Simulation of the Effect of Increased Atmospheric CO₂ on Assimilation and Transpiration of a Closed Crop Canopy³

J. Gondrainless, H. H. van Laar, H. van Keulen and W. Louwerse

Introduction

All terrestrial vegetation is exposed to a steadily growing background concentration of CO₂ (ca. 1.5 ppmv yr⁻¹ at 340 ppmv background) due to release of CO₂ by combustion of fossil fuel. The rate of increase of atmospheric CO₂ corresponds to only about 60% of the CO₂ production from fossil fuel. Most of the remaining 40% is absorbed by the ocean. There is continuous exchange of carbon between the biosphere and the atmosphere.

At present there is probably a net absorption by the biosphere of about 7% of the CO₂ from fossil fuel [9, 1].

It is a classic observation that aerial CO₂ is necessary for plant growth and that CO₂ enrichment usually has a stimulating effect on growth rates [19, 21]. To allow CO₂ diffusion into the leaves, stomata must be open, which at the same time exposes the wet cell surfaces to the drying effect of the ambient air. An increase in atmospheric CO₂ facilitates the plant's dilemma to adjust stomatal aperture in such a way that transpiration is kept within acceptable limits, but that at the same time assimilation is not choked too much.

To examine the effect of an increase in atmospheric CO₂ concentration the simulation model BACROS [20] is applied as by van Keulen et al. [10], but with the following improvements:

a) An aerodynamic resistance, calculated on the basis of the logarithmic wind profile, is inserted above the crop canopy. This resistance modifies the microclimate and moderates high fluxes.

b) The effect of CO₂ on the CO₂-assimilation light response curve of individual leaves has been reformulated, especially in view of interactions with photorespiration.

Stomatal regulation

Van Keulen et al. [10] present literature data [18, 11, 8, 13] indicating the existence of three types of stomatal behaviour:

i) A strong feedback of CO₂ on stomatal aperture, so that the internal CO₂ concentration (i.e. the concentration inside the stomatal cavity) is stabilized at a characteristic value. In this situation an increase in atmospheric CO₂ concentration will not alter assimilation because the photosynthetic apparatus is not exposed to a different CO₂ environment. However, stomata will partially close, consequently transpiration will be strongly reduced, which in case of water-limited production will lengthen the growing season.

ii) A weak feedback of CO₂ on stomatal aperture, resulting in an internal CO₂ concentration that is proportional to the external concentration. This type of behaviour is probably the most frequent one [17]. In this case the benefit of an increased external CO₂ concentration is shared between higher assimilation and lower transpiration. Stomatal aperture is reduced and hence transpiration, but not enough to suppress the effects on assimilation.

iii) No feedback of CO₂ concentration on stomatal aperture. It seems that such behaviour requires presence of water stress throughout, or is operative under very high temperatures. In this situation, transpiration will not be affected by external CO₂ concentration, but assimilation will be stimulated.

Whatever the type of stomatal behaviour, the transpiration-assimilation ratio will be reduced by increased CO₂.

Modelling the aerodynamic or turbulence resistance

Its value

The value of the turbulence resistance is calculated applying the classical theory of the logarithmic wind profile [14]:

\[ r_t = 0.74 \ln \left( \frac{z_s - d}{z_0} \right) \left( k^b a \right) \]

The reference height, \( z_s \), is assumed to be one meter above crop height \( z_r \) (about 1.25 m). With a zero plane displacement, \( d \), of about 0.7 \( z_r \), a roughness length, \( z_0 \), of about 1.1 \( z_r \). Von Karman's constant, \( k \), about 0.4, and wind speed, \( u_* \), about 2 m s⁻¹, the resistance is of the order of 10 to 20 s m⁻². Stomatal resistances are of the order of 100 to 200 m s⁻¹, but because the various leaf layers act in parallel, the resulting crop resistance is much lower and is of the order of 30 s m⁻². Therefore, the aerodynamic resistance in series with stomatal resistance can easily reduce transpiration by 30%.
**Its effect on assimilation**

Under high levels of irradiance the rate of net CO₂ assimilation of a crop may reach values of 60 kg CO₂ ha⁻¹ h⁻¹, causing a drop of 10 to 20 ppmv across the turbulence resistance, \( r_i \) (Fig. 1). This drop in itself may affect the assimilation rate, so that an iterative procedure seems required. To avoid that procedure, the CO₂ content of the air at crop level is defined as a state variable, with a time constant artificially fixed at 1 hour. In this way the iteration is avoided at the expense of a delay of 1 hour in the CO₂ drop. Even under high irradiance the drop does not exceed 20 ppmv, so that the feedback effect on assimilation is limited. Moreover, these deviations have opposite effects in the morning and in the afternoon so that they practically cancel out as far as daily totals are concerned.

\[
T_a = T_i + \frac{r_i}{\alpha} \sum L_{AI} W_i
\]

\[
\epsilon_a = \epsilon_i + \frac{\gamma^*}{\beta^*} \sum L_{AI} \lambda E_i
\]

**Its effect on transpiration**

At a given stomatal resistance the response of transpiration rate to the vapour pressure deficit in the air is linear. This linearity can be used to solve directly the energy balance equations, including the effect of the turbulence resistance. For this purpose, it is assumed that all leaves inside the crop canopy are exposed to an identical ambient temperature and humidity, derived from the atmospheric values modified by the turbulence resistance:

\[
W_i = \frac{\gamma^* R_a - \delta}{s + \gamma^*}
\]

\[
\lambda E_i = \frac{s R_a + \delta}{s + \gamma^*}
\]

where

\[
\gamma^* = \frac{r_b + r_i}{r_b}
\]

and

\[
\delta = \frac{VPD_{in} \beta^*}{r_b}
\]

with

\[
\gamma^* \text{ apparent psychrometric constant} \quad \text{mbar} \quad C^{-1}
\]

\[
R_a \text{ total absorbed radiation per leaf area} \quad \text{W} \quad \text{m}^{-2}
\]

\[
\delta \text{ drying power of the air} \quad \text{mbar} \quad \text{W} \quad \text{m}^{-2} \quad \text{C}^{-1}
\]

\[
r_b \text{ boundary layer resistance} \quad \text{s} \quad \text{m}^{-1}
\]

\[
r_i \text{ leaf resistance (stomata/cuticula)} \quad \text{s} \quad \text{m}^{-1}
\]

Substituting Eqs. 5, 6 and 7 into Eqn. 4 and solving for \( VPD_{in} \) yields:

\[
VPD_{in} \left( 1 + r_i (s + \gamma^*) \frac{L_{AI}}{r_b (s + \gamma^*)} \right) = \frac{VPD_a + \frac{\gamma r_i}{\beta^*} \frac{R_{ad} \gamma}{r_b (s + \gamma^*)} - L_{AI}}{(s + \gamma^*)}
\]

This equation enables a direct calculation of the vapour pressure deficit inside the crop canopy. Typical time courses of the VPD above and inside the crop are shown in Fig. 1.

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**Fig. 1. Diurnal courses of some air properties, simulated for a C₄ species, non-regulating stomata, clear sky, 430 ppmv CO₂, 50°C.**

- **a)** Water vapour pressure (AVP) and CO₂ above and inside the canopy
- **b)** Air temperature (TA) and vapour pressure deficit (VPD) above and inside the canopy

**Table:**

<table>
<thead>
<tr>
<th>Property</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature above</td>
<td>°C</td>
</tr>
<tr>
<td>Temperature within</td>
<td>°C</td>
</tr>
<tr>
<td>Humidity above</td>
<td>mbar</td>
</tr>
<tr>
<td>Humidity within</td>
<td>mbar</td>
</tr>
<tr>
<td>Sensible heat flux</td>
<td>W m⁻²</td>
</tr>
<tr>
<td>Latent heat flux</td>
<td>W m⁻²</td>
</tr>
<tr>
<td>Leaf index of layer</td>
<td>-</td>
</tr>
<tr>
<td>Psychrometric constant</td>
<td>mbar °C⁻¹</td>
</tr>
<tr>
<td>Volumetric heat capacity</td>
<td>J m⁻³ °C⁻¹</td>
</tr>
</tbody>
</table>

The summations in Eqs. 2a and 2b are performed over all leaf layers and yield the fluxes per unit surface area. The vapour pressure deficit inside the crop canopy, \( VPD_{in} \), is now obtained from:

\[
VPD_{in} = VPD_a + \frac{r_i}{\beta^*} \sum L_{AI} (s W_i - \gamma \lambda E_i)
\]
In the calculation time steps of one hour were used. In Eqn. 8 a summation for all leaf classes is required twice, before the vapour pressure deficit can be calculated. Once the vapour deficit inside the crop canopy is known, the transpiration flux can be found by another summation over the same leaf classes. If time steps of one day are used, these two summations must be consequently done each time step. For our purpose the summations were executed simultaneously, thereby accepting the fact that correction terms in Eqn. 8 are one hour delayed. When smooth diurnal courses of weather are used, as in this example, the effect of this error is negligible.

We considered the canopy space as a well mixed reservoir, connected with the atmosphere through a single aerodynamic (or turbulence) resistance. This simplification is permissible if one is not interested in the profiles inside the canopy themselves [1].

Modelling the effect of CO₂ on the CO₂ assimilation—light response curve

The light response curve of leaves is described by an asymptotic exponential (monomolecular) equation. This equation often gives a better fit to experimental data than the rectangular hyperbola [15, 3]. Three parameters characterize the response curve: the light saturated assimilation rate \( F_m \), the initial slope \( \epsilon \) and the dark respiration rate \( R_d \):

\[
F_m = (F_m + R_d)(1 - \exp(-\epsilon H(F_m + R_d))) - R_d
\]

with,

\( F \) actual assimilation rate kg CO₂ ha⁻¹ h⁻¹

\( H \) absorbed radiant flux in the

400 to 700 nm range.

CO₂ concentration presumably does not affect the dark respiration, but it may influence both maximum assimilation rate and initial slope. It is assumed that the inherent assimilatory capacity of the photosynthetic apparatus by far exceeds the constraints imposed by light and CO₂. Therefore, under high irradiance the affinity of the carboxylating enzyme limits assimilation and the response to CO₂ is linear. We can then simply use:

\[
F_m = (C_1 - F')/\epsilon
\]

where \( C_1 \) is the CO₂ concentration inside the stomatal cavity, \( F' \) is the CO₂ compensation point and \( \epsilon \) is the apparent mesophyll resistance. This equation has the same structure as that for a diffusion-limited uptake. However, the limiting step is not diffusion, but carboxylation. Therefore, the so-called mesophyll resistance can be largely identified with the carboxylation resistance. In BACROS this mesophyll resistance is standardized at 260 s m⁻¹ for C₃ plants and 110 s m⁻¹ for C₄ plants, and the CO₂ compensation point \( F' \) at 50 ppmv and 5 ppmv respectively (Table 1). At typical values of 210 and 120 ppmv for the CO₂ concentrations in the stomatal cavity, these values correspond to about 40 and 70 kg CO₂ ha⁻¹ h⁻¹ respectively. When the stomatal resistance is not regulated, the internal CO₂ concentration and the maximum net assimilation rate may be higher.

For modelling purposes we assume that \( R_d \) in Eqn. 9 is independent of light intensity. Consequently we can also write Eqn. 10 as

\[
F_m = F' - F' - R_d
\]

with \( F' \) the maximum gross assimilation, and \( R_d \) the photosynthesis flux.

When \( F' \) is equal to \( C_1/\epsilon \) (no constraint by a maximum enzyme activity) we obtain

\[
R_d = R_d + F'/\epsilon.
\]

In C₃ species, \( R_d \) is zero and \( \epsilon \) is entirely determined by \( C_1 \) (Table 1). In C₄ species the dark respiration rate is responsible for about 12 ppmv out of the 50 in total. The remaining 38 ppmv is caused by photorespiration and may be called the CO₂-photorespiration point \( F* \) [12].

Its value increases linearly with the oxygen concentration. The photosynthetic fraction \( R_d/F_m \) is equal to \( C_1/F* \) [4] and independent of the level of irradiance. Still, photorespiration is relatively more detrimental at low light intensities than at high intensities. Not only is RuBP withdrawn from carboxylation, but also are the oxygenation products recovered by costly energy so that gross photosynthesis is reduced as well. Using data of Peisker and Apel [16] and of Farquhar and Von Caemmerer [5] the apparent initial light use efficiency is given by:

\[
\epsilon = \frac{C - F*}{C + 2F*}
\]

The gross efficiency \( \epsilon \) is higher in C₃ than in C₄ plants [2] but this advantage is more than offset at normal oxygen and CO₂ concentrations (Table 1).

The value of \( C \) to be used in Eqn. 13 is the ambient CO₂ concentration, since the initial efficiency refers to the photosynthetic activity close to the light compensation point where almost no gradient exists between leaf and air. At 300 ppmv the multiplication factor in Eqn. 13 is about 0.68.

### Table 1. Some characteristic values in leaf photosynthesis of C₃ and C₄ plants

<table>
<thead>
<tr>
<th>C₃</th>
<th>C₄</th>
</tr>
</thead>
<tbody>
<tr>
<td>( F_m )</td>
<td>( 40 )</td>
</tr>
<tr>
<td>( C_1 ) regulated</td>
<td>( 210 )</td>
</tr>
<tr>
<td>( F' )</td>
<td>( 30 )</td>
</tr>
<tr>
<td>( I' )</td>
<td>( 38 )</td>
</tr>
<tr>
<td>( \epsilon )</td>
<td>( 260 )</td>
</tr>
<tr>
<td>( R_d )</td>
<td>( 3 )</td>
</tr>
<tr>
<td>( \epsilon_0 )</td>
<td>( 16.7 )</td>
</tr>
<tr>
<td>( \epsilon )</td>
<td>( 11.5 )</td>
</tr>
</tbody>
</table>

In these units the product of resistance and flux must be divided by a conversion factor of 66 to find the CO₂ drop in ppmv.

### Simulation conditions

As a standard day, the 21st of June is used, with a maximum and minimum air temperature of 27.8 and 10.8°C respectively, a water vapour pressure of 17.5 mbar in daytime and an average windspeed of 1.2 m s⁻¹. In daytime the windspeed is 1.6 m s⁻¹ and at night 0.8 m s⁻¹, with the transitions at 6 and 18 h resp. These air conditions are used as driving forces at a level of 1 m above the crop canopy (Fig. 1). As to radiation, a clear day and an entirely overcast day are simulated. The daily total global radiation at a clear day is 30 MJ m⁻² at 30 N. L., and one fifth of that under overcast conditions. The crop characteristics for the C₃ and C₄ type of plants are those of Table 1. The LAI = 4, the height of crop is 5000 kg d. m. ha⁻¹, the end crop height is 1.25 m. The external CO₂ concentrations are assumed to be 330 and 430 ppmv, respectively.

### Results

### Diurnal courses (Fig. 1)

As an illustration of the dynamic behaviour of the model the situation with the highest fluxes (C₄ species, non-regulating stomata, clear sky, 50° N. L., 430 ppmv CO₂) is presented. In Fig. 1 both the vapour pressure above the crop canopy (APP) and the simulated vapour pressure at an average level inside the
crop ($\text{A}_{PP}$) are given. The vapour pressure difference may reach as much as 5 mbar. To support the high latent heat loss sensible heat loss is negative, and so the air temperature shows a drop of about 2 to 3°C.

As a consequence of the higher vapour pressure and lower air temperature in the canopy, the vapour pressure deficit is drastically reduced, and the transpiration flux with it. The peak at 19 h is caused by the sudden drop in wind speed, that occurred an hour before.

The diurnal course of the CO₂ concentration of the air inside the canopy is given in Fig. 1. The maximum drop of 25 ppmv at noon does not impose a serious restriction on the assimilation rate. These results show that the restriction of the turbulence resistance acts much stronger on transpiration than on assimilation.

**Daily totals** (Table 2, Fig. 2)

Compared to a previous simulation study [10] the daily total transpiration for the highest flux situation, as discussed above, dropped from 11 mm d⁻¹ to 7.5 mm d⁻¹ now. This is certainly an extreme case, but it does illustrate the importance of the turbulence resistance. Not always the transpiration rate is reduced. Under high irradiance and relatively closed stomata (C₄ species, fixed internal CO₂ concentration, clear sky, 50° N. L., 430 ppmv) the daily transpiration increased from 3.2 mm d⁻¹ in the previous study to 3.7 mm d⁻¹ here. Because of the rather high share of sensible heat loss in the energy budget, the turbulence resistance increased air temperature at crop level and the vapour pressure deficit decreased, notwithstanding a simultaneous increase in actual vapour pressure.

The results in Table 2 show that the transpiration/assimilation ratio is practically independent of radiation when stomatal regulation occurs. For both types of plants this ratio drops by about 20% when the CO₂ concentration of the air increases from 330 to 430 ppmv.

The turbulence resistance tends to dampen the extreme differences caused by the stomata themselves, and it reduces the range of their regulatory power. Even so, there is still a variation of a factor 2 to 3 in transpiration efficiency, dependent only on the stomatal regulation mechanism. According to these results the importance of stomatal regulation further increases with increasing atmospheric CO₂ concentration.

This is also demonstrated in Fig. 2, where simulated daily net assimilation and water use efficiency are plotted as a function of atmospheric CO₂. Three types of stomatal regulation are used (see text)
successtvely to sun and shade. Therefore, there ts probably a chamber (or Scholander bomb).

characteristics and properties of plant organs, specially owing to the water physiology of a plant which is able to maintain a high water potential, especially micropsychrometer and pressure chamber technique. The standardization on definitions concerning the physical state of water in cells and tissues, with the general acceptance of the water potential concept as "the first and the second levels the major attainments consist of: More clarity and standardization on definitions concerning the physical state of water in cells and tissues, with the general acceptance of the water potential concept as being the most appropriate quantity to characterize the state of water in the soil-plant-atmosphere continuum. Development of new techniques for measuring this water potential, especially micropsychrometer and pressure chamber (or Scholander bomb). Better knowledge of the water characteristics and properties of plant organs, specially owing to the use of the theory of the pressure-volume curves. Increase in interest in the physiology of water stress.

Nevertheless beside these advances, an important chapter of the plant water relations has been missed: the water relations between organs of the same plant. This is yet an important aspect of the water physiology of a plant which is able to maintain a relative water homeostasis in a variable environment. For example, during a sunny day each leaf of the same plant could be exposed successively to sun and shade. Therefore, there is probably a continuous adjustment of the internal fluxes to satisfy at any time the water demand of every part of the plant. This adjustment supposes variable fluxes between organs, depending on climatic conditions, availability of water in soil, state of organs, etc. The description and explanation of these internal fluxes and of their regulation may well constitute the most specific aspect to the water relationships of a plant as being a living organism. The aim of this paper is to give a brief assessment of what is known concerning water relations between organs of the same plant and to show some ways to improve our knowledge in this field of plant physiology.

I. What is known concerning the water relationships between organs of the same plant?

We will concern ourselves with two aspects: structural and functional.

I.1. Structural aspects

a) The vascular system of a plant is often of an extreme complexity. Most of the anatomical works only deal with a minor part of this system (there are some remarkable exceptions like [7, 3] because the classical methods are not adapted to give a complete picture of this complex network. Two authors [13, 14] developed only quite recently a new method, the so-called "optical shuttle method" or "the motion picture analysis" which permits description of the three dimensional structure of the vascular system in higher plants. It has been used to analyse the vascular system of

References
