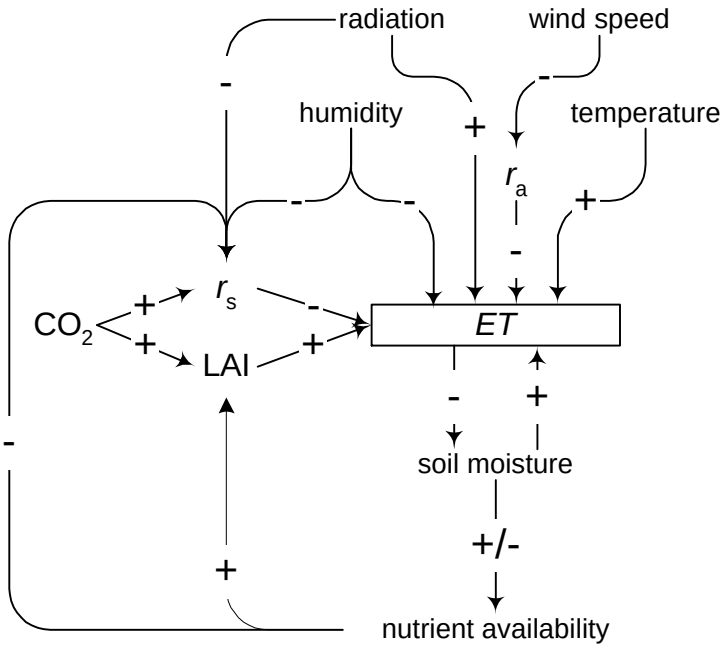
Ministerie van Verkeer en Waterstaat
Directoraat-Generaal Rijkswaterstaat
RIZA Rijksinstituut voor Integraal Zoetwaterbeheer en Afvalwaterbehandeling

KWR 06.004

Januari 2006

The effects of rising CO_2 levels on evapotranspiration



KWR 06.003

Januari 2006

The effects of rising CO_2 levels on evapotranspiration

© 2006 Kiwa N.V.

All rights reserved. No part of this publication may be reproduced, stored in a retrieval system or transmitted in any form or by any means, electronic, mechanical, by photocopying, recording or otherwise, without the written prior permission of the publishers.

Clients

Rijkswaterstaat Riza

Kiwa Water Research

Project number

30.6662.400

Kiwa N.V.

Water Research

Groningenhaven 7

P.O. Box 1072

3430 BB Nieuwegein

The Netherlands

Telephone +31 30 60 69 511

Fax +31 30 60 61 165

Internet www.kiwa.nl

Title

The effects of rising CO_2 levels on evapotranspiration

Project number

30.6662.400

Project manager

J.W. Kooiman

Quality control

P. Droogers, R.A. Feddes and J.N.M. Stricker

Authors

J.PM. Witte, B. Kruijt and C. Maas

This report is not public and is only issued to the client of the Contract research Project / Advice Project. Any further distribution is made solely by the client.

Foreword

Through fossil fuel combustion, the concentrations of carbon dioxide in the atmosphere are increasing, causing a rise in temperatures on the earth. The effect of this temperature rise on potential evapotranspiration has been calculated for The Netherlands by the Dutch meteorological institute KNMI (Beersma et al., 2004): depending on the climate scenario, rising temperatures will cause an increase in annual potential evapotranspiration of between 1.9% and 18%.

However, another consequence of increased levels of CO_2 is that plants do not have to open their stomata as widely, or to create as many stomata, in order to absorb enough CO_2. And the effect of this is that evapotranspiration decreases.

In a very short study, Doomen & Witte (2004) showed that the decrease in evapotranspiration through rising levels of CO_2 could be considerable, with serious consequences for hydrology in The Netherlands. Their study was too brief, however, to adequately substantiate the connection between an increase in CO_2 and a decrease in evapotranspiration. Furthermore, their study raised a number of questions concerning the usability of the experiments described in the literature and the interaction between a decrease in evapotranspiration and environmental factors such as drought stress, temperature and nutrient availability.

For this reason, the Institute of Integrated Water Management and Waste water Treatment, Riza, has asked Kiwa Water Research to do further research into the effects of CO_2 increases on decreasing evapotranspiration. This report is an account of this research, which was jointly financed by Riza's 'Drought Study' (www.droogtestudie.nl) and Kiwa. Comments on both the set-up of the research and the draft report were provided by Peter Droogers (Future Water), Reinder Feddes (Wageningen University, Soil Physics, Ecohydrology and Groundwater Management group) and Han Stricker (Wageningen University, Hydrology and Quantitative Water Management group). In a later stage, Adri Buishand and Jules Beersma from KNMI as well as Timo Kroon from Riza commented on the report.

It was Reinder Feddes who advised me to ask Alterra to calculate the reduction in evapotranspiration using the Penman-Monteith evapotranspiration equation and empirical observations of the relation between CO_2 and stomatal resistance. Thanks to Bart Kruijt of Alterra, this calculation could be performed in a satisfying manner.

Those who are only interested in the results of this study can go straight to the last chapter (page 45), which is readable without the preceding chapters.

Jan-Philip (Flip) Witte

Nieuwegein, January 2006

© Kiwa N.V.

Contents

Foreword **1**

Contents **3**

1 Introduction **5**

1.1 Reasons for this study 5

1.2 Aims and Starting Points 5

1.3 Research method 8

2 The relationship between CO_2 and evapotranspiration: theory **9**

2.1 Introduction 9

2.2 Effects of CO_2 and temperature on photosynthesis and water consumption 10

2.3 The role of transpiration in evapotranspiration 12

2.4 Transpiration and resistance 13

2.5 Factors influencing the experimental relationship between CO_2 and *ET* 17

2.6 What we don't take into account 19

3 Observed effects of CO_2 on a local scale **21**

3.1 Methods 21

3.2 Experimental research methods 21

3.3 Set-up of the database 23

3.4 Discussion and analysis 24

4 Calculating CO_2 effects at plot level **31**

4.1 Introduction 31

4.2 Observations of CO_2 effects on stomatal conductance 31

4.3 Models for stomatal conductance 34

4.4 Calculating evapotranspiration at plot level 35

4.5 Calculation of CO_2 effect at plot level 37

4.6 Discussion 42

5 Conclusions and recommendations **45**

Literature **49**

I List of symbols **57**

II The transpiration share F^T **59**

1 Introduction

1.1 Reasons for this study

In the context of Phase 2 of the Netherlands Drought Study, Kiwa Water Research conducted an exploratory literature study on the effects of CO_2 increases in evapotranspiration, biomass production and competition between plant species (Doomen & Witte, 20 04). One of the most important results of the study is that an increase in CO_2 levels can lead to a significant reduction in potential evapotranspiration. If this result is correct, it has important consequences for hydrology in The Netherlands in a period of climate change: instead of becoming drier, as is generally assumed, The Netherlands would become wetter.

However, this exploratory literature study was too brief to fully substantiate a relation between an increase in CO_2 levels and a decrease in evapotranspiration. Furthermore, their study raised a number of questions concerning the usability of the experiments described in the literature and the interaction between a decrease in evapotranspiration and environmental factors such as drought stress, temperature and nutrient availability. In view of the very significant consequences for hydrology, it is very important that the relationship between increased CO_2 and reduced evapotranspiration be substantiated.

1.2 Aims and Starting Points

Rijkswaterstaat uses the NAGROM and MOZART models to simulate water flow in saturated and unsaturated zones, respectively. These models are linked together by means of the MONA model (Bos et al., 1997). To be able to make its calculations, the MOZART model has to be fed with data about rainfall and the reference crop evapotranspiration, according to Makkink, ET_{ref}.

Since 1987, the Makkink evapotranspiration has been established for several weather stations in The Netherlands. This reference crop evapotranspiration is equivalent to the evapotranspiration of a healthy short grass lawn which is provided with enough nutrients and water; it is, therefore, by definition the potential evapotranspiration of such a hypothetical lawn. The potential evapotranspiration of other vegetations (i.e. crops) is obtained by multiplying the reference crop evapotranspiration by a crop factor:

$$ET_p = f \times ET_{ref} \qquad [1.1]$$

In which (with the usual units between brackets):

ET_p potential evapotranspiration of the vegetation (mm d^{-1})
f crop factor (-)
ET_{ref} reference crop evapotranspiration according to Makkink (mm d^{-1})

The term evapotranspiration covers evaporation from two sources: evaporation from soil and wet surfaces such as raindrops on leaves, and transpiration from the stomata and cuticula of plants.

Crop factors for a range of vegetations have been described in detail in the literature (e.g. Feddes, 1987). The actual evapotranspiration (ET_a) is equal to or lower than the potential evapotranspiration, because if conditions are too dry, too wet or too salty, vegetation reduces the transpiration. ET_a can be calculated with MOZART using a transpiration reduction derived from Feddes et al. (1978), which is a function of the pressure head of the soil moisture in the root zone.

The Rijkswaterstaat models are used to calculate the hydrological consequences of climate change. The KNMI has drawn up climate scenarios, simulating changes in precipitation and potential evapotranspiration per decade (Beersma et al., 2004). According to the KNMI, there will be an increase in weather extremes. Potential evapotranspiration will also increase, due to rising temperatures. Table 1-1 gives the projections for four climate scenarios for the year 2050.

Table 1-1. Climate scenario's for 2050 (Beersma et al., 2004). Multiplying factors are given for precipitation and evapotranspiration (so, 1.015 means an increase of 1.5%).

	Market optimist	Controller	Environmentalist	Drought
Temperature increase (°C)				
Year	0.5	1	2	2.3
Summer	0.5	1	2	3.1
Winter	0.5	1	2	2.0
Increase in precipitation (-)				
Year	1.015	1.030	1.060	0.960
Summer	1.007	1.014	1.028	0.800
Winter	1.030	1.060	1.012	0.870
Increase in potential evapotranspiration (-)[1] (c_1)				
Year	1.019	1.039	1.078	1.180
Summer	1.017	1.033	1.066	1.240
Winter	1.028	1.056	1.112	1.080

[1] Market optimist, Controller and Environmentalist are based on the formula of Penman-Monteith. The temperature effect comes out lower with the Makkink formula, used for MOZART (see Beersma et al., 2004, p. 46).

© Kiwa N.V.

The increase in evapotranspiration caused by rising temperatures is called the temperature effect of climate change.

However, the method for calculating the actual evapotranspiration with MOZART does not take into account the fact that the way vegetation deals with water changes with higher CO_2 concentrations. *On the one hand, if CO_2 levels go up, plants produce more biomass,* leading to an increase in leaf surface (Leaf Area Index or LAI) and therefore in evapotranspiration. This we shall call the lai-effect. *On the other hand, when CO_2 levels are high, plants can fulfil their C-requirements more easily,* meaning that they don't have to open their stomata as wide, or to make as many of them, and they reduce their transpiration: the water use efficiency effect, or wue-effect. Experimental research seems to indicate that the wue-effect is greater than the lai-effect, and the plants therefore use less water for evapotranspiration. The combined lai- and wue-effects are called the CO_2-effect on evapotranspiration of climate change, shortened to CO_2-effect:

$$CO_2\text{-effect} = \text{lai-effect} + \text{wue-effect} \qquad [1.2]$$

When calculating the potential evapotranspiration for a climate scenario, both the temperature effect and the CO_2-effect should be taken into account. This can be done as follows[2]:

$$ET_p^* = c_1 \times c_2 \times f \times ET_{ref} \qquad [1.3]$$

In which:

ET_p^* potential evapotranspiration of the vegetation, *corrected for both the temperature effect and the CO_2-effect* (mm d^{-1})
c_1 factor for the temperature effect (Table 1-1) (-)
c_1 factor for the CO_2-effect (-)

The aim of this study is to quantify the relationship between the reduction factor c_2 and the atmospheric CO_2–concentration.

If this study is successful, Rijkswaterstaat will be able to base its calculations on properly corrected figures for potential evapotranspiration (Klopstra et al., 2005).

We adopt the following three important starting points for this study:

1. Consequences of possible genetic adaptation to the new climate by plant species are not dealt with.
2. The impacts of the vegetation on the regional and global climate are not dealt with.

[2] With our correction method we implicitly link the potential evapotranspiration to the current CO_2 level. An alternative would be to involve the CO_2-effect in the computation of the reference evapotranspiration. For this, the empirical constant in the Makkink equation (*a* in Eq. [4.4]) will have to depend on the CO_2-level.

3. Changes in the moisture and nutrient balance of the soil resulting from changes in evapotranspiration are only incidentally discussed.

In this study we assume a CO_2 concentration of 520 ppm for the year 2050 (KNMI report according to Timo Kroon, Riza). Moreover, we include the year 2100 in our study. With the help of computer simulations, the IPCC has predicted a CO_2 level of 540- 970 ppm for the year 2100 (Gitay et al., 2002). Compared to the CO_2 level in 2000 (368 ppm, according to Gitay et al., 2002), this represents an average rise of approximately:

- 150 ppm in 2050
- 385 ppm in 2100

Especially the latter figure is surrounded by large uncertainties. If desired, effects of other CO_2 rises can be calculated with the aid of this report.

1.3 Research method

The research into the relationship between CO_2 concentration and evapotranspiration will be conducted as follows:

1a. Firstly, the evapotranspiration process will be briefly analyzed, based on a literature study. *This study will focus on the relationship between* CO_2 *and evapotranspiration*, and the factors which may influence it. The results of this first stage are described in Chapter 2.

1b. Armed with the insights gained from the first stage, source research will now be conducted, studying as many publications about CO_2 and evapotranspiration as possible, and recording the results in a database (Chapter 3).

2. In view of the various reservations about field research (a point to which we will return later), a second line of inquiry will be followed as well: calculating CO_2 effects with the Penman-Monteith evapotranspiration equation, from the plot level to the landscape level. (Chapter 4)

3. Finally, the results of both lines of inquiry with be discussed (Chapter 5).

© Kiwa N.V.

2 The relationship between CO_2 and evapotranspiration: theory

2.1 Introduction

Carbon dioxide is the only source of carbon for plants. CO_2 is absorbed primarily through diffusion via the stomata. Plants have to open their stomata in order to absorb CO_2, thereby causing a loss of moisture by transpiration (Figure 2-1). So plants have to lose moisture in order to absorb CO_2. Since photosynthesis stops at night, plants close their stomata, so that moisture loss is limited.

The exact physiological process at cell level that underlies the opening of the stomata is only partially understood. This is not the focus of our study. However, observations consistently indicate that evapotranspiration from leaves and the amount they open their stomata diminish as the CO_2 concentration in the air increases. Intuition suggests, then, that the stomata regulate moisture loss from plants, which is usually advantageous to limit, except in cases where evapotranspiration can help to moderate the leaf temperature.

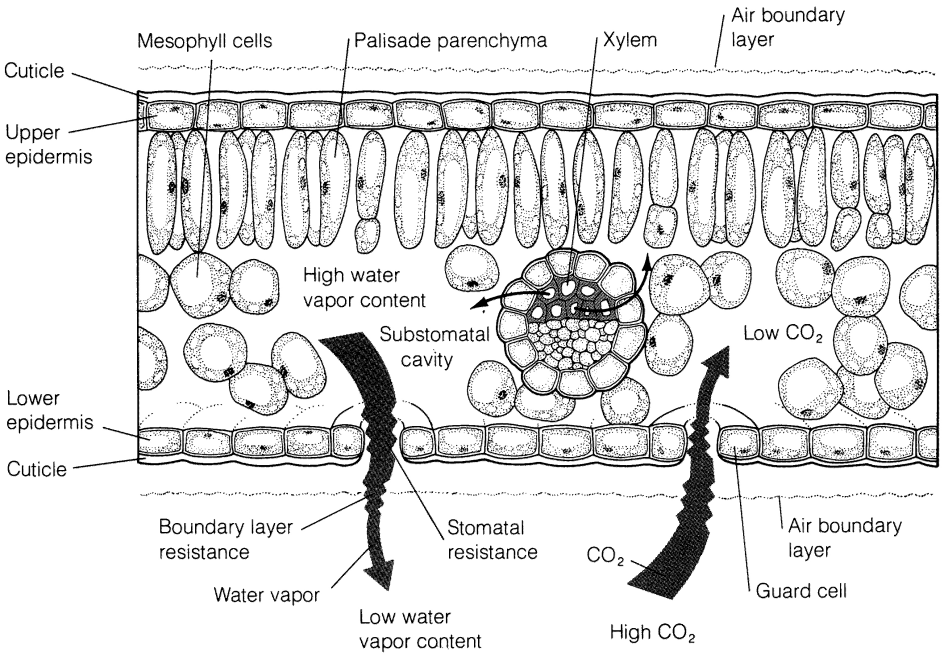


Figure 2-1. Absorption of CO_2 and release of water by a leaf (Taiz & Zeiger, 1991). Water moves from the xylem to the cell walls; from here it evaporates into the air-filled spaces in the leaves. Subsequently, water molecules moves by diffusion through these substomatal spaces, the stomata and the inert layer of air on the leaf surface. CO_2 transport in the opposite direction also takes place by diffusion.

© Kiwa N.V.

The proportion of the number of CO_2 molecules fixed by the plant to the number of H_2O molecules lost by transpiration is called the transpiration ratio, R_T:

$$R_T = \frac{\text{mol } H_2O \text{ transpired}}{\text{mol } CO_2 \text{ fixated}} \qquad [2.1]$$

In most plants in The Netherlands, the first product of photosynthesis is a compound consisting of three carbon atoms. The typical R_T value of these C_3 plants is 500. C_4 plants (of which the first fixation product has four carbon atoms) are more economical with water, and their transpiration ratio averages 250 (Taiz & Zeiger, 1991). The commonest and best-known C_4 plant among agricultural crops in The Netherlands is maize (*Zea mais*).

Another unit used in the literature instead of the transpiration ratio is water use efficiency, *wue*. It is customary to define this unit as the reciprocal of R_T (although there are other definitions in use in the literature):

$$wue = 1/R_T \qquad [2.2]$$

Increases in the concentration of CO_2 in the atmosphere have two important and opposite consequences for evapotranspiration:

1. Plants do not have to open their stomata as wide, or they have to make fewer stomata in order to maintain their supply of carbon dioxide. The consequence is that the *wue* goes up and the transpiration loss goes down (wue-effect).
2. Plants can grow faster, producing more biomass. The evapotranspiration (via transpiration and interception) increases with the increase in biomass (lai-effect).

As previously mentioned, experimental results suggest that the first effect is dominant, and that vegetation generally creates less evapotranspiration at higher concentrations of CO_2.

2.2 Effects of CO_2 and temperature on photosynthesis and water consumption

Under conditions of unlimited light and soil nutrient availability, the influence of CO_2 on photosynthesis is often described by means of experimental curves showing the relationship between CO_2 concentration *C* and assimilation rate *A* (Ammerlaan & De Visser, 1993; Noormets et al., 2001; Sage & Kubien, 2003). It appears from these A-C curves (Figure 2-2) that variations in the CO_2 level particularly affect the assimilation rate at low levels; at high levels, variations hardly play a role. Since the demand for CO_2 levels out with higher availability, the stomata can close up even more and the CO_2 effect (evapotranspiration reduction through rising CO_2 levels) increases.

The saturation point for CO_2 is lower in C_4 plants than in C_3 plants (Taiz & Zeiger, 1991). This would explain why in some experiments, C_4 plants react more strongly than C_3 plants to CO_2–enriched air.

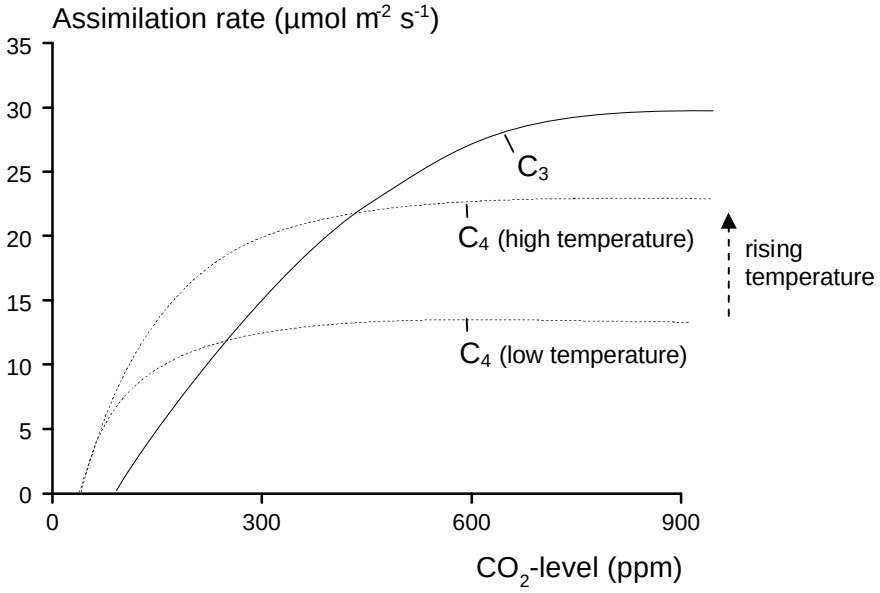


Figure 2-2. Example of the relationship between CO_2 level and assimilation rate A for a hypothetical C_3 and C_4 plant.

According to De Wit (1958), photosynthesis is a process which is far more determined by radiation energy from the sun than by temperature. Respiration in plants is heavily dependent on temperature, but this is usually a minor factor, so that the effect of temperature on the net assimilation (photosynthesis minus respiration) remains small. De Wit (1958) showed that the crop yield (dry matter production) of the vegetation is in direct proportion to the transpiration.

According to Monteith (1981), the temperature is of particular influence on the developmental stages of the plant, such as the timing of germination and the opening of the leaves. In a temperate climate this development goes faster in rising temperatures, until an optimal temperature of c. 20 -25 ^{0}C is reached. Above this optimal temperature, the development rate slows down again until it comes to a complete standstill at 30 -35 ^{0}C. High temperatures damage the plant by attacking proteins.

However, this relatively temperature-sensitive character of photosynthesis does not apply in C_4 plants at high CO_2 concentrations: for this functional species group the assimilation rate (the 'ceiling' in Figure 2-2) actually increases with the temperature (Sage & Kubien, 2003), causing the saturation point on the A-C curve to move to the right (the sharp start to the curve hardly changes). C_4 plants could therefore benefit from rising temperatures combined with an increase in CO_2. Sage & Kubien (2003) suggest this might explain the proliferation of the C_4 plant *Spartina* in Western Europe.

On the basis of paleontological data, Farquhar (1997) speculated as to how water consumption may have changed in the course of geological history due to changes in CO_2 levels. During the last glacial maximum (LGM) - about 20,000 years ago - the earth's climate must have been much drier than it is

now. This is thought to be related to the much lower atmospheric level of 180 ppm of CO_2 during the LGM. At such low concentrations, the wue of plants is in almost direct proportion to the CO_2 concentration. At a concentration level of 180 ppm (LGM), plants have to transpire twice as much to achieve the same amount of photosynthesis as under the current CO_2-level. Furthermore, precipitation is much less at lower CO_2 concentrations. According to Farquhar (1997), the relationship between CO_2 and drought would also explain why 30% more carbon was deposited during the pre-industrial era (270 ppm) than during the LGM. Although plants are now less CO_2 limited than during the LGM, increased CO_2 would still lead to an increase in groundwater recharge. Farquhar (1997) suggests that this could be a positive side-effect of climate change, especially in agricultural areas which now suffer from drought[3].

2.3 The role of transpiration in evapotranspiration

The term evapotranspiration combines two processes: evaporation (symbol: *E)* from wet soil and plant surfaces, and transpiration (symbol: *T)* via the stomata and cuticula of plants. The sum of these two processes is called evapotranspiration (*ET*):

$$ET = E + T \qquad [2.3]$$

Evaporation takes place from the leaf surface after rain (interception) and from the soil (soil evaporation). In general, transpiration contributes the most to the total evapotranspiration *ET*. This is illustrated in Figure 2-3, in which the share of transpiration in the potential evapotranspiration is plotted against the leaf area index *(LAI)* of the vegetation. It is apparent from this figure that the share of transpiration increases with the *LAI* and with increased dryness of the soil. However, as soon as the vegetation covers the soil by more than 70-80% (*LAI*>2), the distinction between wet and dry soils becomes negligible.

In The Netherlands, vegetation usually covers the soil to a large extent, making transpiration the most important factor. For this reason, our research focuses mainly on transpiration.

[3] There are certain reservations about this appealing account: Farquhar (1997) does not take into consideration the effects of changes in biomass production on evapotranspiration, for instance.

© Kiwa N.V.

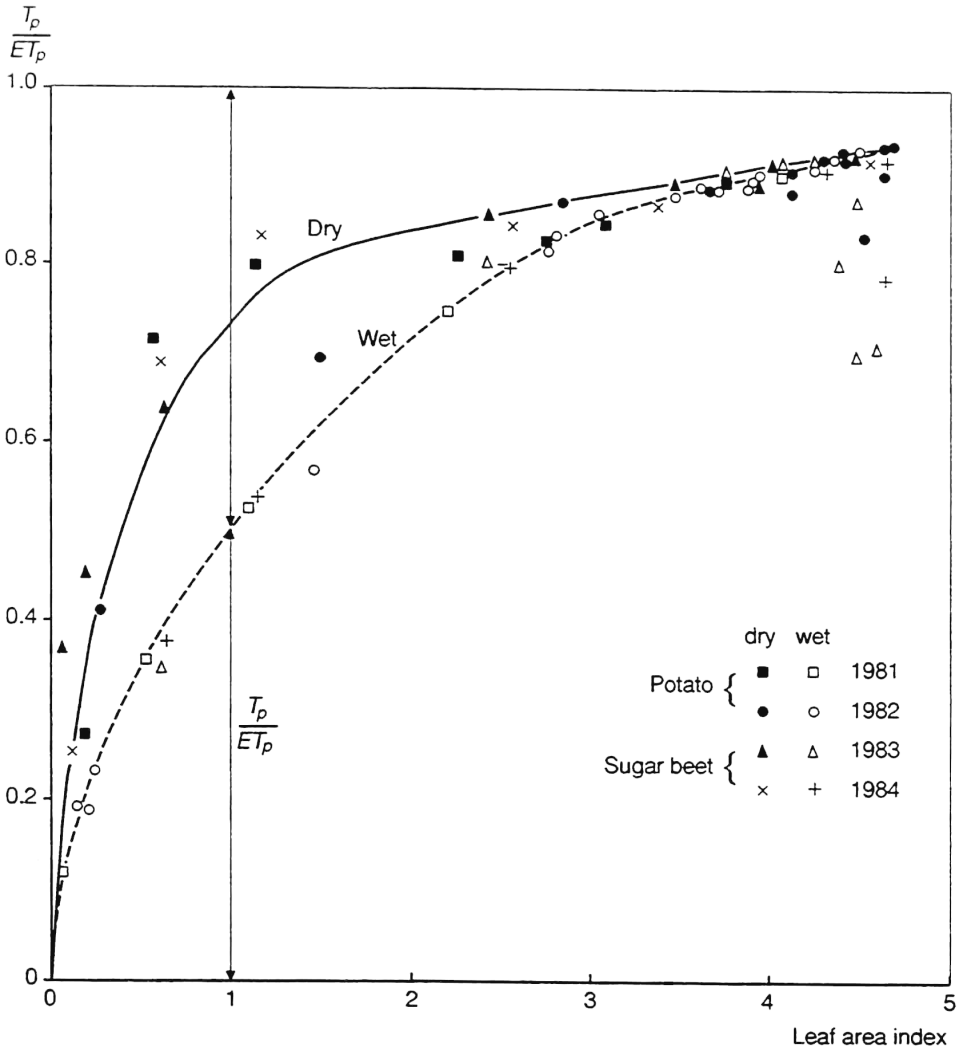


Figure 2-3. The share of potential transpiration T_p in the potential evapotranspiration ET_p as a function of the leaf area index LAI, for a soil that is moistened daily and for a dry soil. ET_p was measured as a remainder of the soil water balance (Sinderhoeve near Renkum); T_p was calculated with the unsaturated zone model SWATRE. From: Feddes et al. (1997).

2.4 Transpiration and resistance

Driving forces behind the transport of water through the system of soil, plant and atmosphere, are differences in osmotic energy and pressure energy (gravitational energy is negligible, except in very tall trees). Absorption of water through the plant roots is partially an active process, caused by the osmotic energy difference that roots build up by (selectively) taking ions from the soil. Transport of water through the stomata on the leaves is an entirely passive process, almost completely caused by the energy difference resulting from a difference in vapour pressure between substomatal spaces (Figure 2-1) and the atmosphere. There is a reduction in the 'water potential' (energy per unit of mass) from the soil to the atmosphere, in which the greatest potential loss occurs during the transition of the water from the substomatal space to the atmosphere (Figure 2-4).

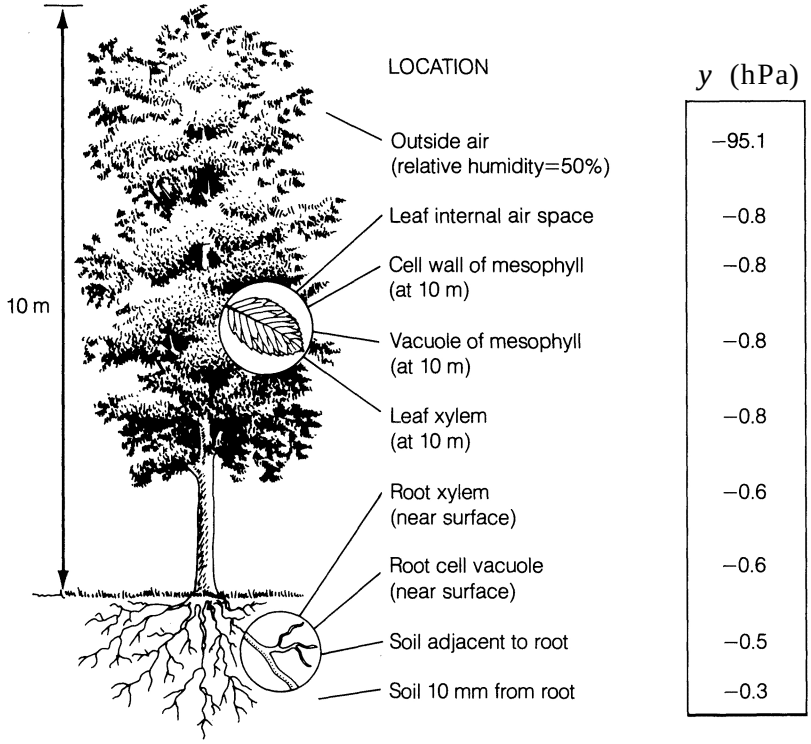


Figure 2-4.Typical course of the water potential ψ during water transport through the soil-plant-atmosphere system (Taiz & Zeiger, 1991).

The transport of water through the soil, the roots, the stem or trunk, branches, leaves and stomata is often described mathematically with a series circuit of resistances, in which the potential gradient of a resistance is in inverse proportion to the resistance. Evapotranspiration experts are particularly interested in the last resistance in the soil-plant-atmosphere continuum: the (diffusion) resistance which moisture meets between the substomatal space and the atmosphere. This is by far the largest resistance in the system (Figure 2-4) and is therefore decisive for the amount of transpiration. The relationship between the diffusion resistance and the transpiration is (see Feddes et al., 1997, among others):

$$T = \frac{M_w}{Rt}\,\frac{e_0^*(t) - e_z(t)}{r} \qquad [2.4]$$

In which:

T	transpiration (kg $m^{-2}s^{-1}$ ˜ mm s^{-1})
M_w	molecular mass of H_2O (0.0018 kg mol^{-1})
R	universal gas constant (8.314 J $mol^{-1}K^{-1}$)
t	absolute temperature (K)
e_0^*	saturated vapour pressure in the substomatal space (Pa)
e_z	vapour pressure in the atmosphere at height z, in this case close to the plant (Pa)
r	diffusion resistance (s m^{-1})

Resistance r is made up of two components (Figure 2-5), namely an aerodynamic resistance and a crop resistance:

$$r = r_a + r_g \qquad [2.5]$$

In which:

r_a aerodynamic resistance (s m^{-1})

r_g crop resistance (s m^{-1})

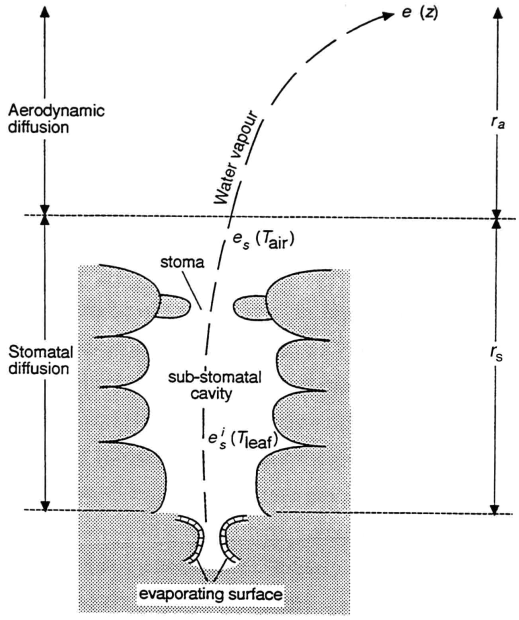


Figure 2-5. The diffusion resistance of water vapour from a leaf is the sum of the aerodynamic resistance and the stomatal resistance: $r = r_a + r_s$ (Feddes et al., 1997).

According to Feddes et al (1997), the total resistance of the plant itself (excluding r_a) is 99% determined by the resistance of the stomata (r_s), so that:

$$r \approx r_a + r_s \qquad [2.6]$$

Both r_a and r_s are important in the Penman-Monteith evapotranspiration equation, which is discussed in Chapter 4.

The aerodynamic resistance depends on both the wind speed and the aerodynamic roughness of the vegetation.

The higher the wind speed and the rougher the vegetation, the more intensive the air exchange and the lower r_a is. Figure 2-6 illustrates the big influence wind can have on the evapotranspiration process. For the sake of clarity, it should be mentioned here that r_a is a matter of how easily the air around a leaf is exchanged with the surroundings, so that vapour can be taken away. This goes more easily in a rough, well-ventilated forest than in a short, smooth grass lawn, so that such a forest has a lower aerodynamic resistance. Transpiration in such a forest is therefore relatively more determined by stomatal resistance. Because there is less mixing above a short grass lawn, water vapour is less quickly removed, so that the humidity gradient from leaf

to outside air, and thus the evapotranspiration, is less dependent on the wind. To sum up: the link between the vegetation and the atmosphere is lower when the vegetation structure is smooth ($r_a > r_s$) than when it is rough ($r_a < r_s$) (McNaughton & Jarvis, 1983; McNaughton & Jarvis, 1991; Bunce, 2004).

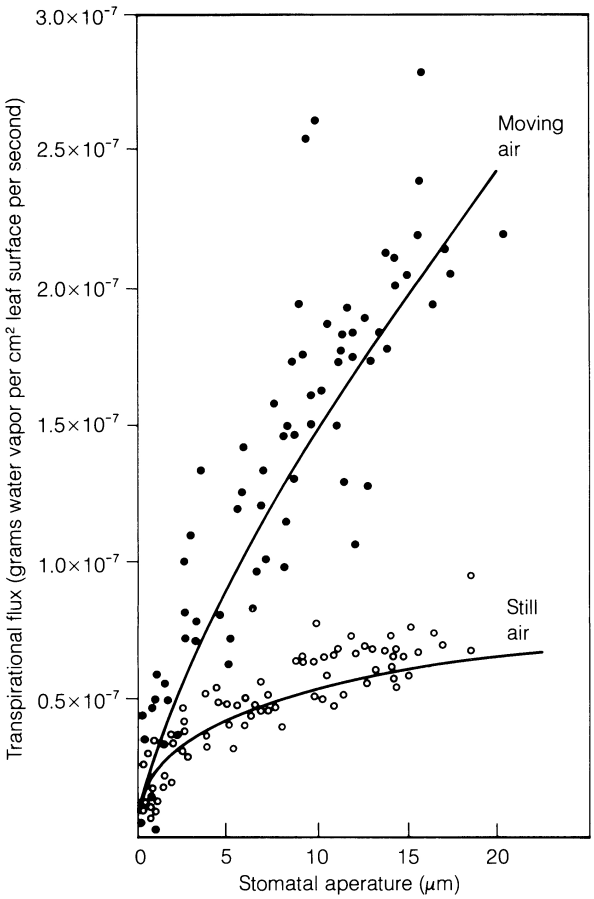


Figure 2-6. Relationship for the Zebra plant (Zebrina pendula) between transpiration flow and stomatal diameter, differentiated for wind still and windy conditions (Bange, 1953; fide Taiz & Zeiger, 1991). The windier it is, the more the boundary layer limits transpiration. Consequently, the stomatal resistance has least influence on the transpiration flow under wind still conditions.

The literature describes stomatal resistance r_s as dependent on:

1. the light intensity (stomata react to the visible light in the radiation spectrum, 0.4-0.7 μm);
2. moisture conditions in the soil (under dry conditions the stomata open less wide so that r_s goes up; the same thing can happen under wet conditions if plants are not adapted to them);
3. the temperature;
4. the 'transpiration demand' from the atmosphere: with a lot of radiation and a strong, dry wind, the plant may be at risk of wilting. To prevent this, the stomata close up;

5. the CO_2 concentration in the atmosphere: the higher this is, the sooner the carbon needs are satisfied and the stomata can close up again.

Many publications about the effects of an anthropogenic CO_2 increase focus on this last factor, the relationship between CO_2 concentration and stomatal resistance.

In micrometeorology, the unit 'conductivity' is often used instead of 'resistance'. Conductivity *g* is the reciprocal of resistance and can therefore be expressed in the unit m s^{-1}. Another unit[4] encountered in the literature is mol $m^{-2}s^{-1}$. Two conductivities dominate the transpiration process: the stomatal conductivity g_s and the aerodynamic conductivity g_a.

2.5 Factors influencing the experimental relationship between CO_2 and *ET*

In this chapter we report on a literature study on the relationship between CO_2 and evapotranspiration in vegetation. Knowledge of the factors and processes affecting this relationship is necessary, to be able to evaluate the literature properly. In this section we briefly summarize the main points. Insights into processes gained from the literature will be covered in Chapter 3.

In the preceding sections it has been explained that the CO_2 effect is species-dependent, with important distinctions between C_3 and C_4 plants and between trees and smaller plants. The scale of an experiment plays a significant role, too. As will be clear in Chapter 3, there is a wide range of measurement methods, from placing a bag of CO_2 on an individual tree branch, to large-scale experiments studying effects on a whole ecosystem. Experimental results depend on the scale (Jarvis & McNaughton, 1986; Bunce, 2004); see Chapter 3.

The most significant relationships between site and evapotranspiration which can influence experimentally established CO_2-effects are schematically displayed in Figure 2-7. A factor-enhancing relationship is indicated with a plus sign, a factor-diminishing one with a minus sign. E.g.: an increase in the CO_2 concentration (CO_2 in Figure 2-7) can lead to a rise (+) in the stomatal resistance r_s which leads in turn to a drop (-) in *ET*.

Three areas can be distinguished in the figure:

1. *To the left of the evapotranspiration (ET) block are relationships with the plant.* These have already been discussed in detail and need no further explanation here.
2. *Above the ET block are relationships with the atmosphere.* Increases in global radiation, wind speed and air temperature, and decreases in humidity lead to an increase in *ET*. This does not always happen, however: if the evapotranspiration demand from the atmosphere

[4] This unit had the same meaning: it is about the conductivity of the amount of *air* (moles or m^3 per m^2 leaf area). Hence, the metre in de m s^{-1} does not refer to metre of water but metre of air column in stead.

is higher than the vegetation can cope with, plants can wither and close their stomata. Vegetation does of course affect the atmosphere, but we assume that this is of much less influence at the level of an experiment.

3. *Below the ET block are relationships with the soil*
   An increase in *ET* leads to a decrease in soil moisture content. If the soil dries out too much, there can be a reduction in *ET* whereas an increase in soil moisture will cause *ET* to increase. However, in agricultural crops, extremely wet conditions lead to a reduction in evapotranspiration (natural vegetation is by definition adapted to its environment; plants that grow in wet conditions have, for example, air roots, such as in reeds, or no roots, such as in Sphagnum mosses).
   Like temperature, soil moisture has a considerable influence on the mineralization of organic matter and therefore on the availability of nutrients for the vegetation. Both excessively dry and excessively wet conditions result in a reduction in the mineralization rate. Nutrient availability influences biomass production and thus also evapotranspiration, via the Leaf Area Index.

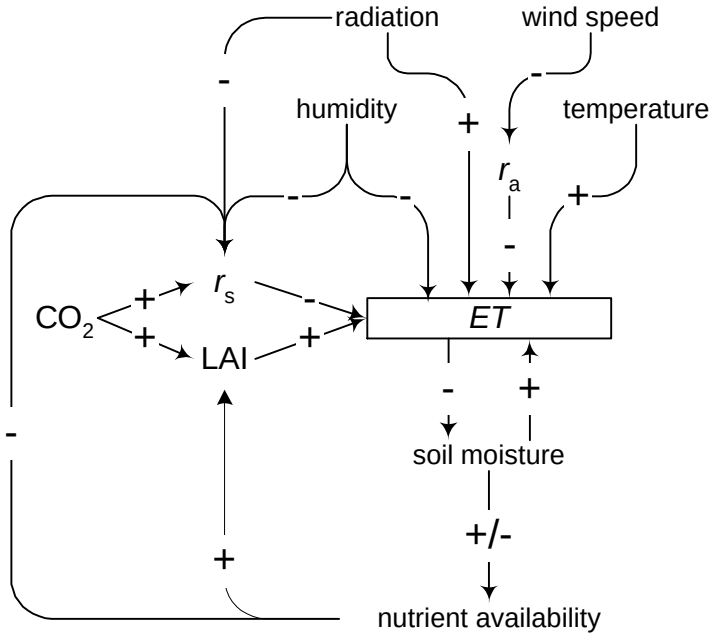


Figure 2-7. Factors influencing the effects of CO_2 on evapotranspiration ET observed in experiments.

The above description is important for the interpretation of observed CO_2 effects, and for selecting the most important factors for the literature study in the next chapter.

Particular attention should be paid to the role of the stomatal resistance r_s in the total resistance *r*. The greater the role of stomatal resistance, the greater the sensitivity of transpiration to increased CO_2. According to [2.4], transpiration is in inverse proportion to *r*. If we ignore the effects of CO_2 enrichment on the aerodynamic resistance, and the effect of vegetation on the

atmosphere, while still assuming that temperature doesn't change, then it follows from [2.4] and [2.6] for the sensitivity that:

$$\frac{\Delta T}{T} = -\frac{\Delta r_s}{r_a + r_s} \qquad [2.7]$$

Or, in terms of conductivity[5]:

$$\frac{\Delta T}{T} = \frac{\frac{\Delta g_s}{g_s}}{\frac{g_s}{g_a} + 1} \qquad [2.8]$$

Equation [2.7] describes the relative change in the transpiration when there is a change in stomatal resistance, making the assumptions mentioned above. If r_a and r_s are of equal size, then, according to [2.7], a doubling of r_s will lead to a 50% reduction in transpiration. This reduction would be 33% if r_a were twice as big as r_s, and 67% if r_a were half as big. These examples illustrate the importance of the ratio between the resistances for the results of experimental research into the relationship between evapotranspiration and CO_2.

As described in §2.4, the aerodynamic resistance is partly determined by wind speed. The possible influence of experiments on the wind profile deserves our attention, therefore. Furthermore, r_a is dependent on the roughness of the vegetation, with rougher vegetation types having a lower r_a than smooth ones. Plant species which naturally grow in dry conditions often have physiological adaptations which increase r_a: e.g. hairs on leaves, and stomata which are sunk into grooves on the leaves. Because moisture transport in these species is heavily dependent on r_a, one might expect that their transpiration would be less dependent on the CO_2 concentration.

In the field, the proportion r_a / r_s varies between approximately 0.03 (in dry forest) and 10 (in well irrigated short grass) (Jones, 1992).

2.6 What we don't take into account

In experimental research, temperature and humidity are often manipulated so that they are the same as those of the surrounding environment. It can be argued that this could lead to an overestimation of the CO_2-effect (§3.4). Direct effects of the air temperature on evapotranspiration are described in the KNMI report, 'Droog, droger, droogst' ('Dry, drier, driest') (Beersma et al., 2004) but the leaf temperature also determines the relative humidity and the lack of vapour pressure close to the leaf, and therefore the evapotranspiration. In turn the evapotranspiration influences the leaf temperature through the energy balance on the surface: higher evapotranspiration makes it cool down. The temperature dependency of stomata and photosynthesis is a process that is seldom described and poorly

[5] Substituting $r_s = \frac{1}{g_s}$, $r_a = \frac{1}{g_a}$ and $\Delta r_s = \Delta \frac{1}{g_s} = -\frac{\Delta g_s}{g_s^2}$ into [2.7] leads to [2.8].

© Kiwa N.V.

understood, yet assumptions made about it in many studies have major consequences for sensitivities (Jacobs & De Bruin, 1997).

Experimental research takes place on a small scale, e.g. the scale of a greenhouse or plot. Such experiments cannot take into account the interaction between this scale and the climate at regional or supra-regional level. This is also true for the theoretical approach to the CO_2-effect at plot level that is presented in Chapter 4. A few remarks about effects on a larger scale are pertinent here.

The previously mentioned interaction via the viscous boundary layer of air around and immediately above the leaves also takes place at macro level. The humidity in the lowest 1-2 km of the atmosphere which is influenced daily by the land surface (the atmospheric boundary layer) depends on the evapotranspiration itself and on import of air from elsewhere (advection). Where there is little advection, the interaction with this boundary layer is significant and results in an extra suppression of the sensitivity of transpiration to CO_2. In Chapter 4, we take the boundary layer into account, but not advection.

On the other hand, atmospheric humidity itself determines the opening of the stomata to a great extent: changes in atmospheric humidity can lead to changes in resistance, etc., until a new equilibrium is established.

Other interaction effects are part of the larger chain of the soil-vegetation-atmosphere system. Soil evaporation is not sensitive to the CO_2 concentration, but it does interact with the air humidity in a way which is influenced by transpiration. In the longer term, there is an interaction with soil moisture and with crop growth and the development of leaf surfaces with varying levels of evapotranspiration. Soil and vegetation feed back to the energy balance of the land surface and therefore influence the boundary layer and the formation of clouds. Clouds influence in turn the exposure to light rays and therefore also the stomata and the evapotranspiration.

3 Observed effects of CO_2 on a local scale

3.1 Methods

We have collected a lot of literature of experimental research into the relationship between CO_2 and evapotranspiration. Because we want to know how potential evapotranspiration is affected by CO_2, the relevant experiments for our study are those in which drought stress and malnutrition do not occur. However, drought stress and malnutrition are sometimes part of an ecosystem and cannot be eliminated from an experiment without interfering with the system.

The results of the literature study are kept up to date in the database 'KWR 06.003 Literature study.xls', available on the website: ww.droogtestudie.nl

Through literature study, we gain knowledge of the methods used by scientists to study the effects of increased CO_2. In §3.2, a brief overview of these methods is given. Section 3.3 outlines the set-up of the database, which gained its final form during the course of the research, and the results are discussed in §3.4.

3.2 Experimental research methods

In research into the effects of increased CO_2, two samples of vegetation cover are compared: one with an increased concentration and one with the current concentration. Two important differences between methods are (1) the treatment with which the samples are exposed to air and (2) the way evapotranspiration is measured.

Treatment methods

There are various methods for exposing vegetation to CO_2–enriched air (from Saxe et al.,1998, among others):

- Branch-bag (BB)
  This is applied to trees. A branch is wrapped in a transparent bag filled with CO_2–enriched air. Disadvantages of this method are that (1) it is difficult to adjust the climate in the bag (in particular, temperatures can rise), (2) it is difficult to scale up measurements from branch to tree level, let alone to forest level, and (3) the system is not closed (exchange via the branch).
- Open-top chamber (OTC)
  Part of the vegetation is shielded with transparent material (glass, Plexiglas, Perspex, foil). To maintain as much uniformity as possible with the surrounding climate, the top is kept open. Climate-controlled and CO_2–enriched air is blown over the vegetation.
  An advantage of OTC is that it is relatively easy to adjust the climate to

the external climate. Regulation of the wind, however, is far from optimal, as ventilation is usually much stronger than it is outside. Due to its limited scale, OTC cannot be used to research whole trees.

- Closed-top chamber (CTC)
  Several different names are used in the literature for the same sort of treatment: the total isolation of a section of an ecosystem from the outside world, treating it with CO_2–enriched and climate-controlled air. The experiments vary in scale, which is reflected in the names: Growth Chamber (small), Glass cabinet (small), mini-ecosystem (small), Greenhouse (large). According to Saxe et al. (1998), climate control is better in these experiments than in OTCs, although the method is expected to have a considerable influence on the wind effect.

- Free-air CO_2 enrichment (FACE)
  Pure CO_2 is applied at several places and at varying heights in the natural environment, where it mixes with the atmosphere. The apparatus used may be for example a number of poles from which application takes place in a circle of 25 m in diameter. Of all the methods, this one has *the least effect on the natural climate*, particularly if the circle is large; the influence in this case is probably negligible (Saxe et al. 1998). One disadvantage is that the apparatus is expensive.

- Mini-FACE
  As in FACE, except that CO_2 is applied in a small circle, e.g. of one meter in diameter. The apparatus is cheaper than that of FACE, but the influence of the experiment on the measurements, due to the greater influence of air outside the circle, is likely to be greater.

- Natural sources
  Tognetti et al. (1998) made use of a natural source of CO_2 near Siena.

Because of their large scale, most experiments on trees are carried out on young trees.

With respect to the influence of aerodynamic resistance, information about the degree of air circulation in the experiment is desirable. Unfortunately, most of the publications do not supply this information (or only in qualitative terms, e.g. “heavy duty air blowers”). Yet it is clear from Stocker et al. (1999) and Dijkstra et al. (1993) – among others – that the influence of wind is considerable: they applied an average air circulation of 37 seconds in OTCs and 14 seconds in small greenhouses (CTCs), respectively[6]. Heijmans et al. (2004) showed in their experiments that the evapotranspiration measured increased with the number of ventilators used.

[6] Stocker et al. (1999) report an air circulation of 2.5 m^3 per minute in OTCs of 1.27m^2 in surface, separate with foil of 120cm high; Dijkstra et al. (1993) report air circulation of 800 m^3 per hour in a small greenhouse of 125x125x200cm.

Methods of measuring evapotranspiration

The literature provides little information about the methods of measuring the evapotranspiration or the transpiration. The main methods are:

- Balance studies
  Evapotranspiration can be determined as a remainder of the soil moisture balance, using lysimeters for example. Changes in the storage of soil moisture can be determined by weighing or by measuring the soil moisture content.
- Analysis of incoming and outgoing air
  The moisture content of incoming and outgoing air is continuously measured automatically. Differences are put down to evapotranspiration.
- Measuring with a measuring cuvette
  A measuring cuvette is placed over part of the plant. It measures gas exchange, including that of water vapour, via electronic sensors. Disadvantages: the measurement period is short (often just a few hours), probably influences the transpiration and is not representative for the whole plant or vegetation cover (so scaling up is required).
- Chamber
  This is like the measuring cuvette, but is larger, so that a more representative picture of the vegetation as a whole can be gained.
- Stem flow measurement
  This gives continuous measurement of the transpiration rate. See Dugas et al. (1996). Disadvantage: difficult to upscale to vegetation level.

3.3 Set-up of the database

The database 'KWR 06.003 Literature study.xls' (www.droogtestudie.nl) contains the results of the literature study and consists of the following columns:

Column A. Seen by
Gives the initials of the person who studied the literature: Cees Maas (CM) or Flip Witte (FW)

Column B. Source
Cites the literature source as done throughout this report: author(s), date.

Column C. Vegetation type
Characterizes the vegetation type (crop, plant species) on which the experiment is carried out.

Column D. CO_2-effect
Observed effects of CO_2-enrichment on transpiration ($\Delta T/T$) or evapotranspiration ($\Delta ET/ET$).

Column E. Treatment
Categorizes the way the vegetation was treated with CO_2 (§3.2: OTC, FACE, etc).

Column F. Details

Information about the measurements of the treatment method, the measurement method (§3.2), etc.

Column G.Duration of the experiment

The duration is important because only longer-term experiments are applicable; i.e. *experiments in which the vegetation was able to adjust to the raised CO_2-concentration*.

Column H. CO_2-concentraton control

Column I. CO_2-concentration experiment

Column J. Location

Country and place where the experiment was carried out. It may be relevant to obtain an impression of the climate, if details of this are not given.

Column K.Climate

Characterizes the climate, thus determining how representative it is for The Netherlands.

Column L. Moisture stress

As explained in §2.5, moisture shortages in the soil lead to a reduction in evapotranspiration. It is to be expected that the CO_2-effect on plants growing on dry soils is smaller since reduced transpiration leads to greater availability of soil moisture.

Column M. Nutrient availability

Nutrient availability influences evapotranspiration via biomass production (§2.5). In nutrient-poor conditions, the CO_2-effect can be suppressed, as discussed in the next paragraph.

Column N. Remarks

Relevant remarks that did not fit in columns A –M.

Column O. Decision

Assessment of the usability of the data source for immediate quantitative assertions about the CO_2-effect.

3.4 Discussion and analysis

Analysis of observed CO_2-effects

On the basis of data from the literature, Figure 3-1 displays the increases in evapotranspiration and in CO_2 side by side (the underlying data are stored on a separate page in the database). In the first instance, the treatment methods are differentiated (CTC, OTC, FACE including mini-FACE, Natural source). Beyond this, information is added about possible drought stress, nutrient poverty, and whether the experiment was carried out on a tree or forest.

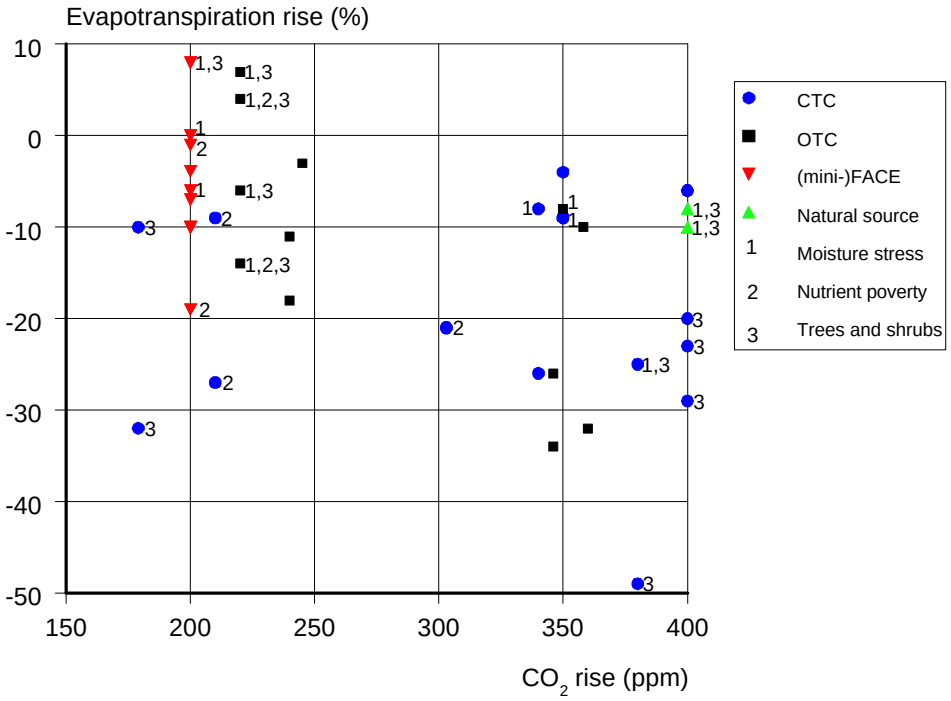


Figure 3-1. Observed changes in evapotranspiration ET with increased CO_2-concentrations compared with the current concentrations in the air.

Before proceeding to a discussion of this figure, some explanation of how it came about is in order:

- The database includes observed effects on both transpiration ($\Delta T / T$) and evapotranspiration ($\Delta ET / ET$). We converted the first figures into evapotranspiration figures by multiplying by a factor of 0.8, on the assumption that transpiration constitutes about 80% of the evapotranspiration (see also Figure 2-3 and §4.5)[7].
- A value that may vary in the literature is reduced to an average in Figure 3-1.
- Data from two publications about steppe vegetation (Szente et al., 1998; Tuba et al., 1996) have been excluded from the analysis because they completely contradict each other, even though they were published by the same scientists. A number of observations in temperatures like 40 ^{0}C, which would be extreme for The Netherlands, have also been left out of the account.
- Many publications have nothing to say about possible drought stress and nutrient poverty. Only when we could make reasonably safe assumptions on these points, is information about them included in Figure 3-1.

In the study which preceded this report, Witte & Doomen (2004) calculated a decrease in evaporation of 5.2% per 100 ppm CO_2 increase. This amounts to a

[7] From $T = 0.8ET$ and $\Delta ET = \Delta T$ follows: $\Delta ET / ET = 0.8 \Delta T / T$

decrease of 20% given an average rise of 385 ppm in the year 2100 (see §1.2). On the basis of linear regression through all the points in Figure 3-1, we arrive at a comparable decrease, namely 23% (regression line: $y = 2.1\text{-}0.054x$; $r^2 = 0.14$, $n = 41$). However, in the current study the variation in the observations increased.

Figure 3-1 seems to suggest that *the CO_2-effect is somewhat diminished by drought stress and is a bit higher in trees.* Predictions of the effect given an increase of 385 ppm confirm this: –13% for drought stress (regression model $y = 12.8\text{-}0.066x$; $r^2 = 0.39$, $n = 14$) and –22% for trees ($y = 8.6\text{-}0.078x$; $r^2 = 0.23$, $n = 14$). The nutrient poverty points in Figure 3-1 lie too close together to provide the basis for any conclusions.

We could describe the various effects of the different treatment methods statistically, and investigate the differences, but we expressly choose not to do this. Firstly, because this is beyond the scope of this limited study, but more importantly because it would not be worthwhile, as our literature study has led us to the conclusion that *the influence of wind on OTCs and CTCs is so great that it is impossible to draw conclusions about evaporation from plants in natural environments from experiments with these kinds of apparatus.* In these experiments, the introduction of air through "heavy duty air blowers" will have led to a lowering of aerodynamic resistance, causing transpiration to be more strongly influenced by CO_2 enrichment than it would be in a natural context.

We have therefore excluded all evaporation measurements taken using OTCs and CTCs from our analysis of the CO_2 effect.

Measurements taken using these methods are, however, useful for several other analyses, such as *the study of the relationship between CO_2 concentration and stomatal resistance.* We shall make use of them in Chapter 4.

For the analysis in this chapter, we are left with the results of FACE experiments and the natural CO_2 source near Siena. These are, respectively, the red and green triangles in Figure 3-1. The most relevant information from these literature sources is summarized in Table 3-1.

We would like to make the following comments on this table:

- The distribution of 'vegetations' is limited: *Sorghum bicolor*, bog, *Triticum aestivum* and three tree species, *Pinus taeda, Quercus ilex* and *Quercus pubescens.*

- The decrease in evapotranspiration from bog signalled by Heijmans et al. (2004) is remarkable, as bog is dominated by peat moss (*Sphagnum spec.*), which has no stomata and therefore cannot be sensitive to CO_2. The authors ascribe the decrease in evapotranspiration to the wind-breaking effect of vascular plants which have grown faster due to higher concentrations of CO_2.

- The experiments of Conley et al. (2001) confirm that drought stress diminishes CO_2 sensitivity.

- The increase in transpiration in a stand of trees dominated by 14 m high *Pinus taeda* observed by Schäfer et al. (2002) is ascribed by the authors to a reduction in soil evaporation. This reduction is assumed to be caused by an increase in leaf fall, and assumed to improve soil moisture content. Transpiration from trees was measured using stem flow measurements, which were scaled up to the level of the entire stand of trees. All things considered, calculating the CO_2 effect from transpiration figures is dubious, and we consider the results less reliable.
- If we exclude two outliers from our calculations, the one of Schäfer et al. (2002) and the one from nutrient-poor conditions of Kimball et al. (1999), the reduction in evapotranspiration reported in Table 3-1 is 6.5% on average (standard deviation 3.5%) with an increase of 200 ppm. The decrease in evapotranspiration is likely to be greater in conditions without drought stress.

*Table 3-1. Data from usable CO_2-experiments (mini-FACE, FACE and natural source).Figures marked with an asterisk are drawn from transpiration figures (?*ET/ET=*0.8?*T/T*).*

Source	Vegetation	CO_2-increase (ppm)	?*ET*/*ET* (%)	Treatment	Limiting factors
Conley et al., 2001	*Sorghum bicolor* (C_4)	200	-9 to -11	FACE	
Conley et al., 2001	*Sorghum bicolor* (C_4)	200	0 to -6	FACE	Drought stress
Heijmans et al., 2001	Peat bog	200	-9 to -10	Mini-FACE	Natural = nutrient-poor
Hunsaker et al., 2000	*Triticum aestivum*	200	-3.7 to -4.0	FACE	
Hunsaker et al., 2000	*Triticum aestivum*	200	-0.7 to -1.2	FACE	Nutrient poor
Kimball et al., 1999	*Triticum aestivum*	200	-7	FACE	
Kimball et al., 1999	*Triticum aestivum*	200	-19	FACE	Nutrient poor
Schäfer et al., 2002	*Pinus taeda*	200	+7.6*	FACE	Drought stress
Tognetti et al., 1998	*Quercus ilex*	150-650	-8*	Natural source	Drought stress
Tognetti et al., 1998	*Quercus pubescens*	150-650	-10*	Natural source	Drought stress

Relevant information from the literature

During our research we came across some information that seems worth mentioning, even though it is of no direct use in the quantification of the CO_2-effect.

- *Nutrients*. The availability of nutrients may affect biomass production and, with it, evapotranspiration (§2.5). Grant et al. (2001) describe the FACE-measurements of Kimball et al. (1999) on Wheat (*Triticum aestivum*), given in Table 3-1, in which the nutrient-poor treatment (7 g N m^{-2}) is more sensitive to CO_2 (*ET* drops 19%) than the nutrient-rich treatment (35 g N m^{-2}) (7%). Their likely explanation is that in N-poor circumstances the biological yield is raised less and therefore the reduction of *ET* is higher (N-limitation).
  In contrast, with the same FACE apparatus Hunsaker et al. (2000) found the lowest CO_2-effect on *Triticum aestivum* in nutrient-poor conditions (Table 3-1): a significant *ET*-decrease of 0.7-1.2% at a supply of 1.5-7.0 g N m^{-2} against 3.7-4.0% at 35 g N m^{-2}. Hunsaker et al. (2000) suggest the small effect at low N-supply might be due to a better utilization of nutrients and soil moisture at the end of growth period, when, in contrast, they measured a higher *ET* then in the control.
  There are more studies which describe that vegetations on nutrient-poor soils are less sensitive to CO_2 enrichment. One explanation for this is that plants try to maintain a certain C / N ratio in their leaves (Jarvis, 1983) so that they respond to CO_2 enrichment by extending their root system in search of N (Sonnleitner et al., 2001). It is likely that the CO_2-effect is especially small on nutrient-poor and dry soil, since in especially that case extending roots leads to a better utilization of soil moisture.
- When there is extreme nutrient poverty in very wet conditions, species may dominate which have a physiognomy more usually associated with drought-resistance. For example, among the vascular plants in a living peat bog, the heather-type plants are dominant (*Erica tetralix*, *Calluna vulgaris*, *Andromeda polifolia*, *Vaccinium myrtillus*, *Oxycoccus palustris*, etc.): plants with thick leathery leaves. They have a 'peinomorphic' (hunger-shaped) form (Weeda et al., 1988), which does not suggest high transpiration rates. Bearing in mind that statements about the purpose of natural characteristics are always speculative, we think that the reason for this is that plants in extremely poor environments are limited in their growth by N and P, so that their CO_2 consumption and therefore their transpiration are also limited.
- *Ozone* in the atmosphere is harmful to plants because it attacks their photosynthesis organs (Pleijel et al., 2003). McKee et al. (1997) put forward the hypothesis that increased CO_2 limits this damage because with less transpiration, less O_3 gets into the plant via the stomata.
- *Fossils.* According to Saxe et al. (1998) and Sellers et al. (1996), analysis of stomata in fossil plant material reveals that stomatal resistance in plants increased in the course of geological history due to rises in CO_2 concentrations.

- *Literature.* During our research we came across a number of excellent publications on the subject, which we recommend to those who wish to explore the subject in greater depth: Ainsworth & Long (2005), Allen et al. (2003), Bunce (2004), Conley et al. (2001), De Wit (1958), Field et al. (1995), Hunsaker et al. (2000), Jacobs & De Bruin (1992), Medlyn et al. (2001), Poorter & Navas (2003), Riedo et al. (1999), Ruddiman (2003), Sage & Kubien (2003), Saxe et al. (1998) and Sellers et al. (1996).

4 Calculating CO_2 effects at plot level

4.1 Introduction

In this chapter we shall try to calculate the CO_2 effect. As discussed in the introduction (Chapter 1), we do not take into consideration either the influence of soil moisture and temperature on stomata, or more complex issues like cloud cover and advection. These effects are either too poorly understood or too complex to deal with in a relatively simple study like this. *We restrict our analysis to well-watered vegetation and thereby ignore effects of water stress.*

4.2 Observations of CO_2 effects on stomatal conductance

The decrease in stomatal conductance with increased CO_2 levels has been described in numerous experiments, most of which make use of OTCs or CTCs in which plants are exposed to higher CO_2 concentrations for a long time while temperature, humidity and radiation are kept in line with those of the surroundings. Such chambers must therefore be well ventilated, which means that there is no vertical humidity gradient such as occurs naturally above plots of land out of doors. Measurements of evapotranspiration in such chambers are made with either small cuvettes for gas exchange measurements, or with a water balance, or lysimeter. In both cases an evapotranspiration measurement is obtained in which the aerodynamic conductance is great, relative to the stomatal conductance; therefore the measured changes in evapotranspiration are approximately proportional to changes in stomatal conductance, and may be interpreted as such[8]. They are not, however, representative for a change in evapotranspiration in the field, although these experiments are usually of long enough duration to give an idea of the adaptation of plants to higher CO_2 concentrations in the medium term.

A number of measurements were taken in a FACE experiments, in which CO_2 concentrations were raised in the open field or even in the forest, by releasing large amounts of CO_2 into the area over a long period. Evapotranspiration readings from lysimeters under such conditions are scarce, but they do give a better direct measurement of the projected changes in evapotranspiration, even though there may be an overestimation of the CO_2-effect, due to artificial ventilation and advection from outside the FACE area.

We investigated a number of studies in greater detail; published results for CO_2-sensitivity in conductance are presented in Table 4-1 and in graph form in Figure 4-1, including the margin of error (standard error), where this was

[8] If $g_a \to \infty$ then Equation [2.8] becomes $\frac{\Delta T}{T} = \frac{\Delta g_s}{g_s}$.

available. A regression line is drawn through the points with reliability intervals of 95%. Two publications provide such deviating results (for potato and barley) that we left them out of the analysis.

This data shows that, with every 100 ppm increase in atmospheric CO_2 concentrations, stomatal conductance goes down by an average of:

- 9.3 ± 1.5% for grass and herbal crops;
- 6.8 ± 2.5% for woody crops and trees;
- 11.8 ± 1% for C_4 crops (based on very few observations).

Taken together, these results suggest that if atmospheric concentrations of CO_2 are doubled in 2100, *we can expect a reduction in conductance g_s in most C_3 plants of about 15 – 40%*.

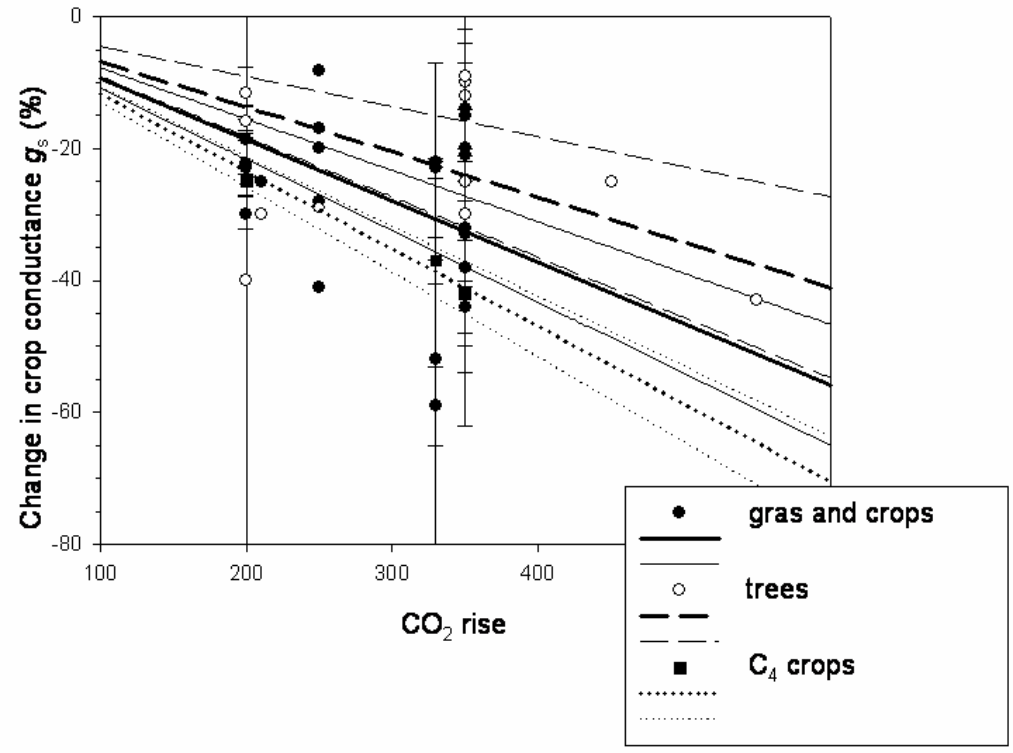


Figure 4-1. Observed effects of increased CO_2 concentrations on crop conductance g_s (~ stomatal conductance), with standard errors and regression lines with 95%reliability intervals. See also the text and Table 4-1.

Table 4-1. Observed effects of CO2 increases on conductance g_s. Figures marked with an asterisk (*) are derived from evapotranspiration measurements.

Vegetation / species	[CO2] ppm	$\Delta g_s / g_s$ (%)	σ (%)	Reference	Crop height (cm)	Photosynthesis type
Potato	680	-59	6	Cure & Acock (1986)	30	C_3
Potato	700	-32	30	*fide* Bunce (2004)	20	C_3
Alfalfa	700	-15		*fide* Bunce (2004)	50	C_3
Birch	700	-10	10	Beerling et al. (1996)	1000	C_3
Birch	800	-25*		Wayne et al. (1998)	100	C_3
Beech	700	-12	10	Beerling et al. (1996)	1000	C_3
Beans	700	-38	10	*fide* Bunce (2004)	50	C_3
Tree	550	-15.9	2.4	Ainsworth & Long (2005)	1000	C_3
Brassica campestris	600	-41		Mishra et al. (1999)	20	C_3
Brassica carinata	600	-8.3		Mishra et al. (1999)	20	C_3
Brassica juncea	600	-20		Mishra et al. (1999)	20	C_3
Brassica nigra	600	-28		Mishra et al. (1999)	20	C_3
Douglas fir	550	-40	43	Apple et al. (2000)	150	C_3
Oak	700	-30	10	Beerling et al. (1996)	1000	C_3
Elder	600	-29		Liang et al. (1995)	150	C_3
Elder	900	-43		Liang & Maruyama (1995)	150	C_3
Forb	550	-18.7	5.1	Ainsworth & Long (2005)	50	C_3
Barley	680	-52	30	Cure & Acock (1986)	100	C_3
Barley	700	-33	8	*fide* Bunce (2004)	50	C_3
Grass	550	-22.2	5	Ainsworth & Long (2005)	20	C_3
Grass	550	-24.9	7.2	Ainsworth & Long (2005)	50	C_4
Grass	700	-33		*fide* Bunce (2004)	20	C_3
Peat bog	560	-25*		Heijmans et al. (2001)	20	C_3
Young tree	700	-25	3	Medlyn et al. (2001)	150	C_3
Legume	550	-22.9	4.1	Ainsworth & Long (2005)	50	C_3
Lolium	700	-20*		Schapendonk et al. (1999)	20	C_3
Maize	680	-37	3.5	Cure & Acock (1986)	200	C_4
Aspen poplar	560	-30		Noormets et al (2001)	200	C_3
Soya	680	-23	1.5	Cure & Acock (1986)	50	C_3
Soya	700	-25*		Serraj et al. (1999)	50	C_3
Shrub	550	-11.6	3.9	Ainsworth & Long (2005)	200	C_3
Wheat	680	-22	15	Cure & Acock (1986)	50	C_3
Adult tree	700	-9	5	Medlyn et al. (2001)	2000	C_3
Winter wheat	700	-21*		Dijkstra et al, (1999)	50	C_3
Summer wheat	550	-30		Hunsaker et al. (2000)	50	C_3
Summer wheat	600	-17		Agrawal & Deepak (2003)	50	C_3

4.3 Models for stomatal conductance

There are various models for predicting stomatal conductance g_s in relation to the environment. A classic and still-used model is that of Jarvis & Stewart (Jarvis, 1976; Stewart, 1988). This empirical model calculates the conductance by multiplying a maximum value with a number of reduction functions, including one for CO_2-sensitivity. Since each reduction function has to be adjusted to the data, this model will provide good prediction for most vegetations. *However, this model is of limited value for extrapolations in time, and for generalizations.*

Another type of model integrates the various sensitivities into one equation with fewer empirical parameters, making it easier to evaluate the interactions and extrapolations. Models of the type used by Ball-Berry (see Jacobs, 1994) express conductance as a function of photosynthesis rate, CO_2 concentration and atmospheric humidity; combined (for details, see Jacobs & De Bruin, 1997):

$$g_s = g_c + 1.6\frac{A_n}{C_s f(e_s^* - e_s)} \qquad [4.1]$$

In which:

g_c minimum conductance of the epidermis of leaves when stomata are closed (m s^{-1} or µmol m^{-2} s^{-1})

A_n net photosynthesis (which in turn depends on radiation, nutrient availability, temperature, CO_2 and g_s itself) (µmol $m^{-2}s^{-1}$)

C_s CO_2-concentration on the leaf surface (µmol m^{-3} or µmol mol^{-1})

f function of atmospheric humidity deficit on the leaf surface $\left(e_s^* - e_s\right)$

e_s vapour pressure in the atmosphere on the leaf surface (Pa)

e_s^* saturated vapour pressure on the leaf surface (Pa)

There has been a lot of discussion in the literature about the validity of Equation [4.1], because it appears to be a physiological-mechanistic model, and is often described as such, and yet very little is known about the underlying mechanism. In practice the model seems to work well for a wide range of vegetation types, and with little variation in parameters. It can therefore be seen as a well-chosen empirical method to practically describe how stomatal conductance dependents on CO_2 and atmospheric humidity on the leaf surface. It follows from this that g_s can only be determined through iteration (repeated calculation, mathematically). Medlyn et al. (2001) compared experimental results, as described in Chapter 3, with predictions of both the Jarvis- Stewart model and the Ball-Berry model. Both models seem to work well; the Ball-Berry concept seems to describe all the measurements particularly well, and also to predict changes from doubling CO_2 concentrations well. The study by Jacobs & de Bruin (1997) also analyzes this concept in adapted form, and integrated into a boundary layer model. The projected *change in* g_s in this study is around -30% with a doubling of CO_2, which is within the experimental margin of -15 to -40% mentioned in §4.2.

4.4 Calculating evapotranspiration at plot level

For a prediction of changes in evapotranspiration at plot level, measurements on stomatal conductance g_s have to be fed into an evapotranspiration model which also simulates the aerodynamic conductance in the boundary layer g_a.

The most relevant approaches to the evapotranspiration calculations are those of:

$$\text{Penman-Monteith: } l\,ET = \frac{sQ + g\,g_a \times \left(e_z^* - e_z\right)}{s + g\,(1 + g_a / g_s)} \qquad [4.2]$$

$$\text{Priestly-Taylor: } l\,ET = a\,\frac{s}{s+g}\,Q \qquad [4.3]$$

$$\text{Makkink: } l\,ET = a\,\frac{s}{s+g}\,K\downarrow \qquad [4.4]$$

In which:

?	evaporation heat of water (J kg^{-1})
ET	evapotranspiration (kg m^{-2}s^{-1})
s	temperature-dependant gradient of the saturated vapour pressure curve (Pa K^{-1})
Q	net radiation (W m^{-2})
?	temperature-dependant psychometric constant (Pa K^{-1})
e_z	actual vapour pressure in the atmosphere at altitude z (Pa)
e_z^*	saturated vapour pressure in the atmosphere at altitude z (Pa)
a	constant (-)
a	constant (-)
K?	incoming shortwave (global) radiation (W m^{-2})

The variable g_s in these equations is the effective total stomatal conductance of the entire vegetation (the same, therefore, as the crop conductance).

Equation [4.2] provides a good description of local evapotranspiration, given the necessary variables measured at a certain height above a homogeneous crop. This equation is *the* standard procedure in scientific research. The quantities in [4.2] vary continually, especially the atmospheric humidity deficit $\left(e_z^* - e_z\right)$, the temperature and the conductance.

The aim of this study is to research the CO_2 sensitivity of *ET*, and not that of *?ET*. In other words: we still have to divide the equation by *?*. However, this evaporation heat is only sensitive to temperature, and will therefore have no influence on the results of this study, since temperature is not taken into consideration. N.B.: in the Drought study of Beersma et al. (2004) the effect of temperature on *?* is very small, perhaps even negligible (e.g.: at a temperature of 10 ^{0}C, *?* decreases 0.1% with every temperature rise of 1 ^{0}C).

Equations [4.3] and [4.4] give a particularly reliable value for the evapotranspiration of a crop if *a* and *a* can be assumed to be constant and if advection is negligible. The atmospheric humidity deficit and the

conductance are implicitly included in these constants and may vary as long as they vary little in proportion to each other. It is easy to demonstrate that for the Priestly-Taylor constant (Moors et al., 1996):

$$\alpha = \Omega(1+\frac{\gamma g_a D_a}{sQ}) \qquad [4.5]$$

In which O represents McNaughton & Jarvis's (1983) coupling factor, i.e. the vegetation-atmosphere coupling (see §2.4). If O is not far from 1 then [4.3] or [4.4] are the most applicable, and evapotranspiration can be estimated from a previously determined crop factor, the radiation and the temperature. This is the case with a smooth vegetation surface, a low wind speed, and a high stomatal conductance. Equation [4.4] has the advantage that it requires few measurements and that it prevents problems in the winter, with a positive evapotranspiration in spite of a negative energy balance. It is routinely used by the KNMI. It is important to stress that, just as is the case with the equation of Priestly-Taylor ([4.3]), we cannot assume that the atmospheric humidity remains constant when we use the Makkink equation, and that by implication, the equation includes advection and all feedback from the boundary layer that plays a role in the empirical determination of crop factors. *Like the Priestly-Tylor equation, the Makkink equation is very suitable for interpolation, but for the reasons given, less suitable for use in climate scenarios in which radiation, temperature and humidity vary*.

However, it is possible to use Equation [4.5] to research the sensitivity of the crop factor to variations in g_a and g_s and to make predictions about future crop factors. Both these sorts of analysis were made by Jacobs & de Bruin (1992, 1997). These studies were carried out for various conditions (high wind speed combined with deep boundary layer and vice versa; rough and smooth surfaces). They made use either of Equation [4.2] (without boundary layer feedback), or of a fully linked boundary layer model, in which the effect of g_s on Equation [4.3] and [4.4] was investigated. The results of a sensitivity analysis with [4.2] can also be expressed as a sensitivity in α, or $?E/Q$. Jacobs & De Bruin (1997) analyzed a model that was fully linked to the boundary layer, Equation [4.1] and a photosynthesis model. The study estimates the changes in g_s and in crop factor for various climates, whether or not feedback from the boundary layer or atmospheric humidity is taken into account.

We have drawn up Figure 4-2 from Jacobs & De Bruin (1992). It shows that *the sensitivity of evapotranspiration to g_s in the first place depends on the aerodynamic conductance*, or the roughness of the surface. In the second place, the boundary layer determines the sensitivity for g_s: *the boundary layer tempers the sensitivity* (compare the boundary layer model and Penman-Monteith in Figure 4-2). Finally, the figure shows that this sensitivity depends on the value of g_s itself: with higher stomatal conductance, sensitivity is lower, because the link with the atmosphere is weaker (g_s/g_a is higher). The effect is therefore not linear, and a reduction in g_s as a result of an increase in CO_2 has a bigger and bigger effect on evapotranspiration. Well-irrigated and non-stressed vegetation has a relatively high stomatal conductance. For this study we can therefore use sensitivities from Figure 4-2 that are on the high side of g_s. We can deduce from Figure 4-2 that:

- for a smooth surface (such as short grass), the transpiration changes by 15-20% of the change in g_s;
- for a rough surface (such as forest), the transpiration changes by 40-75% of the change in g_s.

From Jacobs & De Bruin (1992) it appears that, within these two ranges, the lower percentage represents cases in which the boundary layer plays a greater role, and the higher percentage a highly advective situation.

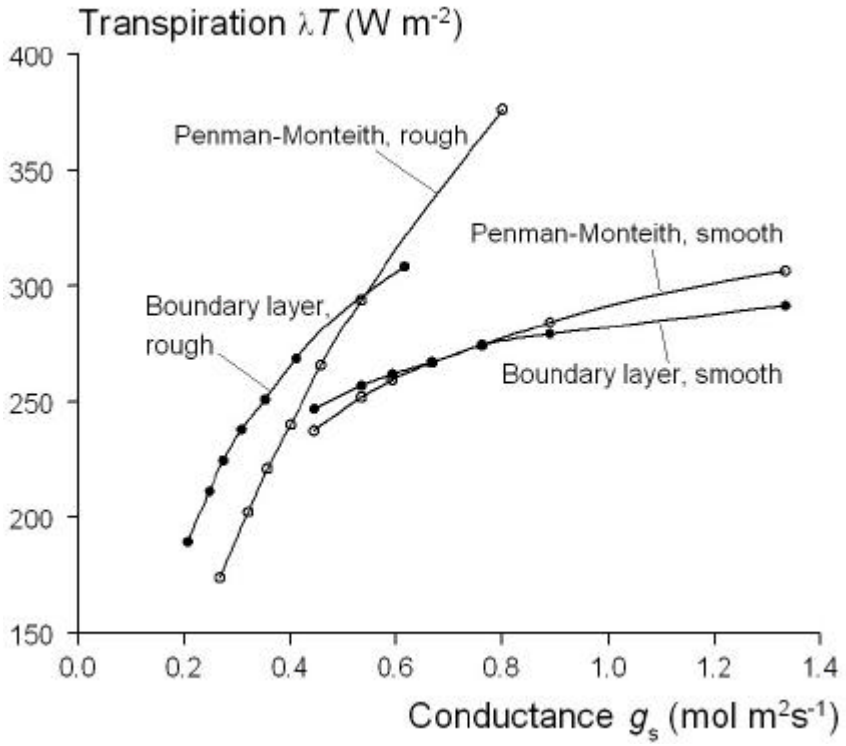


Figure 4-2. The sensitivity of the transpiration to crop conductance g_s under conditions such as Jacobs & De Bruin (1992) describe. A re-plotting of data from this publication.

4.5 Calculation of CO_2 effect at plot level

With the information about effects of CO_2 on g_s from §4.2, and the effects of roughness and boundary layers on the sensitivity of evapotranspiration from §4.4, we can now estimate the effect at plot level.

In §4.2 we showed for example that when CO_2 concentrations go up by 100 ppm, the g_s of grass and herbal crops goes down by an average of 9.3%: $?g_s / g_s$ = -0.093 per 100 ppm. In §4.4 we came to the conclusion that the transpiration from a smooth surface changes by 15-20% - an average of 17.5% - of the change in g_s: $(?T / T) / (?g_s / g_s)$=0.175. Combining these two factors gives an average decrease in transpiration of 1.6% per 100 ppm (0.093×0.175). Making various combinations of crop type and roughness, and taking uncertainties into account, we end up with the transpiration sensitivities *S* for CO_2 rise, set out in Table 4-2. *S* is defined here as the relative change in transpiration caused by a CO_2 rise of 100 ppm.

We now have to consider two other aspects before we can determine the effect on evapotranspiration: (1) the share of transpiration in the evapotranspiration, F^T, and (2) the lai-effect of CO_2-rise, mentioned in §2.1 (positive feedback on *ET* via increased Leaf Area Index, see also Figure 2-7).

Table 4-2. Transpiration sensitivities S (percentages; min = minimum, max = maximum). S is defined as the relative change in transpiration caused by a CO_2 rise of ?CO_2 = 100 ppm. Reduction of stomatal conductance g_s taken from §4.2. In these figures the temperature in the boundary layer is assumed to be constant.

	Change in conductance		Roughness of the vegetation					
			Smooth			Rough		
	?g_s	σ	min	mean	max	min	mean	max
Herbal	-9.3	1.5	-1.2	-1.6	-2.2	-3.1*	-5.3*	-8.1*
Woody	-6.8	2.5	-0.6*	-1.2*	-1.9*	-1.7	-3.9	-7.0
C_4	-11.8	1.0	-1.6	-2.1	-2.6	-4.3*	-6.8*	-9.6*

* These combinations occur seldom or never.

The transpiration share

The transpiration share F^T is mainly determined by vegetation cover. Suppose the transpiration of a well-developed crop constitutes 80% of the total evapotranspiration (Figure 2-3), and that the 20% evaporation in *ET* is not sensitive to CO_2, then the decrease, per 100 ppm CO_2 rise, in *ET* in our previous example in not 1.6%, but 0.8×1.6 = 1.3% instead. So, in order to compute effects on evapotranspiration we have to know the transpiration share F^T. This share may vary with the seasons, depending on vegetation cover. In winter, fields usually lie fallow so that $F^T = 0$. In winter, potential evapotranspiration is also low so that *ET* is less sensitive to F^T. On the other hand, grasslands have a high cover throughout the year and, with that, F^T is permanently high too.

With the integrated soil-water-atmosphere-plant model SWAP (Van Dam, 2000) we calculated for 10 successive years (1980-1990) and on a soil without moisture stress, the F^T of four crops: potato, maize, grassland and wheat. The results are shown in Figure 4-3 and Appendix II, with mean values per decade. Table 4-3 that was derived from Appendix II gives the average F^T-values for the summer season and for the winter season. On the basis of this we define the following two categories:

- Grasslands and other short, lasting vegetations (like heather), with an F^T value of 80% throughout the year.
- Agricultural fields and other deciduous vegetations (like deciduous forests and gardens), with an F^T value of 60% on average, 80% in the summer season and 10% in the winter season. Also evergreen conifers

(such as spruce) are in this category because their high interception loss in winter causes a low F^T.

It may seem that this rules of thumb estimate the transpiration share of wheat too high, but this may not be the case since we did not consider the effect of a second crop, which is often planted by farmers for green manuring. So, for a parcel of wheat F^T is probably higher than we computed with the SWAP model.

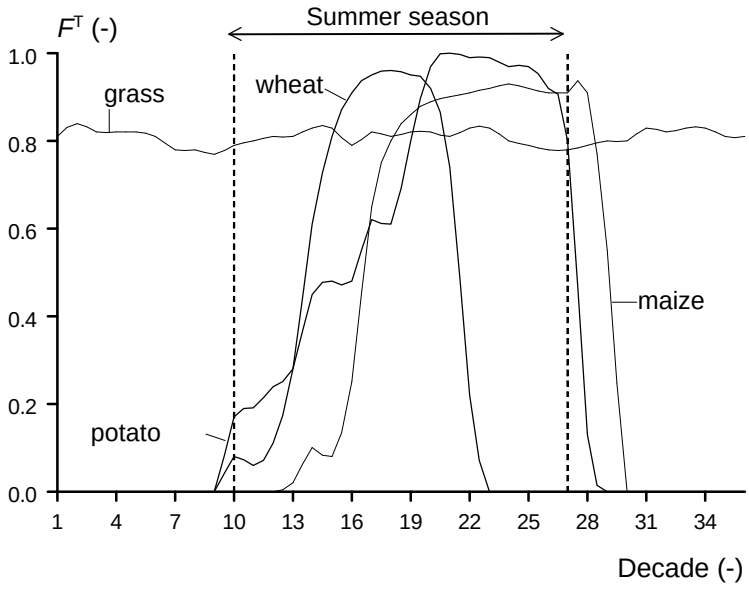


Figure 4-3. Course of transpiration share F^T in the evapotranspiration of four crops: potatoes, maize, grassland en wheat. Based on average simulated decadal figures of transpiration and evapotranspiration (1980-1990), see Appendix II.

Table 4-3. Mean transpiration share F^T of four crops, for the whole year, summer season (decade 9-27 = 1 April - 30 September), and winter season (decade 1-8 and 28-36).

	Potatoes	Grass	Maize	Wheat
Year	0.61	0.81	0.63	0.49
Summer	0.81	0.81	0.79	0.67
Winter	0.06	0.80	0.15	0.02

The lai-effect

In the literature it has been suggested that CO_2 rise may stimulate Leaf Area Index to such an extent, that this may nullify the effect of a lower stomatal conductance: wue-effect and lai-effect fully compensate each other and the net-effect is that evapotranspiration remains the same. Poorter & Navas (2002) show in a meta-analysis comprising a large number of experiments, that biomass can increase tens of percents when CO_2-concentration doubles.

However, according to the authors the results do not tell us how biomass increases in natural conditions outdoors, since these large effects on biomass were measured on well ventilated pots in which plants had enough space to use the extra CO_2 for their growth. Experiments with monocultures, in which plants compete, showed a small biomass response.

In order to reliable estimate effects on biomass or LAI, we have to rely on FACE studies. Bunce (2004) gives a review of his own FACE experiments and those of others, in which effects on LAI of CO_2 supply (550-700 ppm) have been measured. From the crops studied, there was no (Beans, Cotton, Orchard grass - *Dactylis glomerata*, Potatoes, Sorghum, Winter barley, Winter wheat) or just a small (<10%; Rice, Summer wheat) observed increase in LAI. In the latter case, the small increase occurred at the beginning of the growing season. An exception was Soya bean, on which an average increase of 27% was observed, throughout the growing season. However, according to a simulation with a soul-vegetation-atmosphere model (Wilson et al., 1999), this increase had no effect on evapotranspiration.

According to Bunce (2004) "the lack of response of LAI to elevated CO_2 in most crop species under field conditions is somewhat surprising and suggests that leaf area growth often is not carbon limited under field conditions". For our study this means *that we can neglect the lai-effect*.

Bunce (2004) makes a number of statements about the response of crops that are worth mentioning:

- In stands of crops, interception of radiation is generally nearly complete at a LAI of about 3, and evapotranspiration changes little above a LAI of 3 or 4.
- In naturally ventilated plant canopies additional shaded leaf area contributes little to *ET* partly because shaded leaves receive not much radiation, but also because a greater leave area results in humification of the air as well as a reduction of wind speed inside the canopy.
- In artificially ventilated systems additional leaf area can result in a higher *ET* because the supply with blowers of CO_2 enriched air causes a lower humidity and a higher wind speed inside the canopy. Therefore, results of such experiments cannot be simply extrapolated to the field.
- Many annual crops spend a substantial fraction of the growing season with a LAI of <3. Therefore during this period LAI could be stimulated and, with that, *ET* as well. As we discussed, however, in most cases there is no effect on LAI and in cases there is any, it only has a small impact on *ET*. According to Bunce (2004) the small response of *ET* might be due to the lower soil evaporation than in the ambient CO_2 treatment.

Effects on evapotranspiration

Now that we know the transpiration share and that we may neglect the lai-effect, we can calculate the decrease of evapotranspiration as a result of CO_2 level rise by ? CO_2:

$$\frac{\Delta ET}{ET} = \frac{\Delta CO_2}{100} \times F^T \times S \qquad [4.6]$$

With the aid of this equation, the two categories for transpiration share mentioned on page 39, and the transpiration sensitivities of Table 4-2, we have drawn up Table 4-4, showing the evapotranspiration decrease in terms of percentage for 2050 and 2100.

Table 4-4. Calculated decrease of evapotranspiration in 2050 en 2100 due to a CO_2 level rise of 150 and 385 ppm, respectively (min = minimum, max = maximum). In these figures, temperature in the boundary layer is assumed to be constant.

Vegetation	F^T	Roughness of the vegetation					
		Smooth			Rough		
		min	mean	max	min	max	max
2050 (+150 ppm)							
Year							
Short grasslands	0.8	-1.4	-2.0	-2.6	-3.7*	-6.4*	-9.7*
Fields, conifers	0.6	-1.1	-1.5	-1.9	-2.8*	-4.8*	-7.3*
Deciduous, shrubs	0.6	-0.6*	-1.1*	-1.7*	-1.5	-3.5	-6.3
C_4 crops	0.6	-1.5	-1.9	-2.3	-3.9*	-6.1*	-8.6*
Summer							
Short grasslands	0.8	-1.4	-2.0	-2.6	-3.7*	-6.4*	-9.7*
Fields, conifers	0.8	-1.4	-2.0	-2.6	-3.7*	-6.4*	-9.7*
Deciduous, shrubs	0.8	-0.8*	-1.4*	-2.2*	-2.1	-4.7	-8.4
C_4 crops	0.8	-1.9	-2.5	-3.1	-5.2*	-8.1*	-11.5*
Winter							
Short grasslands	0.8	-1.4	-2.0	-2.6	-3.7*	-6.4*	-9.7*
Fields, conifers	0.1	-0.2	-0.2	-0.3	-0.5*	-0.8*	-1.2*
Deciduous, shrubs	0.1	-0.1*	-0.2*	-0.3*	-0.3	-0.6	-1.0
C_4 crops	0.1	-0.2	-0.3	-0.4	-0.6*	-1.0*	-1.4*
2100 (+385 ppm)							
Year							
Short grasslands	0.8	-3.6	-5.0	-6.7	-9.6*	-16.5*	-24.9*
Fields, conifers	0.6	-2.7	-3.8	-5.0	-7.2*	-12.4*	-18.7*
Deciduous, shrubs	0.6	-1.5*	-2.7*	-4.3*	-4.0	-9.0	-16.1
C_4 crops	0.6	-3.7	-4.8	-5.9	-10.0*	-15.7*	-22.2*
Summer							
Short grasslands	0.8	-3.6	-5.0	-6.7	-9.6*	-16.5*	-24.9*
Fields, conifers	0.8	-3.6	-5.0	-6.7	-9.6*	-16.5*	-24.9*
Deciduous, shrubs	0.8	-2.0*	-3.7*	-5.7*	-5.3	-12.0	-21.5
C_4 crops	0.8	-5.0	-6.4	-7.9	-13.3*	-20.9*	-29.6*
Winter							
Short grasslands	0.8	-3.6	-5.0	-6.7	-9.6*	-16.5*	-24.9*
Fields, conifers	0.1	-0.5	-0.6	-0.8	-1.2*	-2.1*	-3.1*
Deciduous, shrubs	0.1	-0.2*	-0.5*	-0.7*	-0.7	-1.5	-2.7
C_4 crops	0.1	-0.6	-0.8	-1.0	-1.7*	-2.6*	-3.7*

*These combinations hardly occur in practice.

© Kiwa N.V.

4.6 Discussion

Comparison with measurements

Measurements of evapotranspiration decreases in cases of CO_2 increases of 200 ppm are according to Table 3-1 6.5% on average, with a standard deviation of 3.5% (including experiments under conditions of drought stress and nutrient poverty). If we calculate the decrease at 200 ppm according to the method described in §4.5, excluding unrealistic combinations of vegetation and aerodynamic resistance, we obtain a value of between 2 and 11% (see sheet 'calculations' in the data base). Like Table 3-1, in our method a C_4 plant and trees have a relatively high value, whereas the low value is computed for the other agricultural fields. So, m*easurements seem to confirm the usability of the calculation method presented here.*

Comparison with model simulations

The effect on evapotranspiration of doubling of CO_2 level has been simulated in a number of studies. According to our method, $2\times CO_2$ leads to an evapotranspiration reduction of 3.3-6% of short grasslands and aerodynamically smooth C_4 crops. High crops like maize are not that smooth, aerodynamically, so that the reduction will be somewhat higher.

Bunce (2004) discusses five model studies in which the stomatal conductance depends on environmental conditions, such as CO_2 concentration and moisture stress. With one-dimensional soil-vegetation-atmosphere models, a reduction of *ET* was simulated at $2\times CO_2$ of 1-2% for Alfalfa, 2-5% for Orchard grass, 5-9% for Soybean, and 0-9% for Maize. A reduction of *ET* of 2.3-3.5% for all vegetation was simulated with a Ball-Berry model of stomatal conductance ([4.1]), linked to a Global Circulation Model (GCM). According to Bunce (2004) these studies suggest that doubling atmospheric CO_2 would probably reduce *ET* by a few percent, but probably by <10%.

With a one-dimensional model Grant et al. (2001) simulated a 9% reduction of evapotranspiration of Wheat, sufficiently supplied with water and nutrients. Also using a one-dimensional model, Riedo et al. (1999) simulated reductions of 6 and 11 % for two grasslands in the Alps. Given soil texture (loam) and species composition (Orchard grass, Perennial ryegrass - *Lolium perenne*, Tall oatgrass - *Arrhenatherum elatius*), both grassland probably had enough water and nutrients.

Finally, Sellers et al. (1996) used a biosphere model linked to a GCM to calculate for the northern latitudes ((50.4 ^{0}N to 72.0 ^{0}N) a reduction of *ET* of 2.2 and 4.1%. The low figure (2.2%) is based on the assumption that all the extra carbon is used for extra photosynthesis, the high figure (4.1%) on the assumption that photosynthesis does not change. Since we may probably neglect the lai-effect, the highest figure seems most appropriate.

The results of these model simulations are in reasonable agreement with the results of our calculation method. Deviations may be due to model assumptions and sub-optimal growth conditions in the simulations.

Future research

The predicted evapotranspiration decreases, with all their uncertainties, could be included, whether in these or in more simplified forms, in future hydrological calculations. The predictions for increased evapotranspiration in Beersma et al. (2004) should also be included. Given that the increases are of similar dimensions, we can expect that *the net effect of climate change on evapotranspiration will be small*, but that *there are many uncertainties*. The type and structure of vegetation plays a big role, with CO_2, temperature and crop evapotranspiration having a bigger effect on rougher (and usually taller) vegetation forms. The uncertainties increase here too, and it is more important for rougher vegetation than for lower, smoother vegetation to integrate evapotranspiration processes explicitly in models.

Finally, we would like to point out that, as mentioned in §2.6, we have left out a number of processes, both on the smaller scale at leaf and stomata level, and on the larger, regional scale. These processes are potentially very influential and it is therefore important to conduct *further studies with integrated models simulating and linking both small-scale and large-scale processes*.

5 Conclusions and recommendations

1. The greenhouse and Open Top Chamber experiments described in the literature (Chapter 3) reveal a bigger decrease in evapotranspiration due to increased CO_2 than that which is observed out in the field. In such experiments, the aerodynamic resistance is so reduced by the efficient application of CO_2 enriched air that the transpiration of plants displays an increased sensitivity to CO_2 enrichment.
2. For the Drought study, Doomen & Witte (2004) estimate an evapotranspiration reduction of 5% per 100 ppm increase in CO_2. Given that this study is based on the experiments mentioned in (1), this reduction figure has to be considered unrealistic and must therefore be rejected.
3. Experimental research into the effect of CO_2 application on evapotranspiration is complicated by various feedback mechanisms, including:
   - Reduction in evapotranspiration increases the vapour pressure gradient from leaf to air through a rise in the leaf temperature and a drop in atmospheric humidity, which in turn stimulates evapotranspiration.
   - Rising temperatures and falling atmospheric humidity levels near the leaves can make the stomata close, causing a further decrease in transpiration. There has been little research into this positive feedback and its effect in practice is highly uncertain.
   - Under nutrient-poor conditions, CO_2 may stimulate plants to extend their root system in order to obtain nutrients, which are then a limiting factor. A larger root system ensures a better supply of moisture, which stimulates transpiration.
   - Rising CO_2 leads to greater above-ground growth, increasing leaf surface area and with it evapotranspiration.
   - On dry soils, evapotranspiration reduction through increased CO_2 ensures that soil moisture is available for longer, which promotes evapotranspiration.
4. Most experimental research has focused on agricultural crops and natural vegetations, probably with a view to consequences for agricultural production and for biodiversity, respectively. For hydrological scenarios in The Netherlands, it is very important that more experimental research is done on common vegetations such as grasslands (dominated by *Lolium perrene),* maize fields and heather. This research should be done using FACE, and should also investigate the increased closing of the stomata as a consequence of reduced atmospheric humidity around the leaves.

   The effect of CO_2 on evapotranspiration can be researched using historical lysimeter results, preferably from at least fifty years ago. CO_2

concentrations have increased so much in the past century that their effect on evapotranspiration must be demonstrable with the help of historical data.

5. For a truly reliable estimate of the effects of changing climate and CO_2 levels, a study should be carried out using a linked soil-water-vegetation-atmosphere model on a landscape scale. Such a model includes the seasonal dynamics of growth and leaf development and is applied to whole regions over at least one year. Only under such conditions can we be sure that the most significant feedback mechanisms are taken into account.

6. In spite of all the uncertainties, we can use the literature study (Chapter 3), model simulations described in the literature (§4.6), and our calculations (Chapter 4; Table 4-4) to give estimates of the reduction in evapotranspiration caused by increases in the CO_2 level of 150 and 385 ppm, which are (§1.2) the averages predicted for 2050 and 2100 respectively: *see Table* 5-1. These estimates take into consideration the aerodynamic roughness of the vegetation (the rougher the vegetation, the better the air mixing and the lower the aerodynamic resistance), the photosynthesis type (C_3 or C_4) and the moderating influence of nutrient poverty mentioned under point (3).

7. The reduction in evapotranspiration presented in Table 5-1 is more or less the same as the increase in evapotranspiration calculated by the KNMI for scenarios of yearly average temperature increases of 0.5, 1 and 2 ^{0}C (Table 1-1: 1.9, 3.9 and 7.8% increase in evapotranspiration). However, when the predicted increase in rainfall (Table 1-1) is taken into account, the expectation is that The Netherlands will become rather wetter, on average (see example calculation on page 48). According to the example calculation, the summer season may become wetter or dryer, depending on the scenario and the value c_2 for the CO_2-effect.
   It is only in the 'Drought scenario' that the increase in evapotranspiration by higher temperatures and the reduction of precipitation will yield a large reduction of the precipitation excess, irrespective the CO_2-effect on evapotranspiration.

8. In view of the fact that the effects on evapotranspiration of temperature increases (Table 1-1) and of CO_2 increases (Table 5-1) are surrounded by large uncertainties, have an opposite result, and are comparable in scale, we recommend that both effects be incorporated, with their margins of uncertainty, in any hydrological risk calculations for different climate scenarios.

© Kiwa N.V.

Table 5-1. Proposed factor c_2 for the correction of potential evapotranspiration ET_p (according to Equation[1.3]) for 2050 and 2100 (CO_2 concentration of 150 and 385 ppm respectively)[9]. Presented are the estimated minimal (min), mean and maximum (max) figures for evapotranspiration reduction. Effects on the evapotranspiration of the expected rise in temperature are not taken into account. The relative change in ET_p amounts $?ET_p/ET_p = 1 - c_2$.

Vegetation	2050			2100		
	min	mean	*max*	*min*	mean	*max*
Year						
1. Grasslands, dry + nutrient-poor reserves*	*0.99*	0.98	*0.97*	*0.96*	0.95	*0.93*
2. Deciduous, shrubs, C_4 crops	*0.98*	0.96	*0.94*	*0.96*	0.91	*0.84*
3. Other fields, conifers	*0.98*	0.97	*0.95*	*0.95*	0.92	*0.88*
4. Other nature reserves	*0.97*	0.96	*0.94*	*0.93*	0.89	*0.84*
Summer						
1. Grasslands, dry + nutrient-poor reserves*	*0.99*	0.98	*0.97*	*0.96*	0.95	*0.93*
2. Deciduous, shrubs, C_4 crops	*0.98*	0.95	*0.92*	*0.95*	0.88	*0.78*
3. Other fields, conifers	*0.97*	0.96	*0.94*	*0.93*	0.89	*0.84*
4. Other nature reserves	*0.97*	0.96	*0.94*	*0.93*	0.89	*0.84*
Winter						
1. Grasslands, dry + nutrient-poor reserves*	*0.99*	0.98	*0.97*	*0.96*	0.95	*0.93*
2. Deciduous, shrubs, C_4 crops	*1.00*	0.99	*0.99*	*0.99*	0.99	*0.98*
3. Other fields, conifers	*1.00*	0.99	*0.99*	*0.99*	0.99	*0.98*
4. Other nature reserves	*0.97*	0.96	*0.94*	*0.93*	0.89	*0.84*

*dry dunes, dry heath

[9] Explanation of how the figures were established:

- The estimates for category 1 and 2 are directly based on Table 4-4.
- Although nutrient-poor and dry nature reserves have, on average, a higher aerodynamic roughness than grasslands, they are assigned to category 1 because nutrient-poverty tempers evapotranspiration reduction.
- Maize is assigned to category 2. This crop is moderately rough, aerodynamically, so less rough than deciduous forest, but, on the other hand, the C_4 photosynthesis increases the sensitivity of maize to CO_2.
- 'Other fields' have a season dependent transpiration share in the evapotranspiration. Aerodynamically speaking, they are 'moderately rough'. The estimates are averages from the calculation method described in §4.5 of 'smooth' and 'rough' for grasslands. Coniferous trees are assigned to category 3 because of their low transpiration share, which is caused by a high interception rate.
- Category 4 got the same transpiration share as that of grassland (80%), but an aerodynamic roughness just between 'smooth' and 'rough'.

© Kiwa N.V.

Example calculation : effects on precipitation excess in 2050

Approximately 800 mm of precipitation falls in The Netherlands every year, and approximately 550 mm of moisture evaporates under good water supply conditions, giving a precipitation excess of 250 mm yr^{-1}. (www.knmi.nl).

For short grassland, Table 5-1 gives a reduction in evapotranspiration through the CO_2-effect of 2% for 2050 (c_2 = 0.98). If we adopt the market optimist's scenario (Table 1-1: increase in precipitation of +1.5%, increase in evapotranspiration through higher temperatures of +1.9% (c_1 = 1.019)), then the precipitation excess for this grassland in 2050 will be 5%: 800×1.015 - 550×1.019×0.98 = 263 mm. The table below can be put together in the same way, for different climate scenarios and c_2-values.

In the table below, figures for the summer season are based on a precipitation of 400 mm and an evapotranspiration of 500 mm; positive values indicate a *decrease* of the evapotranspiration excess.

It is of course a rough calculation method, but it does indicate that most scenarios suggest that The Netherlands will become somewhat wetter *on average*. To accurately calculate the effects on the actual evapotranspiration and the precipitation excess, a model for unsaturated zone is needed, e.g. SWAP or MOZART. Models like NAGROM, MONA and MOZART could be used to investigate how evapotranspiration, the precipitation excess and the hydrology of The Netherlands change in various climate scenarios (including other precipitation, potential evapotranspiration, and downwardly adjusted crop factors).

Predicted increase in precipitation excess (%) in different climate scenarios (with average temperature rises as in Table 1-1), for correction factors c_2.

	Year			*Summer*		
Scenario	c_2=0.95	c_2=0.97	c_2=0.98	c_2=0.95	c_2=0.97	c_2=0.98
Market optimist (+0.5 ^{0}C)	+12	+7	+5	+20	+10	+4
Controller (+1 ^{0}C)	+12	+8	+6	+15	+5	-1
Environmentalist (+2 ^{0}C)	+14	+9	+7	+5	-6	-11
Drought (+2.3 ^{0}C)	-39	-45	-47	-170	-180	-190

Literature

Anonymous, 2004. *Evapotranspiration-Summary*. Center for the Study of Carbon Dioxide and Global Change.

Anonymous, ?. *Impact of climate change on crop and soil processes.* Climate Change & Agriculture in the United Kingdom. www.defra.gov.uk.

Adam, N.R., C.E. Owensby & J.M. Ham, 2000. The effect of CO_2 enrichment on leaf photosynthetic rates and instantaneous water use efficiency of Andropogon regardii in the tallgrass prairie. *Photosynthesis Research* 65: 121-129.

Allen, L.A., D. Pan, K.J. Boote, N.B. Pickering & J.W. Jones, 2003. Carbon dioxide and temperature effects on evapotranspiration and water use efficiency of Soybean. *Agronomy Journal* 95: 1071-1081.

Ainsworth, E. A. & S. P. Long, 2005. What have we learned from 15 years of free-air CO_2 enrichment (face)? A meta-analytic review of the responses of photosynthesis, canopy. *New Phytologist* 165: 351-371.

Apple, M.E, D.M. Olszy, D.P. Ormrod, J. Lewis, D. Southworth & D.T. Tingey, 2000. Morphology and stomatal function of Douglas fir needles exposed to climate change: elevated CO_2 and temperature. *International Journal of Plant Science* 161: 127-132.

Agrawal, M. & S.S. Deepak, 2003. Physiological and biochemical responses of two cultivars of wheat to elevated levels of CO_2 and SO_2, singly and in combination. *Environmental Pollution* 121:189-97.

Bazzaz, F.A. & K. Garbutt, 1988. The response of annuals in competitive neighborhoods: effects of elevated CO_2. *Ecology* 69:937-946.

Beerling D.J., J. Heath, F.I. Woodward & T.A. Mansfield, 1996. Drought-CO_2-interactions in trees: observations and mechanisms. *New Phytologist* 134: 235-245.

Beersma, J.J., T.A. Buishand & H. Buiteveld, 2004. *Droog, droger, droogst — KNMI/Riza bijdrage aan de tweede fase van de droogtestudie Nederland.* KNMI-publicatie 199-II, Lelystad.

Bos, H., R. van Ek, J. Hoogeveen, A. Kors, W. de Lange, H. Vermulst, G. Arnold & T. Kroon, 1997. *Water onder land tussen regen en plant ofwel landelijke modellen voor verdrogingsbestrijding.* RIZA rapport 97.062, RIZA, Lelystad.

Brinkman, R. & W.G. Sombroek, 2004. *The effects of global change on soil conditions in relation to plant growth and food production*. www.fao.org / docrep / W5183E.

Brutsaert, W. & B. Parlange, 1998. Hydrologic cycle explains the evaporation paradox. *Nature* 6706: 396.

Bunce, J.A., 2004. Carbon dioxide effects on stomatal responses to the environment and water use by crops under field conditions. *Oecologia* 140:1-10.

Calvet, J.C., V. Rivalland, C. Picon-Cochard & J.M. Guehl, 2004. Modelling forest transpiration and CO_2 fluxes-response to soil moisture stress. *Agricultural and Forest Meteorology* 124: 143-156.

Cardoso-Vilhena, J., L. Balaguer, D. Eamus, J. Ollerenshaw & J. Barnes, 2004. Mechanisms underlying the amelioration of O_3-induced damage by

elevated atmospheric concentrations of CO_2. *Journal of Experimental Botany* 55: 771-781.
Carlson, N.C. & J.A. Bunce, 1995. Will a doubling of atmospheric carbon dioxide concentration lead to an increase or a decrease in water consumption by crops? *Ecological Modelling* 88: 241-246.
Centritto, M., F. Magnini, H.S.J. Lee & P.G. Jarvis, 1999. Interactive effects of elevated CO_2 and drought on Cherry seedling photosynthesis and water relations. *New Phytologist* 141: 141-153.
Conley, M.M., B.A. Kimbal, T.J. Brooks, P.J. Pinter Jr., D.J. Hunsaker, G.W. Wall, N.R. Adams, R.L. LaMorte, A.D. Matthias, T.L. Thompson, S.W. Leavitt, M.J. Ottman, A.B. Cousins & J.M. Triggs, 2001. CO_2 enrichment increases water-use efficiency in sorghum. *New Phytologist* 151: 407-412.
Cure, J.D. & B. Acock, 1986. Crop responses to carbon dioxide doubling: a literature survey. *Agricultural and Forest Meteorology* 38: 127-145.
Daepp, M., D. Suter, J.P.F. Almeida, H. Isopp, U.A. Hartwig, M. Frehner, H. Blum, J. Nösberger & A. Lüscher, 2000. Yield response of Lolium perenne swards to free air CO_2 enrichment increased over six years in a high N input system on fertile soil. *Global Change Biology* 6: 805-816.
De Wit, C.T., 1958. *Transpiration and crop yields.* Verslagen landbouwkundig onderzoek no. 64.6, 's-Gravenhage.
Dijkstra, P., A.H.M.C. Schapendonk & K. Groenwold, 1993. *Effects of CO_2 enrichment on canopy photosynthesis, carbon economy and productivity of wheat and faba bean under field conditions.* In: Van de Geijn et al., 1993.
Dijkstra, P., A.H.M.C. Schapendonk, K. Groenwold, M. Jansen & S.C. Van de Geijn, 1999. Seasonal changes in the response of winter wheat to elevated atmospheric CO_2 concentration grown in open-top chambers and field tracking enclosures. *Global Change Biology* 5: 563-576.
Doomen, A. & J.P.M. Witte, 2004. *Invloed van CO_2 -toename op verdamping en groei van planten; Een literatuuronderzoek voor de Droogtestudie Nederland.* Kiwa-rapport.
Dolman, A.J., E.J. Moors, J.A. Elbers & W. Snijders, 1998. Evaporation and surface conductance of three temperate forests in the Netherlands. *Ann. Sci. For.* 55:255-270.
Dong-Xiu, W., W. Gen-Xuan, B. Yong-Fei, L. Jian-Xiong & R. Hong-Xu, 2002. Response of growth and water use efficiency of spring wheat to whole season CO2 enrichment and drought. *Acta Botanica Sinica* 44: 1477-1483.
Droogers, P., R. Loeve & B. van den Hurk, 2004. De (on)zekerheid van klimaatverandering. *H_2O* 19: 85-88.
Dugas, W.A. , S.A. Prior & H.H. Rogers, 1996. Transpiration from sorghum and soybean growing under ambient and elevated CO_2 concentrations. *Agricultural and Forest Meteorology* 83: 37-48.
Farquhar, G.D., 1997. Carbon dioxide and vegetation. *Science* 278: 1411.
Feddes, R.A., 1987. *Crop factors in relation to Makkink's reference crop evaporation*. In: Hooghart, J.C. (red) *Evaporation and Weather*; CHO-TNO, Proceedings and Information No. 39, Den Haag.
Feddes, R.A., R.W.R. Koopmans & J.C. van Dam, 1997. *Agrohydrology*. Dictaat Wageningen Universiteit, Wageningen.
Feddes, R.A., P.J. Kowalik & H. Zaradny, 1978. *Simulation of field water use and crop yields.* Simulation monographs. Pudoc, Wageningen.

Field, C.B., R.B. Jackson RB & H.A. Mooney, 1995. Stomatal responses to increased CO_2: implications from the plant to the global scale. *Plant, Cell and Environment* 18: 1214-1225.

Gavazzi, M., J. Seiler, W. Aust & S. Zedaker, 2000. The influence of elevated carbon dioxide and water availability on herbaceous weed development and growth of transplanted loblolly pine (*Pinus taeda*). *Environmental and Experimental Botany* 44: 185-194.

Gitay, H., Suárez, A., Dokken, D.J. & R.T. Watsen, 2002. *Climate change and biodiversity*. Intergovernmental Panel on Climate Change (IPCC).

Grant, R.F., B.A. Kimball, T.J. Brooks, G.W. Wall, P.J. Pinter Jr., D.J. Hunsaker, F.J. Adamsen, R.L, Lamorte, S.W. Leavitt, T.L. Thompson & A.D. Matthias, 2001. Modeling Interactions among carbon dioxide, nitrogen, and climate on energy exchange of wheat in a free air carbon dioxide experiment. *Argonomy Journal* 93: 638-649.

Haasnoot, M., J.A.P.H. Vermulst & H. Middelkoop, 1999. *Impacts of climate change and land subsidence on the water systems in the Netherlands — Terrestrial areas*. RIZA rapport 99.049, Lelystad.

Hakala, K., 1998. Growth and yield potential of spring wheat in a simulated changed climate with increased CO_2 and higher temperature. *European Journal of Agronomy* 9: 41-52.

Heijmans, M.M.P.D., W.J. Arp & F. Berendse, 2001. Effects of elevated CO_2 and vascular plants on evapotranspiration in bog vegetation. *Global Change Biology* 7: 817-827.

Heijmans, M.M.P.D., W.J. Arp, & F.S. Chapin, 2004. Carbon dioxide and water vapour exchange from understory species in boreal forest. *Agricultural and Forest Meteorology* 123: 135-147.

Heijmans, M.M.P.D., H. Klees, W. de Visser & F. Berendse, 2002. Response of a Sphagnum bog plant community to elevated CO_2 and N supply. *Plant Ecology* 162: 123-134.

Hodkinson, I.D., N.R. Webb, J.S. Bale & W. Block, 1999. Hydrology, water availability and tundra ecosystem function in a changing climate: the need for a closer integration of ideas? *Global Change Biology* 5: 359-369.

Hunsaker, D.J., B.A. Kimball, P.J. Pinter Jr., G.W. Wall, R.L. LaMorte, F.J. Adamsen, S.W. Leavitt, T.L. Thompson, A.D. Matthias & T.J. Brooks, 2000. CO_2 enrichment and soil nitrogen effects on wheat evapotranspiration and water use efficiency. *Agricultural and Forest Meteorology* 104: 85-105.

Hungate, B.A. , E.A. Holland, F.S. Chapin III, H. Zhong & C.B. Field, 1997. Stimulation of grassland nitrogen cycling under carbon dioxide enrichment. *Oecologia* 109: 149-153.

Hungate, B.A., E.A. Holland, R.B. Jackson, F.S. Chapin III, F.S., H.A. Mooney & C.B. Field, 1997. The fate of carbon in grasslands under carbon dioxide enrichment. *Nature* 388: 576-579.

Jackson, R.B., O.E. Sale, J.M. Paruelo & H.A. Mooney, 1998. Ecosystem water fluxes for two grasslands in elevated CO_2: a modelling analysis. *Oecologia* 113: 537-546.

Jacobs, C. M. J., 1994. *Direct impact of atmospheric CO_2 enrichment on regional transpiration*. Wageningen, Wageningen University: 179.

Jacobs, C. M. J. & H. A. R. de Bruin, 1992. The sensitivity of regional transpiration to land-surface characteristics - significance of feedback. *Journal of Climate* 5: 683-698.

Jacobs, C. M. J. & H. A. R. de Bruin, 1997. Predicting regional transpiration at elevated atmospheric CO_2: Influence of the pbl-vegetation interacton. *Journal of Applied Meteorology* 36: 1663-1675.

Janácek, J., 1997. Stomatal limitation of photosynthesis as affected by water stress and CO_2 concentration. *Photosynthetica* 113: 537-546.

Jarvis, P. G., 1976. Interpretation of variations in leaf water potential and stomatal conductance found in canopies in field. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 273: 593-610.

Jones, H.G., 1992, *Plants and microclimate: a quantitative approach to environmental plant physiology (2nd ed).* Cambridge University Press, Cambridge, UK.

Kimball, B.A., R.L. LaMorte, P.J. Pinter Jr., G.W. Wall, D.J. Hunsaker, F.J. Adamsen, S.W. Leavitt, T.L. Thompson, A.D. Matthias & T.J. Brooks, 1999. Free-air CO_2 enrichment (FACE) and soil nitrogen effects on energy balance and evapotranspiration of wheat. *Water Resources Research* 35: 1179-1190.

Kimball, B.A., P.J. Pinter Jr., R.L. Garcia, R.L. LaMorte, G.W. Wall, D.J. Hunsaker, G. Wechsung, F. Wechsung & T. Kartschall, 1995. Productivity and water use of wheat under free-air CO_2 enrichment. *Global Change Biology* 1: 429-442.

Klopstra, D., R. Versteeg & T. Kroon, 2005. *Aard, ernst en omvang van watertekorten in Nederland; Eindrapport droogtestudie Nederland.* Rapport Droogtestudie, Lelystad.

Kruijt, B., C. Barton, A. Rey & P.G. Jarvis, 1999. The sensitivity of stand-scale photosynthesis and transpiration on changes in atmospheric CO_2 concentration and climate. *Hydrology and Earth System Sciences* 3: 55-69.

Lawson, T., J. Craigon, C.R. Black, J.J. Colls, A.-M. Tulloch & G. Landon, 2001. Effects of elevated carbon dioxide and ozone on the growth and yield of potatoes (Solanum tuberosum) grown in open-top chambers. *Environmental Pollution* 111: 479-491.

Leishman, M.R., K.J. Sanbgrooke & R.M. Woodfin, 1999. The effects of elevated CO_2 and light environment on growth and reproductive performance of four annual species. *New Phytologist* 144: 455-462.

Leverenz J.W., D. Bruhn D & H. Saxe, 1999. Responses of two provenances of Fagus sylvatica seedlings to a combination of four temperature and two CO2 treatments during their first growing season: gas exchange of leaves and roots. *New phytologist*, 144: 437-454.

Lewis, J.D., M. Lucash, D.M. Olszyk & D.T. Tingey, 2002. Stomatal responses of Douglas-fir seedlings to elevated carbon dioxide and temperature during third and fourth years of exposure. *Plant, Cell and Environment* 25: 1411-1421.

Li, F., S. Kang & J. Zhang, 2004. Interactive effects of elevated CO2, nitrogen and drought on leaf area, stomatal conductance, and evapotranspiration of wheat. *Agricultural Water Management* 67: 221-223.

Liang, N. & K. Maruyama, 1995. Interactive effects of CO_2 enrichment and drought stress on gas exchange and water-use efficiency in Alnus Firma. *Environmental and experimental botany* 35(3): 353-361.

Liang, N., K. Maruyama & Y. Huang, 1995. Interactions of elevated CO_2 and drought stress in gas-exchange and water-use efficiency in 3 temperate deciduous tree species. *Photosynthetica* 31: 529-539.

Lin, G., J.R. Ehleringer, P.T. Rygiewicz, M.G. Johnson & D.T. Tingey, 1999. Elevated CO_2 and temperature impacts on different components of soil CO_2 efflux in Douglas-fir terracosms. *Global Change Biology* 5: 157-168.

Lockwood, J.G., 1999. Is potential evapotranspiration and its relationship with actual evapotranspiration sensitive to elevated atmospheric CO_2 levels? *Climatic Change* 41: 193-212.

Louche-Tessandier, G. Samson, C. Hernández-Sebastià, P. Chagvardieff & Y. Desjardins, 1999. Importance of light and CO_2 on the effects of endomycorrhizal colonization on growth and photosynthesis of potato plantlets (*Solanum tuberosum*) in an *in vitro* tripartite system. *New Phytologist* 142: 539-550.

Luo, Y., J. Reynolds, Y. Wang & D. Wolfe, 1999. A search for predictive understanding of plant responses to elevated [CO_2]. *Global Change Biology* 5: 143-156.

Mendelsohn, R. & L. Williams, 2003. Comparing forecasts of the global impacts of climate change. *Mitigation and Adaptation Strategies for Global Change* 9: 315-333.

McKee, I.F., J.F. Bullimore & S.P. Long, 1997. Will elevated CO_2 concentrations protect the yield of wheat from O_3 damage? *Plant, Cell and Environment* 20: 77-84.

McNaughton, K. G. & P. G. Jarvis, 1983. *Predicting the effects of vegetation changes on transpiration and evaporation. Water deficits and plant growth*. T. T. Kozlowski, New York, Academic Press. Vol. VII: 1-47.

McNaughton, K. G. & P. G. Jarvis, 1991. Effects of spatial scale on stomatal control of transpiration. *Agricultural and Forest Meteorology* 54: 279-302.

Medlyn, B. E., C. V. M. Barton, M. S. J. Broadmeadow, R. Ceulemans, P. de Angelis, M. Forstreuter, M. Freeman, S. B. Jackson, S. Kellomaki, E. Laitat, A. Rey, P. Roberntz, B. D. Sigurdsson, J. Strassemeyer, K. Wang, P. S. Curtis & P. G. Jarvis, 2001. Stomatal conductance of forest species after long-term exposure to elevated CO_2 concentration: A synthesis. *New Phytologist* 149: 247-264.

Miglietta, F., M.R. Hoosbeek, J. Foot, F. gigon, A. Hassinen, M. Heijmans, A. Peressotti, T. Saarinen, N. van Breemen & B. Wallen, 2001. Spatial and temporal performance of the miniface (free air CO_2 enrichment) system on bog ecosystems in northern and central Europe. *Environmental Monitoring and assessment* 66: 107-127.

Mishra, R.S., M.Z. Abdin & D.C. Uprety, 1999. Interactive effects of elevated CO_2 and moisture stress on the photosynthesis, water relation and growth of Brassica species. *Journal of Agronomy & Crop Science* 182: 223-229.

Mitchell, R.A.C., D.W. Lawlor, V.J. Mitchell, C.L. Gibbard, E.M. White & J.R. Porter, 1995. Effects of elevated CO_2 concentration and increased

temperature on winter wheat: test of ARCWHEAT1 simulation model. *Plant, Cell and Environment* 18: 736-748.

Monteith, J.L., 1981. Climatic variation and the growth op crop. *Quarterly journal of the Royal meteorological society* 107: 749-774.

Moors, E. J., A. J. Dolman, W. Bouten & A. W. L. Veen, 1996. De verdamping van bossen. *H2O* 29(16): 462-466.

Murphy, J.M., D.M.H. Sexton, D.N. Barnett, G.S. Jones, M.J. Webb, M. Collins & D. A. Stainforth, 2004. Quantifying of modeling uncertainties in a large ensemble of climate change simulations. *Nature* 430: 768-772.

Noormets, A., A. Sôber, E.J. Pell, R.E. Dickson, G.K. Podila, J. Sôber, J.G. Isebrands & D.F. Karnosky, 2001. Stomatal and non-stomatal limitation to photosynthesis in two trembling aspen (*Populus tremuloides* Michx.) clones exposed to elevated CO_2 and / or O_3. *Plant, Cell end Environment* 24: 327-336.

Peterson, T.C., V.S. Golubev & P. Groisman, 1995. Evaporation data refute claims of global warming. *Nature* 377: 687-688.

Peterson, A.G. & P.G. Neofotis, 2004. A hierarchical analysis of the interactive effects of elevated CO_2 and water availability on the nitrogen and transpiration productivities of velvet mesquite seedlings. *Oecologia* 141: 629-640.

Pleijel, H., J. Gelang, E. Sild, H. Danielsson, S. Younis, P.-E. Karlsson, G. Wallin, L. Skarby & G. Sellden, 2000. Effects of elevated carbon dioxide, ozone and water availability on spring wheat growth and yield. *Physiologia Plantarum* 108: 61-70.

Polley, H.W., H.B. Johnson, C.R. Tischler & H.A. Torbert, 1999. Links between transpiration and plant nitrogen: variation with atmospheric CO_2 concentration and nitrogen availability. *International Journal of Plant Sciences* 160: 535-542.

Poorter, H. & M.L. Navas, 2003. Tansley review — Plant growth and competition at elevated CO_2: on winners, losers and functional groups. *New Phytologist* 157: 175-198.

Poorter, H. & M. Pérez-Soba. The growth of plants to elevates CO_2 under non-optimal environmental conditions. *Oecologia* 129: 1-20.

Pospisilova, J. & J. Catsky, 1999. Development of water stress under increased atmospheric CO_2 concentration. *Biologia Plantarum* 42: 1-24.

Read, J.J. & J.A. Morgan, 1996. Growth and partitioning in Pascopyrum smithii (C_3) and Bouteloua gracilis (C_4) as influenced by carbon dioxide and temperature. *Annuals of Botany* 77: 487-496.

Riedo, M., D. Gyalistras, A. Fischlin & J. Fuhrer, 1999. Using an ecosystem model linked to GCM-derived local weather scenarios to analyse effects of climate change and elevated CO_2 on dry matter production and partitioning, and water use in temperate managed grasslands. *Global Change Biology* 5: 213-223.

Ruddiman, W.F., 2003. The anthropogenic greenhouse era began thousands of years ago. *Climate Change* 61: 261-293.

Sabaté, S, C.A. Gracia & A. Sánchez, 2002. Likely effects of climate change on growth of Quercus ilex, Pinus halepensis, Pinus pinaster, Pinus sylverstris and Facus sylvatica forests in the Mediterranean region. *Forest ecology and management* 162: 23-37.

Sage, R.F. & D.S. Kubien, 2003. Quo vadis C_4? An ecophysiological perspective on global change and the future of C_4 plants. *Photosynthesis Research* 77: 209-225.

Saxe, H., D.S. Ellsworth & J. Heath, 1998. Tansley review No. 98 — Tree and forest functioning in an enriched CO_2 atmosphere. *New Phytologist* 139: 395-436.

Schapendonk, A., P. Dijkstra, J. Groenwold, C. S. Pot & S. C. van de Geijn, 1997. Carbon balance and water use efficiency of frequently cut lolium perenne swards at elevated carbon dioxide. *Global Change Biology* 3: 207-216.

Schäfer, K.V.R., R. Oren, C.-T. Lai & G.G. Katul, 2002. Hydrologic balance in an intact temperate forest ecosystem under ambient and elevated atmospheric CO_2 concentration. *Global Change Biology* 8: 895-911.

Sellers, P.J., L. Bounoua, G.J. Collatz, D.A. Randall, D.A. Dazlich, O.Los, J.A. Berry, I. Fung, C.J. Tucker, C.B. Field & T.G. Jensen, 1996. Comparison of radiative and physiological effects of doubled atmospheric CO_2 on climate. *Science* 271: 1402-1406.

Serraj, R., L.H. Allen Jr. & T.R. Sinclair, 1999. Soybean leaf growth and gas exchange response to drought under carbon dioxide enrichment. *Global Change Biology* 5: 283-291.

Sonnleitner, M.A., M.S. Günthardt-Goerg, I.K. Bucher-Wallin, W. Attinger, S. Reis & R. Schulin, 2001. Influence of soil type in the effects of elevated atmospheric CO_2 and N deposition on the water balance and growth of a young spruce and beech forest. *Water, Air and Soil Pollution* 126: 271-290.

Stanhill, G., 2005. Global dimming: a new aspect of climate change. *Weather* 60: 11-14.

Stewart, J. B., 1988. Modeling surface conductance of pine forest. *Agricultural and Forest Meteorology* 43: 19-35.

Strocker, R., Ch. Körner, B. Schmid, P.A. Niklaus & P.W. Leady, 1999. A field study of the effects of elevated CO_2 and plant species diversity on ecosystem-level gas exchange in a planted calcareous grassland. *Global Change Biology* 5: 95-105.

Szente, K., Z. Nagy & Z. Tuba, 1998. Enhanced water use efficiency in dry loess grassland species grown at elevated air CO_2 concentration. *Photosynthetica* 35: 637-640.

Taiz, L. & E. Zeiger, 1991. *Plant Physiology*. The Benjamin / Cummings Publishing Company, California.

Tognetti, R., J.D. Johnson, M. Michelozzi & A. Raschi, 1998. Response of foliar metabolism in mature trees of Quercus pubescens and Quercus ilex to long-term elevated CO_2. *Environmental and Experimental Botany* 39: 233-245.

Tuba, Z., K. Szente & J. Koch, 1994. Response of photosynthesis, stomatal conductance, water use efficiency and production to long-term elevated CO_2 in winter wheat. *Journal of Plant Physiology* 144: 661-668

Tuba, Z., K. Szente, Z. Nagy & J. Koch, 1994. Response of CO_2 assimilation, transpiration and water use efficiency to long-term elevated CO_2 in perennial C_3 xeric loes steppe species. *Journal of Plant Physiology* 148: 356-361

Unsworth, M.H. & W.E. Hogsett, 2004. *Combined effects of changing CO_2 temperature, UV-B radiation and O_3 on crop growth.*

Van Dam, J., 2004. *Food production and climate change in the Rhine basin.* Notitie Water Resources Group, Wageningen UR.

Van de Geijn, S.C. & J. Goudriaan, 2004. *The effects of elevated CO_2 and temperature change on transpiration and crop water use*. www.fao.org / docrep / W5183E.

Van de Geijn, S.C., J. Goudriaan & F Berendse (eds), 1993. *Climate Change; crops and terrestrial ecosystems.* Agrobiologische thema's 9, CABO-DLO, Wageningen.

Vesala, T., T. Ahonen, P. Hari, E. Krissinel & N. Shokhirev, 1996. Analysis of stomatal CO_2 uptake by a three-dimensional cylindrically symmetric model. *New Phytologist* 132: 235-245.

Wayne, P.M., E.G. Reekie & F.A. Bazzaz, 1998. Elevated CO_2 ameliorates birch response to high temperature and frost stress: implications for modeling climate-induced geographic range shifts. *Oecologia* 114: 335-342.

Weeda, E.J., R. Westra, Ch. Westra & T. Westra, 1988. *Nederlandse oecologische flora — Wilde planten en hun relaties 3.* De Lange en Van Leer, Deventer.

Witte, J.P.M., 2004. *Droogtestudie: bepaling ecologische effecten op terrestrische natuur.* Kiwa-rapport, Nieuwegein.

Wilson, K.B., T.N. Carlson & J.A. Bunce, 1999. Feedback significantely influences the simulated effect of CO_2 on seasonl evapotranspiration from two agricultural species. *Global Change Biology* 5: 903-917.

Wolf, J. & C.A. van Diepen, 1995. Effects of climate change on grain maize yield potential in the European community. *Climate Change* 29: 299-331.

Wolf, J. & M. van Oijen, 2003. Model simulation of effects of changes in climate and atmospheric CO_2 and O_3 on tuber yield potential of potato (cv. Bintje) in the European Union. *Agriculture, Ecosystems and Environment* 94: 141-157.

I List of symbols

a	Makkink constant (-)
A_n	net photosynthesis (mol m^{-2} s^{-1})
c_1	factor for the temperature effect (Table 1-1) (-)
c_1	factor for the CO_2-effect (-)
C	CO_2-concentration (mol m^{-3} or mol mol^{-1})
C_s	CO_2-concentration on the leaf surface (mol m^{-3} or mol mol^{-1})
e_0^*	saturated vapor pressure in the substomatal space (Pa)
e_s	vapor pressure in the atmosphere on the leaf surface (Pa)
e_s^*	saturated vapor pressure s on the leaf surface (Pa)
e_z	vapor in the atmosphere at height z (Pa)
e_z^*	saturated vapor in the atmosphere at height z (Pa)
E	evaporation (kg $m^{-2}s^{-1}$ or mm d^{-1})
ET	evapotranspiration (kg $m^{-2}s^{-1}$ or mm d^{-1})
ET_a	actual evapotranspiration (kg $m^{-2}s^{-1}$ or mm d^{-1})
ET_p	potential evapotranspiration (kg $m^{-2}s^{-1}$ or mm d^{-1})
ET_p^*	potential evapotranspiration from the vegetation, corrected for both the temperature effect and the CO_2 effect (kg $m^{-2}s^{-1}$ or mm d^{-1})
ET_{ref}	reference evapotranspiration according to Makkink (kg $m^{-2}s^{-1}$ or mm d^{-1})
f	crop factor (-)
F^T	share of transpiration in the evapotranspiration (-)
g_a	aerodynamic conductance (m s^{-1} or mol m^{-2} s^{-1})
g_c	minimum conductance of the epidermis of leaves with closed stomata (m s^{-1} or mol m^{-2} s^{-1})
g_s	stomatal or crop conductance (m s^{-1} or mol m^{-2} s^{-1})
$K?$	incoming shortwave (global) radiation (W m^{-2})
LAI	Leaf Area Index (-)
M_w	molecular mass of H_2O (kg mol^{-1})
Q	the available energy (~ net radiation energy) (W m^{-2})
r	diffusion resistance (s m^{-1})
r_a	aerodynamic resistance (s m^{-1})
r_g	crop resistance (s m^{-1})
r_s	stomatal resistance (s m^{-1})
R	universal gas constant (J $mol^{-1}K^{-1}$)
R_T	transpiration ratio (-)
s	temperature-dependant gradient of the saturated vapor pressure curve (Pa K^{-1})
S	transpiration sensitivities S for CO_2 rise, defined as the relative change in transpiration caused by a CO_2 rise of 100 ppm (-)
t	absolute temperature (K)
T	transpiration (kg $m^{-2}s^{-1}$ of mm d^{-1})
T_p	potential transpiration (kg $m^{-2}s^{-1}$ of mm d^{-1})
wue	water use efficiency (-)
a	Prienstly-Taylor constant (-)

? evaporation heat of water (J kg^{-1})
? temperature-dependant psychometric constant (Pa K^{-1})
O coupling factor (-)
ψ water potential (Pa)

II The transpiration share F^T

Mean decadal values of transpiration T (cm), evaporation E (cm), and transpiration share F^T (-), computed with the SWAP model for Potatoes, Grass, Maize and Wheat. Based on meteorological data from weather station De Bilt (1980-1990), and ideal soil conditions (not too wet, nor too dry).

Month	decade	Potatoes			Grass			Maize			Wheat		
		T	E	F^T	T	E	F^T	T	E	F^T	T	E	F^T
		cm	cm	(-)	cm	cm	(-)	cm	cm	(-)	cm	cm	(-)
Jan	1	0.00	2.67	0.00	2.21	0.51	0.81	0.00	2.67	0.00	0.00	2.67	0.00
	2	0.00	3.30	0.00	3.33	0.63	0.84	0.00	3.30	0.00	0.00	3.30	0.00
	3	0.00	3.91	0.00	3.56	0.79	0.82	0.00	3.91	0.00	0.00	3.91	0.00
Feb	4	0.00	5.31	0.00	4.87	1.10	0.82	0.00	5.31	0.00	0.00	5.31	0.00
	5	0.00	5.40	0.00	5.98	1.28	0.82	0.00	5.40	0.00	0.00	5.40	0.00
	6	0.00	4.24	0.00	5.51	1.29	0.81	0.00	4.24	0.00	0.00	4.24	0.00
Mar	7	0.00	6.95	0.00	6.03	1.74	0.78	0.00	6.95	0.00	0.00	6.95	0.00
	8	0.00	7.38	0.00	8.43	2.39	0.78	0.00	7.38	0.00	0.00	7.38	0.00
	9	0.00	10.73	0.00	11.31	3.39	0.77	0.00	10.73	0.00	0.00	10.73	0.00
Apr	10	1.53	7.49	0.17	12.89	3.48	0.79	0.00	7.71	0.00	0.70	7.65	0.08
	11	1.77	7.59	0.19	14.84	3.74	0.80	0.00	8.13	0.00	0.54	7.95	0.06
	12	2.27	7.18	0.24	17.37	4.16	0.81	0.00	7.50	0.00	0.89	7.31	0.11
May	13	3.29	8.41	0.28	19.41	4.41	0.81	0.17	9.11	0.02	3.15	8.30	0.28
	14	6.78	8.44	0.45	24.94	5.18	0.83	1.03	9.02	0.10	12.37	7.81	0.61
	15	8.55	9.35	0.48	25.60	5.43	0.83	0.85	10.20	0.08	25.07	5.91	0.81
Jun	16	9.63	10.30	0.48	21.45	5.66	0.79	3.85	11.65	0.25	24.73	2.43	0.91
	17	13.24	8.01	0.62	25.11	5.46	0.82	14.81	7.91	0.65	29.87	1.69	0.95
	18	13.70	8.76	0.61	22.18	5.34	0.81	24.55	6.03	0.80	26.35	1.21	0.96
Jul	19	25.30	6.24	0.80	25.91	5.82	0.82	32.52	5.08	0.86	30.70	1.66	0.95
	20	30.64	0.85	0.97	24.85	5.45	0.82	32.66	4.22	0.89	28.75	2.42	0.92
	21	33.24	0.10	1.00	27.06	6.20	0.81	36.70	3.95	0.90	20.33	7.18	0.74
Aug	22	29.78	0.23	0.99	24.10	5.05	0.83	33.11	3.13	0.91	2.42	8.72	0.22
	23	30.86	0.43	0.99	25.28	5.26	0.83	34.68	2.88	0.92	0.00	9.53	0.00
	24	26.69	0.69	0.97	22.04	5.41	0.80	30.18	2.33	0.93	0.00	12.01	0.00
Sep	25	19.32	0.67	0.97	15.89	4.23	0.79	21.81	1.82	0.92	0.00	9.51	0.00
	26	14.38	1.30	0.92	11.98	3.42	0.78	16.16	1.55	0.91	0.00	10.87	0.00
	27	11.28	2.87	0.80	10.58	2.90	0.78	14.37	1.38	0.91	0.00	8.95	0.00
Oct	28	1.19	8.09	0.13	9.60	2.52	0.79	12.74	1.24	0.91	0.00	8.52	0.00
	29	0.00	7.86	0.00	7.67	1.91	0.80	5.17	4.17	0.55	0.00	7.85	0.00
	30	0.00	7.10	0.00	6.19	1.50	0.80	0.00	7.07	0.00	0.00	7.09	0.00
Nov	31	0.00	4.22	0.00	4.58	0.91	0.83	0.00	4.24	0.00	0.00	4.22	0.00
	32	0.00	3.95	0.00	3.79	0.82	0.82	0.00	3.96	0.00	0.00	3.97	0.00
	33	0.00	3.21	0.00	2.89	0.59	0.83	0.00	3.19	0.00	0.00	3.19	0.00
Dec	34	0.00	2.11	0.00	2.45	0.49	0.83	0.00	2.13	0.00	0.00	2.13	0.00
	35	0.00	2.83	0.00	2.41	0.57	0.81	0.00	2.84	0.00	0.00	2.82	0.00
	36	0.00	2.97	0.00	2.99	0.69	0.81	0.00	2.93	0.00	0.00	2.96	0.00