	2334
Maximum LAI (m^2 m^{-2})	CNF	5.7	5.8	5.3	5.5
Maximum leaf biomass (kg m^{-2})	CNF	0.49	0.50	0.46	0.48
Maximum aboveground biomass (kg m^{-2})	CNF	–	–	–	–

Table 4. Median difference of daily values of leaf area index (LAI), hourly values of canopy conductance (relative difference), leaf temperature, net ecosystem exchange of CO_2 (NEE), water vapour flux, heat flux, and yearly values of peak aboveground biomass (relative difference) and optimum irrigation, between the 1960 and 2050 scenarios and the 2000 reference simulation, for 3 vegetation types: winter wheat (WTW), irrigated corn (IRC), and coniferous forest (CNF). The mean of the yearly (Y1-Y4) values are given, with the standard deviation. The values of leaf nitrogen concentration (N_L), in % of dry mass, derived from Eq. (2), are indicated.

| Variable	WTW 1960	WTW 2050	IRC 1960	IRC 2050	CNF 1960	CNF 2050
LAI (m^2 m^{-2})	−0.22±0.02	+0.62±0.08	−0.10±0.02	+0.07±0.07	−0.20±0.01	+0.39±0.02
Canopy conductance (relative difference in %)	−3.0±1.7	+2.6±4.5	+3.2±0.6	−18.2±2.2	+1.4±0.2	−6.2±1.0
Leaf temperature (degree C)	+0.04±0.02	−0.05±0.05	−0.06±0.01	+0.42±0.05	−0.01±0.01	+0.07±0.02
Net CO_2 flux (μmol m^{-2} s^{-1})	+2.5±0.5	−7.9±1.7	+4.5±0.3	−9.2±1.1	+3.8±0.3	−11.8±0.5
Water vapour flux (W m^{-2})	−1.4±0.6	+1.5±1.6	+2.1±0.3	−13.5±1.2	+1.6±0.2	−6.6±1.4
Heat flux (W m^{-2})	+0.9±0.4	−1.0±1.0	−1.2±0.3	+8.6±1.0	−1.3±0.2	+5.6±1.3
Yearly peak aboveground biomass (relative difference in %)	−12±2	+32±4	−7±0	+15±2	–	–
Yearly optimum irrigation (mm y^{-1})	–	–	0±0	−30±0	–	–
N_L (%)	1.13	1.03	2.25	2.07	2.37	2.12
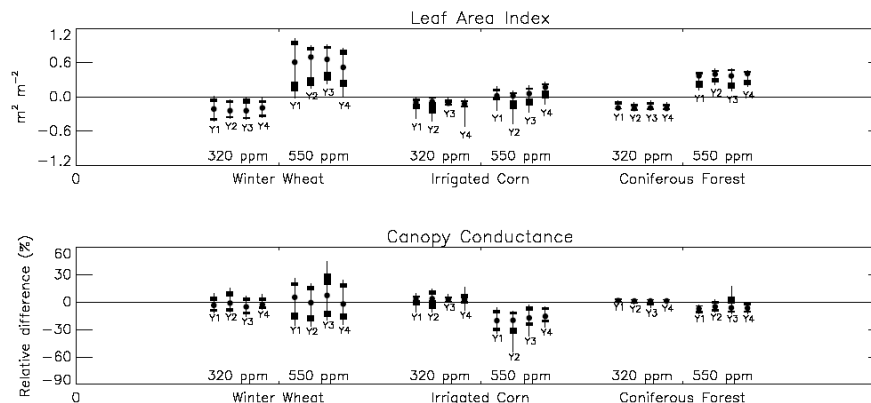
Fig. 1. Impact of 2 scenarios (1960, 2050, i.e. [CO_2] of 320 and 550 ppm, respectively) on (top) leaf area index, and (bottom) canopy conductance (relative difference). Median difference: closed circles; 5–95% percentiles: fine line; 10–20% percentile: closed box (bottom); 80–90% percentile: closed box (top). Positive differences correspond to higher values in the scenario, compared with the 2000 reference simulation. The results are presented for four contrasting annual cycles (Y1 to Y4, Table 1) in southwestern France.
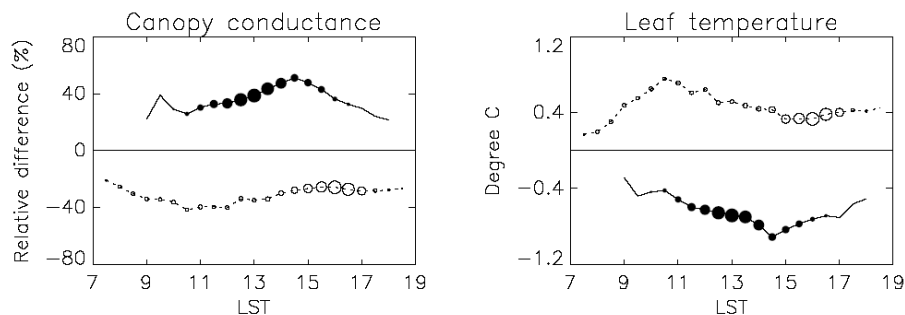
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Fig. 2. Impact of the 2050 scenario ([CO_2] of 550 ppm) on (left) the canopy conductance (relative difference) of winter wheat vs time (from 08:00 to 18:00 local standard time): average values above the 90% percentile and below the 10% percentile (closed and open circles, solid and dotted lines, respectively). The probability of occurrence is represented by the radius of the circles. Right: the corresponding mean leaf temperature difference.
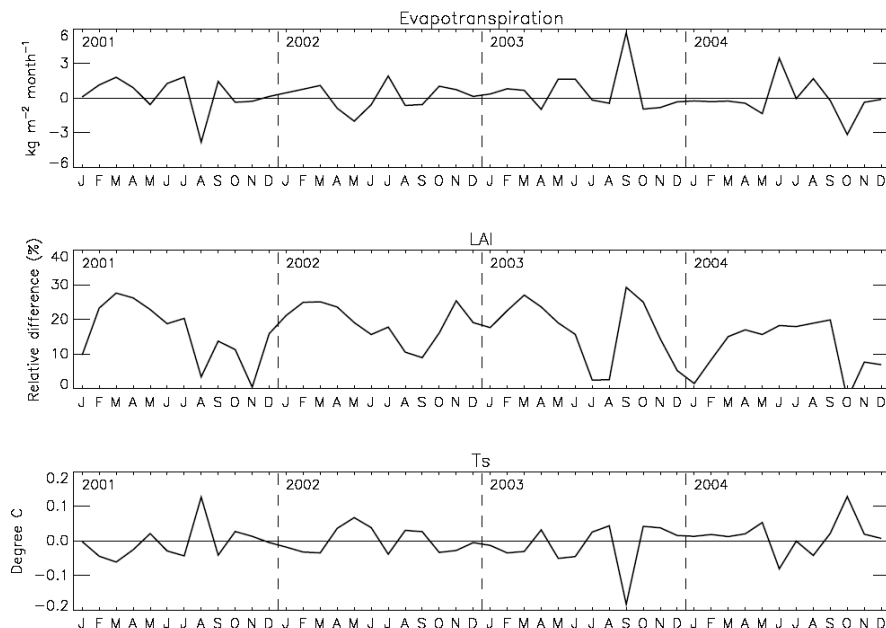
J.-C. Calvet et al.

Fig. 3. Impact of the 2050 scenario ($[CO_2]$ of 550 ppm) on winter wheat, for four contrasting years (Y1 to Y4, Table 1). From top to bottom: difference in monthly evapotranspiration, relative difference in LAI, monthly average difference in leaf temperature.

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

|◄ | ►|

◄ | ►

Back | Close

Full Screen / Esc

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