

Effects of elevated atmospheric CO₂ on canopy transpiration in senescent spring wheat

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S. Grossman ^a, B.A. Kimball ^b, D.J. Hunsaker ^b, S.P. Long ^c, R.L. Garcia ^d, Th. Kartschall ^a, G.W.

Wall ^b, P.J. Pinter, Jr. ^b, F. Wechsung ^a, R.L. LaMorte ^b

^a *Potsdam Institute for Climate Impact Research, PO Box 60 12 03, 14412 Potsdam, Germany*

^b *USDA, Agricultural Research Service, U.S. Water Conservation Laboratory, Phoenix, Arizona
85040, U.S.A*

^c *University of Essex, Dept. of Biological Sciences, John Tabor Laboratories, Colchester, CO4
3SQ, U.K.; Brookhaven National Laboratory, Dept. of Applied Science, Building 318, Upton,
New York, U.S.A.*

^d *LI-COR, Inc., 4221 Superior Street, Lincoln, Nebraska 68504, U.S.A.*

*

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Abstract

The seasonal course of canopy transpiration and the diurnal courses of latent heat flux of a spring wheat crop were simulated for atmospheric CO₂ concentrations of 370 μmol mol⁻¹ and 550 μmol mol⁻¹. The hourly weather data, soil parameters and the irrigation and fertilizer treatments of the Free-Air Carbon Dioxide Enrichment wheat experiment in Arizona (1992/93) were used to drive the model. The simulation results were tested against field measurements with special emphasis on the period between anthesis and maturity.

A model integrating leaf photosynthesis and stomatal conductance was scaled to a canopy level in order to be used in the wheat growth model. The simulated intercellular CO₂ concentration, C_i , was determined from the ratio of C_i to the CO₂ concentration at the leaf surface, C_s , the leaf to air specific humidity deficit and a possibly unfulfilled transpiration demand. After anthesis, the measured assimilation rates of the flag leaves decreased more rapidly than their stomatal conductances, leading to a rise in the C_i/C_s ratio. In order to describe this observation, an empirical model approach was developed which took into account the leaf nitrogen content for the calculation of the C_i/C_s ratio.

Simulation results obtained with the new model version were in good agreement with the measurements. If changes in the C_i/C_s ratio accorded to the decrease in leaf nitrogen content during leaf senescence were not considered in the model, simulations revealed an underestimation of the daily canopy transpiration of up to twenty percent and a decrease in simulated seasonal canopy transpiration by ten percent. The measured reduction in the seasonal sum of canopy transpiration and soil evaporation owing to CO₂ enrichment, in comparison, was only about five percent.

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1. Introduction

A primary response of C₃-plants to elevated atmospheric CO₂ concentrations is an increase in the net assimilation rate and an associated decrease in the transpiration rate per unit leaf area (Morrison 1987, Kimball 1995). In order to simulate the cumulative effect of increasing atmospheric CO₂ on productivity and transpiration of ecosystems, short-term changes in stomatal conductance and photosynthesis as well as the longer term CO₂-fertilizer effect on plant and root growth have to be considered. Therefore detailed physiologically-based models of leaf photosynthesis and stomatal conductance (Farquhar and von Caemmerer 1982, Ball et al. 1987, Leuning et al. 1995a, Jacobs 1996) are now more frequently included in crop and forest growth models by means of spatial scaling from leaf to canopy level and temporal parameterization (Grant 1993, Amthor 1994, Nikolov et al. 1994, Friend et al. 1995, de Pury and Farquhar 1997).

In this study a model integrating leaf photosynthesis (Farquhar and von Caemmerer 1982) and stomatal conductance (Jacobs et al. 1996) was used in the wheat growth model DEMETER (Kartschall et al. 1995, Grossman et al. 1995) to simulate the response of a wheat crop to atmospheric CO₂ concentrations of 370 μmol mol⁻¹ and 550 μmol mol⁻¹. The simulated seasonal sum of canopy transpiration and soil evaporation as well as diurnal courses of latent heat flux were tested against field data which were obtained from the Free-Air Carbon Dioxide Enrichment (FACE)-wheat experiment in Arizona, USA (1992/93). Our emphasis was given to the period between anthesis and maturity.

Significant changes in the physiological properties of the wheat crop occur after anthesis and must be considered in the model for season-long simulations. During grain-filling, canopy photosynthesis declines as a result of the diminishing photosynthetic area (leaf area index). The

ribulose-1,5-bisphosphate (RuP₂) carboxylase/oxygenase (Rubisco) content decreases as chlorophyll and protein are remobilized from the aging leaves (Evans 1983). Associated changes in stomatal conductance, g_s , and mesophyll conductance, g_m , occur in the leaves of the aging canopy and might effectively contribute to limit photosynthesis by limiting the CO₂ concentration in the chloroplasts (Loreto 1994, Parkhurst 1994, Evans and von Caemmerer 1996).

Throughout most of the life of a leaf, the changes in g_s and g_m are in parallel, with the consequence that any increase in the intercellular CO₂ concentration, C_i , as a result of reduced photosynthetic capacity is countered by reduced stomatal conductance (Mott 1991). This observation is usually used to model the interaction of C_i , net assimilation rate, A_n , and g_s , even though it might not be cause-and-effect. Often C_i is back-calculated from the ratio of C_i to the CO₂ concentration at the leaf surface, C_s , which is assumed to be about 0.7 for C₃-plants and might be decreased by the leaf to air humidity deficit, D_s , and effects of plant hormones such as ABA, caused by short term water stress (Wong et al. 1979, Goudriaan 1986, Grant 1993, Jacobs 1996, Haxeltime 1997). In the model of Ball et al. (1987) and Leuning (1995b) the stomatal conductance for CO₂, g_{sc} , is related to A_n and C_s , but it was shown that the empirical model parameter a_1 in the equation $g_{sc}=g_0+a_1A_n/(C_s-\Gamma)(1+D_s/D_0)$ is related to the C_i/C_s ratio at saturating irradiance (Leuning et al. 1995a). The conductance has the value g_0 for $A_n=0$, and D_0 is another empirical model parameter.

Parallel reductions of g_s and g_m were observed in senescing wheat leaves during spike maturation (Loreto 1994). However, several studies reported a faster decline in mesophyll than in stomatal conductance of the flag leaves of field grown wheat plants after anthesis (Araus et al. 1986; Atkinson et al. 1989, Davies and Pereira 1992) leading to a continuous increase in the C_i/C_s ratio and a reduced stomatal sensitivity to increasing C_i (Evans 1983). Evans (1986) showed that

the C_i/C_s ratio was about 0.67 for young flag leaves of *Triticum aestivum* and remained close to this until senescence began when C_i/C_s rose to 1 almost linearly with the decreasing leaf nitrogen content.

A similar behaviour was found during the FACE-wheat experiment, where a stronger decline in the assimilation rates of the flag leaves of *Triticum aestivum* L. cv Yecora Rojo than in stomatal conductance after anthesis indicated a rise in the C_i/C_s ratio during flag leaf senescence (Garcia et al. 1998). In parallel, the daily sum of canopy transpiration and soil evaporation increased since leaf area index and g_s remained high while the transpiration demand increased due to changing weather conditions (Hunsaker et al. 1996). At the very end of the growing season a rapid decrease in canopy transpiration was caused by the diminishing leaf area index.

In this paper it will be shown that the consideration of asynchronous changes in mesophyll and stomatal conductance in the model has a significant influence on the simulated canopy transpiration during grain-filling and is essential for describing the effect of elevated atmospheric CO_2 on canopy transpiration. Based on the data of Evans (1986) a new model approach was developed, which calculates the C_i/C_s ratio as a function of the leaf nitrogen content. Observed increases in C_i/C_s not only due to age but nutritional status leading to lower photosynthetic rates can be described. Causality is not included in the model, since the nature of the interaction between g_s and g_m is not clear (Loreto 1994).

2. Materials and Methods

2.1. Model description

The wheat model DEMETER includes submodels for the simulation of soil water and nitrogen content, soil temperature dynamics, plant and root growth as well as energy fluxes and assimilation rates. All submodels use an hourly simulation time step. The ability of DEMETER to describe such canopy properties as phenology, leaf area index and biomass under ambient and elevated atmospheric CO₂ during the entire growing season was shown in a previous study (Kartschall et al. 1995).

By means of a 'big-leaf' model, canopy temperature, T_c , transpiration and energy fluxes are calculated as explicit functions of the atmospheric boundary conditions (measured hourly air temperature, vapour pressure, wind velocity and CO₂ concentration at a reference height 2m above ground, solar radiation, precipitation) and of physiological variables which are supplied by the growth model (leaf area index, canopy height, root density distribution). The assumption is made that the whole canopy is exposed to the same microclimate, which is sufficient to simulate canopy processes (Raupach and Finnigan 1988). Therefore, calculated CO₂ concentration, air temperature, vapour pressure and T_c are taken as being constant throughout the canopy. It is assumed further that the light intensity profile is the main cause of variations of the assimilation rates and g_s inside the canopy.

The amount of photosynthetic and near infrared radiation entering the canopy is divided into direct and diffuse light (Spitters et al. 1986) and is assumed to decrease exponentially within the canopy and with different extinction coefficients. The amount of direct and diffuse radiation to which sunlit and shaded leaves are exposed is determined. The fraction of sunlit leaf area at any

particular level inside the canopy is equal to the fraction of leaves intercepting direct light at that level. The fraction of shaded leaves is the difference between one and the fraction of sunlit leaves. A spherical leaf angle distribution is assumed.

The five-point Gaussian integration method (Bronstein and Semiendjajev 1981) is applied at different levels inside the canopy, which vary with changes in the simulated leaf area index to keep canopy layer thicknesses less than or equal to half a leaf layer (Stockle 1991). It was shown by Goudriaan (1986) that the Gaussian integration method provides an accurate and fast numerical method to calculate the light intensity profiles inside crop canopies.

The model of Farquhar and von Caemmerer (1982) is applied to calculate the assimilation rates for the sunlit and shaded leaf fractions of each layer. Activation energies to describe the temperature response of the kinetic constants of Rubisco are taken from Long (1991). The summation of the assimilation rates for each layer results in the canopy CO₂ assimilation rate. The maximum capacity of RuP₂ carboxylation per unit leaf area, V_{Cmax} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), is expressed as a function of the simulated or measured leaf nitrogen content, N_l (mmol N m^{-2}):

$$V_{Cmax} = 1.25 k_t k_{cat} f_{Rub} N_l \quad (1)$$

where the factor 1.25 is the number of mmoles of Rubisco reaction sites per mole nitrogen in Rubisco, k_t is a dimensionless temperature coefficient (1.0 at 25°C), k_{cat} is the catalytic constant for RuP₂ carboxylation ($3.3 \text{ mol CO}_2 \text{ mol}^{-1} \text{ s}^{-1}$), f_{Rub} is the fraction of leaf nitrogen contained in Rubisco (0.23, Evans et al.1989). The potential rate of electron transport per unit leaf area, J_{max} ($\mu\text{mol m}^{-2} \text{ s}^{-1}$), is calculated from the fixed ratio $J_{max}/V_{Cmax}=2.1$ at 25°C (Wullschlaeger 1993).

The CO₂ compensation point, Γ ($\mu\text{mol mol}^{-1}$), in the presence of day respiration, R_d , is calculated by

$$\Gamma = \frac{\Gamma_* + K_c(1 + O_i/K_o)R_d/V_{C_{\max}}}{1 - R_d/V_{C_{\max}}} \quad (2)$$

with

$$\Gamma_* = \frac{0.5V_{O_{\max}}K_cO_i}{V_{C_{\max}}K_o} \quad (3)$$

where Γ_* is the CO₂ compensation point in the absence of day respiration, K_c and K_o are the Michaelis-Menten constants for CO₂ ($\mu\text{mol mol}^{-1}$) and O₂ (mmol mol^{-1}) respectively, O_i is the intercellular concentration of O₂ (mmol mol^{-1}) and $V_{O_{\max}}$ is the maximum RuP₂ saturated rate of oxygenation ($0.21 V_{C_{\max}}, \mu\text{mol m}^{-2} \text{s}^{-1}$). The equations for calculating the RuP₂-saturated and RuP₂-limited rates of CO₂ assimilation are well-known (Farquhar and von Caemmerer 1982) and are not repeated here.

$V_{C_{\max}}$ can respond to elevated atmospheric CO₂ in the model in different ways. The leaf nitrogen concentration can be reduced under elevated atmospheric CO₂ (Hocking and Meyer 1991, Conroy 1992) resulting in lower $V_{C_{\max}}$ values at the same phenological stage. CO₂-induced stomatal closure and an increase in T_c under elevated atmospheric CO₂ as measured and simulated for spring wheat (Kimball et al. 1995, Grossman et al. 1995) can affect $V_{C_{\max}}$ via its temperature response.

The simulated CO₂ concentration in the chloroplasts, C_c ($\mu\text{mol mol}^{-1}$), which is used to calculate the assimilation rates, is determined from:

$$C_c = C_i - \frac{A_{n,c}}{g_m L} \quad (4)$$

where $A_{n,c}$ is the net canopy CO₂ assimilation rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). The leaf mesophyll conductance g_m ($\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) characterizes the transport of CO₂ inside the leaves from the intercellular airspaces to the sites of carboxylation in the chloroplasts. The calculation of g_m is based on the evidence of a strong correlation between g_m and photosynthetic capacity which was found for young as well as aging wheat leaves, where both photosynthetic capacity and g_m declined in parallel (von Caemmerer and Evans 1991, Evans and von Caemmerer 1996, Loreto et al. 1994) and is defined as follows (Amthor 1994):

$$g_m = \frac{V_{C_{\max}}}{200 + V_{C_{\max}}} \quad (5)$$

The reduction of $V_{C_{\max}}$ during canopy aging due to the reduction of the simulated leaf nitrogen content leads to a decrease in A_n and g_m after anthesis.

According to the approach of Goudriaan (1986) and Jacobs (1994 and 1996) C_i is calculated from the ratio $f = (C_i - \Gamma) / (C_s - \Gamma)$, which depends on the difference between the saturation specific humidity at leaf temperature and the specific humidity of the air at the leaf surface, D_s (g kg^{-1}). This approach was modified by introducing an independent water stress effect, which is caused

by soil moisture depletion leading to a possible unfulfilled transpiration demand:

$$f = \frac{C_i - \Gamma}{C_s - \Gamma} = f_{\max} (1 - D_s / D_{\max}) (E_c / E_{\max}) + f_{\min} (D_s / D_{\max}) \quad (6)$$

where f_{\max} is the value of f at $D_s=0$, D_{\max} is the value of D_s where the stomata are assumed to close completely (50 g kg^{-1}), E_c is the canopy transpiration rate ($\text{kg m}^{-2} \text{ s}^{-1}$) and E_{\max} is the potential canopy transpiration rate ($\text{kg m}^{-2} \text{ s}^{-1}$). The term f_{\min} is the value of f at D_s greater than or equal to D_{\max} and accounts for the cuticular conductance, g_c , for CO_2 ($0.01 \text{ mol m}^{-2} \text{ s}^{-1}$, Körner 1994):

$$f_{\min} = g_c / (g_c + g_m) \quad (7)$$

The effects of the CO_2 concentration (Goudriaan et al. 1985, Mott 1988) and day respiration on the C_i/C_s ratio are described by eq. (6). In agreement with experimental results which showed that f has a value of 0.7 to 0.8 at $D_s=10 \text{ g kg}^{-1}$ for C_3 -plants (Goudriaan and Van Laar 1978, Wong et al. 1979), f_{\max} is determined by the relationship:

$$f_{\max} = (f_0 - f_{\min} (D_0 / D_{\max})) / (1 - D_0 / D_{\max}) \quad (8)$$

where f_0 has the value 0.7 and D_0 is a specific humidity deficit of 10 g kg^{-1} .

The C_i/C_s ratio was observed to vary with age and nutritional status of the plants with C_i/C_s being greater in plants with lower photosynthetic rates (Farquhar and Wong 1984). Under ample water supply and a specific humidity deficit small enough that stomata were not affected, Evans

(1986) showed that the C_i/C_s ratio was about 0.67 for young flag leaves of *Triticum aestivum* and remained close to this until senescence began, when C_i/C_s rose to 1 almost linearly with the decreasing leaf nitrogen content. Based on these data, f_0 in eq. (8) is calculated as a linear function of N_l :

$$f_0 = \alpha(N_l - N_r) + b \quad (9)$$

where N_r is the residual non-remobilizable leaf nitrogen content (mmol N m^{-2}), for which C_i/C_s is assumed to be one. According to van Keulen and Seligman (1987) N_r is a function of the phenological stage of the crop and varies between 25 mmol m^{-2} at the beginning and 5 mmol m^{-2} at the end of the season. The values of the empirical parameters α and b depend on N_l and are given in Table 1.

Taking into account the CO_2 concentration gradient between C_s and C_i and the effect of an increased assimilation rate on stomatal conductance, transient effects of elevated atmospheric CO_2 on energy fluxes and transpiration rate are described. Canopy conductance $g_{s,c}$ ($\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$) for the transport of water vapour from inside to outside the canopy leaves is given by:

$$g_{s,c} = \frac{1.6 A_{n,c}}{(C_s - C_i)} \quad (10)$$

The CO_2 concentration at the big-leaf surface, C_s , is calculated from the CO_2 concentration at reference height, C_r , by means of

$$C_s = C_r - A_{n,c} P_a (1.37 / g_{b,c} + 1.4 r_a) \quad (11)$$

where P_a is the atmospheric pressure (Pa), $g_{b,c}$ is the canopy boundary layer conductance (mol H₂O m⁻²s⁻¹) and r_a is the aerodynamic resistance (m² s¹ mol⁻¹ H₂O). The stability correction of r_a is calculated according to Choudhury (1986) for stable conditions and Mahrt and Ek (1984) for unstable conditions.

The latent heat of transpiration or dew formation, λE_c (Wm⁻²), as part of the canopy energy balance equation is given by:

$$\lambda E_c = \rho_a c_p V_m (e_s - e_a) / (\gamma (1 / (g_{s,c} + 1.6 g_c L) + 1 / g_{b,c})) \quad (12)$$

where λ is the latent heat of vapourization (J kg⁻¹), ρ_a is the air density (kg m⁻³), c_p is the heat capacity of the air (J kg⁻¹K⁻¹), e_s is the saturation vapour pressure at canopy temperature (Pa), γ is the psychrometric constant (J m⁻³ K⁻¹) and V_m is the molar volume ($V_m = RT_a / P_a$, m³ mol⁻¹ where $R = 8.314$ Pa m³ mol⁻¹ K⁻¹, molar gas constant) to convert the conductances from units of (mol m⁻² s⁻¹) to (m s⁻¹).

Latent heat of soil evaporation λE_s (W m⁻²) is given by:

$$\lambda E_s = \rho_a c_p V_m (e_s - e_a) / (\gamma (1 / g_{s,s} + 1 / g_{b,s})) \quad (13)$$

where e_s is the saturation vapour pressure at soil surface temperature (Pa), $g_{s,s}$ is the soil surface

conductance ($\text{mol m}^{-2}\text{s}^{-1}$) and $g_{b,s}$ is the soil boundary layer conductance for water vapour ($\text{mol m}^{-2}\text{s}^{-1}$). The canopy and soil boundary layer conductances as well as $g_{s,s}$ are calculated according to Goudriaan (1977). The vapour pressure inside the canopy, e_a (Pa), is calculated from:

$$E_c + E_s = \rho_a c_p V_m (e_a - e_r) / (\gamma \lambda r_a) \quad (14)$$

where e_r is the vapour pressure at reference height (Pa).

A coupled equation system, containing the canopy energy balance equation, the biochemical equations for determining the assimilation rates in each layer, the equations for calculating the various CO_2 concentrations, the micrometeorological variables inside the canopy as well as $g_{s,c}$ has to be solved for every simulation time step. The energy balance equation of the canopy is an ordinary differential equation of the canopy temperature, T_c , and is solved by means of the Newton-Raphson iteration. The iteration stops if T_c does not change more than 0.05 K per iteration step or the residuum of the canopy energy balance is less than 30 W m^{-2} .

The soil surface temperature and soil water content from the previous time step are used for solving the energy balance equation of the canopy. After iteration the various water fluxes are used to update the current sinks of the soil water model, which includes the solution of the Richards' equation by means of an explicit procedure. The energy balance of the soil surface is also the upper boundary condition for solving the soil heat conductivity equation.

2.2. Field experiment

The FACE wheat experiment was conducted on a field at the Maricopa Agricultural Center of the University of Arizona, about 50 km south of Phoenix in the midst of an extensive agricultural region (33.07° N latitude, 111.98° W longitude, 358-m altitude), to investigate the effects of elevated atmospheric CO₂ on field grown wheat (Kimball et al. 1995, Pinter et al. 1996, Hunsaker et al. 1996). Spring wheat was sown in December 1992 and harvested in late May 1993. FACE apparatus was used to enrich the air to about 550 μmol·mol⁻¹ in four 25m diameter circular plots. Four replicate control rings at ambient atmospheric CO₂ were also installed. Half of each plot was subject to a water-stress treatment. This study reports only on the plants grown with adequate water, which were irrigated when the available water in the root zone was depleted by 70%. The cumulative irrigation total between crop emergence and harvest was 600mm. Cumulative rainfall during the same period was 76 mm. Irrigation water and fertilizer were delivered through a subsurface drip system. The wheat crop received 277 kg N ha⁻¹. CO₂ enrichment began shortly after emergence, continuing until shortly before harvest and was in operation 24 hours a day. During the experiment, it was possible to control atmospheric CO₂ concentration in the FACE arrays to 550 ± 20% for most of the time (Hendrey et al. 1993).

Micrometeorological variables were recorded from instrumentation scanned every minute using a data logging system (Campbell Scientific, Logan, UT; Model CR7X). Diurnal changes in the sum of canopy transpiration and soil evaporation were determined as a residual in the energy balance (Kimball et al. 1994), i.e. as the difference between net radiation of the canopy, soil heat flux and sensible heat flux. Net radiation was measured with duplicate net radiometers (Radiation Energy Balance System, Seattle, WA; Model Q6) and soil heat flux was determined

by soil heat flux plates (Radiation Energy Balance System, Seattle, WA; Model HFT-3). Sensible heat flux was determined by measuring the temperature difference between the crop surface and the air and then dividing the temperature difference by an aerodynamic resistance calculated from a measurement of wind speed (R.M. Young Co., Traverse City, MI; Model 12170C 3-cup anemometer with photochopper) at the 2-m height at one position in the field. The air temperature was measured at the 2-m height in each plot with an aspirated psychrometer. Crop surface temperature was measured with duplicate infrared thermometers (Everest Interscience, Fullerton, CA; IRT Model 4000AL, 15° field of view) mounted above each plot to view the canopy toward north at an angle of 20° below horizontal.

Daily and seasonal sum of canopy transpiration and soil evaporation were determined by measuring the change in soil water over a period of time and calculating the soil water balance for those periods between soil water measurements where rainfall was small (less than 10 mm), irrigation water was not applied, and where deep percolation could be reasonably assumed negligible, i.e. waiting at least two days after irrigation or heavy rainfall before taking the water content measurements. Volumetric soil water contents were measured in each plot using Time-Domain Reflectometry (TDR) and neutron scattering equipment. A 2-m-long neutron probe access tube was installed vertically in the plant row, 0.9 m from the TDR probe, and with the same placement as the TDR probe relative to the drip emitters. A neutron moisture gauge, calibrated at the field site, was used to measure volumetric soil water contents in 0.2-m intervals from 0.4 to 2.0 m. Water contents were measured about once every week from crop emergence through the first regular irrigation. After that, water contents were measured every two to five days depending on the frequency of irrigation.

Wheat plants were sampled at 7-to10-day intervals. A minimum of six plants was obtained

from four sampling zones in each plot. Leaf area index was computed from specific leaf weight of a subsample of 12 median-sized plants per plot, green leaf biomass of all plants, and plant density. Leaf nitrogen analysis was done by the micro-Kjeldahl procedure from the same subsample.

Measurements of photosynthesis as well as determination of the C_i/C_s ratios at an individual leaf level were conducted by using LI-COR Model 6200 photosynthesis systems (LI-COR, Inc., Lincoln, NE) that were equipped with 0.25 l cuvettes and moved between subplots from dawn until dusk at ~2 week intervals from February until crop harvest.

The maximum capacity of RuP₂ carboxylation, $V_{C_{max}}$, was determined from the initial, linear slope of the response curve of light-saturated photosynthesis to variation in C_i after the method of Wullschlegel (1993) and the temperature correction of Harley et al. (1992). The $A-C_i$ response curve was determined by using fully controlled micro-environment cuvettes incorporated into two open gas exchange systems (MPH-1000 Plant Gas Exchange System, Campbell Scientific, Logan, Utah). Each system contained an infra-red CO₂/H₂O analyzer (IRGA; LI-6262, LI-COR, Inc.), calibrated for CO₂ using gravimetrically prepared calibration mixture of CO₂ in air ($\pm 1\%$, "Primary Standard", Matheson Gas Products, Inc., Cucamonga, California), and for water vapour with a dew point generator (LI-610, LI_COR, Inc.). Leaf temperature was maintained at 22.5 ± 0.1 °C.

2.3. Simulation experiment

The model DEMETER was applied from 15 January to 15 May 1993. Simulations were made for atmospheric CO₂ concentrations of 370 μmol mol⁻¹ (ambient CO₂) and 550 μmol mol⁻¹ (elevated CO₂) with two different versions of the model, in which the C_i/C_s ratio was either a function of N_l according to eq. (9), or not.

The measured hourly air temperature, humidity, wind velocity, solar radiation and precipitation as well as fertilizer and irrigation treatments were used as input data for the model (Fig. 1). The physical characteristics of the soil (saturated hydraulic conductivity, wilting point, field capacity, albedo, particle density) were taken from Kimball et al. (1993). The RETC Code of van Genuchten et al. (1992) was applied to fit the soil water retention curve through the data points and to calculate soil hydraulic conductivity and water diffusivity. The applied drip irrigation was modeled by means of a water source at a soil depth of 0.2 m, which could be enriched with fertilizer. Significant water stress caused by a lack of soil moisture was excluded since the irrigations were scheduled according to the transpiration demand of the crop. Water stress was not detected in the simulations. All state variables and rates were calculated for every hour for the entire growing season.

Since the data were available, the measured leaf nitrogen content on dates 1/2/93, 24/2/93, 7/4/93, 25/4/93 and 12/5/93 was used for the simulations. Leaf nitrogen contents between the measurements were obtained by linear interpolation.

3. Results and Discussion

3.1. Photosynthesis and stomatal conductance

The seasonal courses of the simulated and measured values of V_{Cmax} of the flag leaves at 22.5°C are shown in Fig. (2). Both measured and simulated data show the decrease in V_{Cmax} after anthesis due to a drop in N_l (Fig. 3), but the values of V_{Cmax} for ambient CO₂ are overestimated during grain filling. The assumption of an unchanged ratio of Rubisco capacity to leaf nitrogen content for the whole growing season, as used in the model, might be inaccurate. A decrease of Rubisco content during the same experiment was shown by Nie et al. (1995). The standard deviations for the measurements of the leaf nitrogen content were less than 8 mmol m⁻² for all data points.

The simulated seasonal courses of the C_i/C_s ratio of the flag leaves at 12 noon as well as the measured data on dates 16/3/93, 30/3/93, 9/4/93, 15/4/93 and 28/4/93 are given in Fig. (4). The simulated C_i/C_s ratio rose after anthesis in both versions of the model. This was caused by an increase in the simulated respiration due to its temperature response and the development of heads. Higher respiration rates resulted in a higher simulated CO₂ compensation point as well as C_i/C_s ratios. However, the increase in the C_i/C_s ratio due to the increase in respiration could not account completely for the observed values after anthesis. Good results were achieved when considering N_l in the calculation of the C_i/C_s ratio, but it was still underestimated for ambient CO₂. The C_i/C_s ratio might be dependent on the carboxylation capacity rather than on N_l , which was not investigated in this study. Also, there is a wide range in the measured values of the C_i/C_s ratio dependent on N_l in the data of Evans (1986) and the parameters a and b in equation (9) might not describe the behavior of a particular plant.

The corresponding measured and simulated net assimilation rates and stomatal conductances of the flag leaves for the same dates are given in Fig.(5). In accordance with the decrease in $V_{C_{max}}$, the simulated and measured net assimilation rates decreased after anthesis until the end of April by about 50%, whereas g_s remained high. The standard deviations for the measured net assimilation rates and stomatal conductances were less than $1.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $0.08 \text{ mol m}^{-2} \text{s}^{-1}$ respectively. Simulated and measured A_n were in good agreement for ambient and elevated CO_2 . The simulated stomatal conductances were lower for elevated than for ambient CO_2 , as expected from CO_2 induced stomatal closure, but g_s was significantly underestimated for ambient CO_2 . A significant drop in C_c at the end of the season was not simulated, since A_n and g_m declined in parallel.

3.2. Canopy transpiration

The observed daily sum of E_C and E_S increased after anthesis (4 April 1993) for both ambient and elevated CO_2 (Fig. 6, but shown only for elevated CO_2). The decline in canopy transpiration at the end of the season (starting at about 28 April 1993) was caused by the decrease in leaf area index (Fig. 7). The simulated daily sum of E_C and E_S was in good accordance with the observations for both model versions until anthesis. After anthesis, it was underestimated by about 25% if the influence of the leaf nitrogen content on the C_i/C_s ratio was not considered in the model. This underestimation of the canopy transpiration had a significant influence on the prediction of the seasonal sum of E_C and E_S . The difference between the measured and simulated values increased continuously to about 51mm (ambient CO_2) and 61mm (elevated CO_2) at 5 May 1993 when using a C_i/C_s ratio independent of N_l in the model (Fig. 8). This corresponds to a 9.3%

and 12% deviation respectively. The simulated seasonal sum of E_C and E_S was 12% lower for elevated than for ambient CO_2 . However, the simulation results obtained with the new model version were in good agreement with the measurements. The reduction in the seasonal sum of E_C and E_S owing to CO_2 enrichment was calculated as 8%. This corresponds better with the measured value, which was 5.3% (Hunsaker 1996) and can be explained mainly by the differences in leaf area index between the ambient elevated CO_2 plots at the end of the season. The reduction in the seasonal sum of E_C and E_S accorded to enriched CO_2 was smaller than deviations due to changes in the C_i/C_s ratio during grain filling.

The simulated and measured diurnal courses of latent heat fluxes are given for elevated CO_2 in Fig. (9) for the representative dates of 5/4/93, 15/4/93, 28/4/93 and 5/5/93. The data shown are the averages of data obtained from four different plots with standard deviations less than 40 W m^{-2} . The deviations between the calculated fluxes and the measurements increased later in the season to 50% when using a C_i/C_s ratio independent of the leaf nitrogen content in the model. Good agreement between simulation results and recorded data were achieved with the new model version.

The impact of deviations in the simulated transpiration accorded to the different model versions on the canopy temperature was investigated. The two model versions disagreed in simulated canopy temperature by up to 2K. Many metabolic and physiological processes such as photosynthesis, respiration and phenology depend upon canopy temperature in the model. An increased simulated temperature can affect these processes significantly, depending on the temperature-response curves. The maximum capacity of RuP₂ carboxylation V_{Cmax} for example would change by about 20% with a change in temperature of 2K.

The results of this study show that the reduced sensitivity of g_s to changes in C_i after anthesis

resulted in a decoupling of A_n and g_s and lead to a reduction in water use efficiency, i.e. the ratio of the amount of carbon fixed photosynthetically to the amount of water lost due to transpiration. There is evidence that stomatal function is not degraded until the very late stages of senescence to preserve the integrity of leaf function (Field 1987). According to Thimann and Satler (1982), maintaining open stomata might be paralleled by a significant delay of senescence, which would prolong the grain-filling period and support higher grain yields.

Another phenomenological explanation was suggested by Atkinson et al. (1989), who measured a decline in water use efficiency of old wheat leaves which was caused by the decoupling of A_n and g_s during leaf senescence. Mature wheat leaves should act as sensors and regulators of the plant/environment water balance through control of whole plant levels of abscisic acid. This is achieved by water loss from old leaves which is primarily influenced by energy balance. However, calculating E_C and E_S as a function of the canopy and soil energy balance only lead to a significant overestimation of seasonal transpiration in the model.

The applicability of a model which relates A_n and g_s in the wheat growth model DEMETER was limited after anthesis by asynchronous changes in photosynthetic capacity, g_m and g_s . Appropriate seasonal parameter changes had to be made to describe the relation between leaf conductance and net assimilation rate during grain filling.

4. Summary and Conclusions

In this study it was shown that the seasonal variations of the physiological parameters concerning photosynthesis and stomatal conductance in the wheat growth model DEMETER had a significant impact on the simulated annual water balance and the ability of the model to describe the response of the crop's water balance to elevated CO₂. The applicability of a model relating A_n and g_s was limited by asynchronous seasonal changes in A_n and g_s after anthesis. By means of the calculation of the C_i/C_s ratio depending on the leaf nitrogen content, canopy transpiration could be simulated in good agreement with the measurements during grain filling.

Although the focus in this study was on a particular spring wheat crop, most of the factors discussed also apply to other terrestrial ecosystems and can support the identification of sensitive parameters for long-term simulation studies more generally. Systematic investigations of the causality in the relationship between A_n , g_m and g_s during leaf senescence are necessary to be able to define causality in the model approach.

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Appendix

Definition of symbols

<i>Term</i>	<i>Units</i>	<i>Definition</i>
A_n	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Net leaf rate of CO ₂ uptake per unit leaf area
$A_{n,c}$	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Net canopy rate of CO ₂ uptake per unit ground area
c_p	$\text{J kg}^{-1} \text{K}^{-1}$	Heat capacity of the air
C_c	$\mu\text{mol mol}^{-1}$	CO ₂ concentration in the chloroplasts
C_i	$\mu\text{mol mol}^{-1}$	Intercellular CO ₂ concentration in air
C_s	$\mu\text{mol mol}^{-1}$	CO ₂ concentration at the leaf surface
C_r	$\mu\text{mol mol}^{-1}$	CO ₂ concentration at reference height
D_{max}	g kg^{-1}	Value of D_s where stomata close completely
D_s	g kg^{-1}	Specific humidity deficit at leaf surface
e_a	Pa	Vapour pressure inside the canopy
e_r	Pa	Vapour pressure at reference height
e_s	Pa	Saturation vapour pressure at T_c or soil surface temperature
E_c	$\text{kg m}^{-2} \text{s}^{-1}$	Canopy transpiration rate per unit ground area
E_{max}	$\text{kg m}^{-2} \text{s}^{-1}$	Potential transpiration rate per unit ground area
E_s	$\text{kg m}^{-2} \text{s}^{-1}$	Soil evaporation rate per unit ground area
f	-	$(C_i - \Gamma)/(C_s - \Gamma)$
f_{max}	-	$(C_i - \Gamma)/(C_s - \Gamma)$ at $D_s = 0$
f_{min}	-	$(C_i - \Gamma)/(C_s - \Gamma)$ at $D_s = D_{max}$

f_0	-	$(C_r - \Gamma)/(C_s - \Gamma)$ at $D_s \leq 10 \text{ g kg}^{-1}$, $E = E_{max}$ and depending on N_l
f_{rub}	-	Fraction of leaf nitrogen content contained in Rubisco (0.23)
$g_{b,c}$	$\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$	Canopy boundary layer conductance for H_2O per unit ground area
$g_{b,s}$	$\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$	Soil boundary layer conductance for H_2O
g_c	$\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	Leaf cuticular conductance for CO_2 per unit leaf area
g_m	$\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	Leaf mesophyll conductance for CO_2 per unit leaf area
g_s	$\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$	Leaf stomatal conductance for H_2O per unit leaf area
g_{sc}	$\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$	Leaf stomatal conductance for CO_2 per unit leaf area
$g_{s,c}$	$\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$	Canopy conductance for H_2O per unit ground area
$g_{s,s}$	$\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$	Soil surface conductance for H_2O
J_{max}	$\mu\text{mol m}^{-2} \text{ s}^{-1}$	Potential rate of electron transport per unit leaf area (2.1 V_{Cmax} at 25°C)
K_c	$\mu\text{mol mol}^{-1}$	Michaelis Menten constant for CO_2 (460)
k_{cat}	$\text{mol CO}_2 \text{ mol}^{-1} \text{ s}^{-1}$	Catalytic constant for RuP ₂ carboxylation (3.3)
K_o	mmol mol^{-1}	Michaelis Menten constant for O_2 (330)
k_t	-	Temperature coefficient for V_{Cmax}
N_l	mmol N m^{-2}	Leaf nitrogen content
N_r	mmol N m^{-2}	Residual leaf nitrogen content
O_i	mmol mol^{-1}	Intercellular concentration of O_2 in air (210)
P_a	Pa	Atmospheric air pressure

r_a	$\text{m}^{-2} \text{s}^{-1} \text{ mol H}_2\text{O}$	Aerodynamic resistance
R	$\text{Pa m}^3 \text{ mol}^{-1} \text{ K}^{-1}$	Molar gas constant (8.314)
R_d	$\mu\text{mol m}^{-2} \text{ s}^{-1}$	Leaf day respiration per unit leaf area
T_a	$^{\circ}\text{C}$	Air temperature inside the canopy
T_c	$^{\circ}\text{C}$	Canopy temperature
T_r	$^{\circ}\text{C}$	Air temperature at a reference height of 2m
V_{Cmax}	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	Maximum capacity of RuP ₂ carboxylation per unit leaf area
V_{Omax}	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	Maximum capacity of RuP ₂ oxygenation per unit leaf area ($0.21 V_{Cmax}$)
V_m	$\text{m}^3 \text{ mol}^{-1}$	Molar volume
γ	$\text{J m}^{-3} \text{ K}^{-1}$	Psychrometric constant
Γ	$\mu\text{mol mol}^{-1}$	CO ₂ compensation point of photosynthesis
Γ^*	$\mu\text{mol mol}^{-1}$	CO ₂ compensation point of photosynthesis in the absence of R_d
λ	J kg^{-1}	Latent heat of vaporization
ρ	Kg m^{-3}	Air density

α (mmol ⁻¹ m ²)	b	N_l (mmol m ⁻²)
-0.00073	0.79	$N_l > 100$
-0.00167	0.875	$100 \geq N_l > 80$
-0.00313	1.0	$80 \geq N_l$

Table 1: Values of the empirical parameters a and b , which are used in the model to calculate the C_i/C_s ratio depending on the leaf nitrogen content, N_l , according to eq. (9). Parameters were obtained from a curve fit through data of Evans (1986).

Figure Captions

Figure 1

Measured daily (a) total incoming solar radiation, (b) minimum and maximum of air temperature, (c) average wind speed and (d) minimum and maximum of vapour pressure deficit for the growing season 1993 (15 Jan to 15 May).

Figure 2

Seasonal variation (15 Jan to 15 May 1993) of the maximum capacity of RuP₂ carboxylation, V_{Cmax} , at 22.5°C for the flag leaves of wheat plants grown in elevated CO₂ (• measured, — simulated) and ambient CO₂ (o measured, --- simulated)

Figure 3

Leaf nitrogen content, N_l , of wheat for five days of the growing season 1993 for plants grown in elevated CO₂ (• measured) and ambient CO₂ (o measured).

Figure 4

Seasonal variation (15 Jan to 15 May 1993) of the ratio of C_i/C_s at 12 noon for the flag leaves of wheat plants grown in elevated CO₂ (• measured, — simulated with C_i/C_s dependent and --- not dependent on N_l) and ambient CO₂ (o measured, --- simulated with C_i/C_s dependent on N_l).

Figure 5

(a) Net leaf photosynthetic CO₂-uptake, A_n , and (b) stomatal conductance, g_s , for the flag leaves of wheat at 12 noon for five days of the growing season 1993 for plants grown in elevated CO₂ (• measured, + simulated) and ambient CO₂ (o measured, Δ simulated).

Figure 6

Seasonal variation (15 Jan to 15 May 1993) of leaf area index of wheat plants grown in elevated CO₂ (• measured, --- simulated) and ambient CO₂ (o measured).

Figure 7

Seasonal variation (15 Jan to 15 May 1993) of the daily sum of canopy transpiration and soil evaporation, E , of a wheat crop grown in elevated CO₂ (• measured, — simulated with C_i/C_s dependent and --- not dependent on N_i).

Figure 8

Seasonal variation (15 Jan to 15 May 1993) of the cumulative sum of canopy transpiration and soil evaporation, E , of a wheat crop grown in (a) elevated CO₂ (• measured, — simulated with C_i/C_s dependent and --- not dependent on N_i) and (b) ambient CO₂ (o measured and simulated: — C_i/C_s dependent and, --- not dependent on N_i).

Figure 9

Diurnal variation of latent heat flux, λE , of a wheat crop grown in elevated CO_2 on four days during the 1993 growing season (\bullet measured, — simulated with C_i/C_s dependent and --- not dependent on N_i).

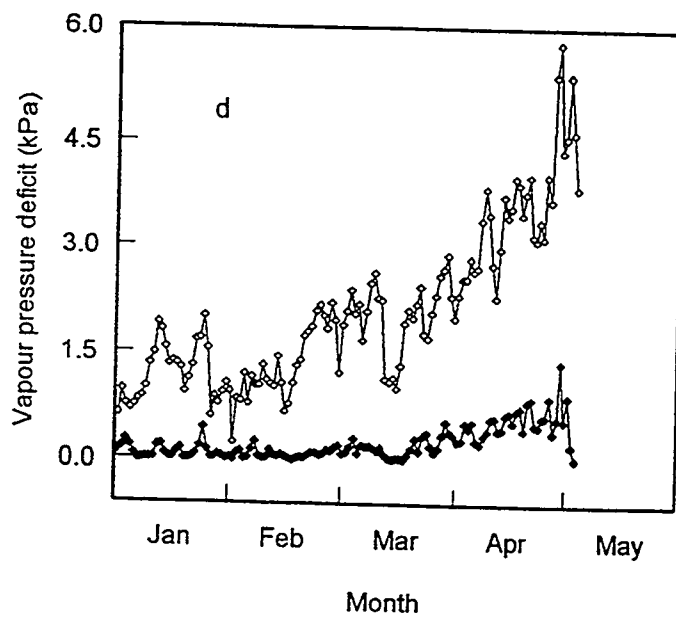
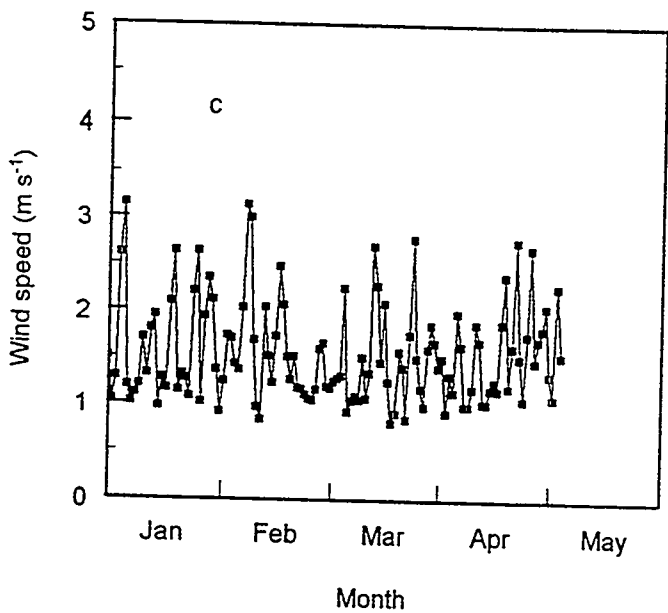
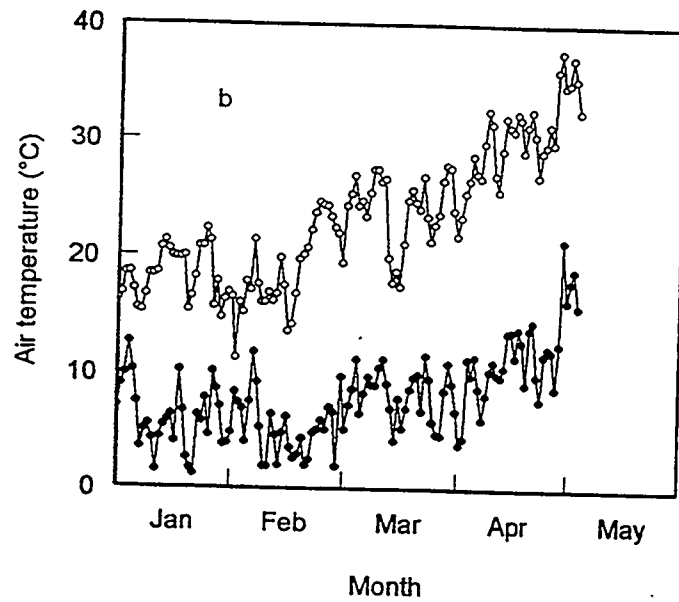
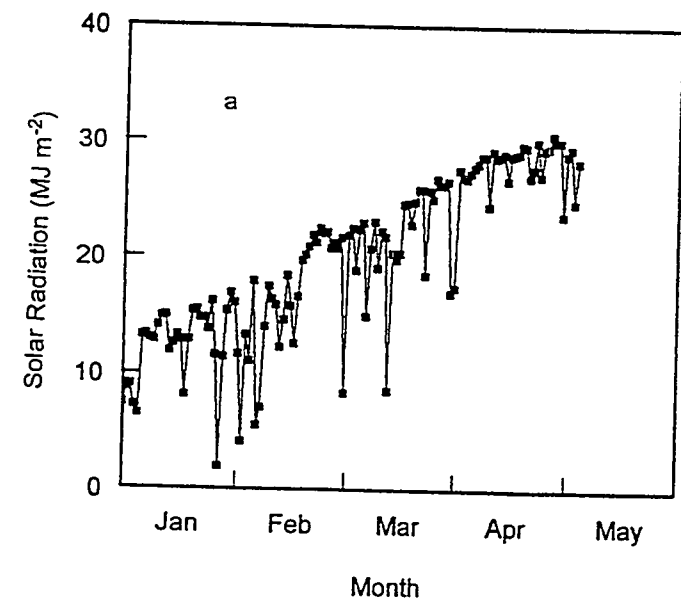


Figure 1 Prossman et al.

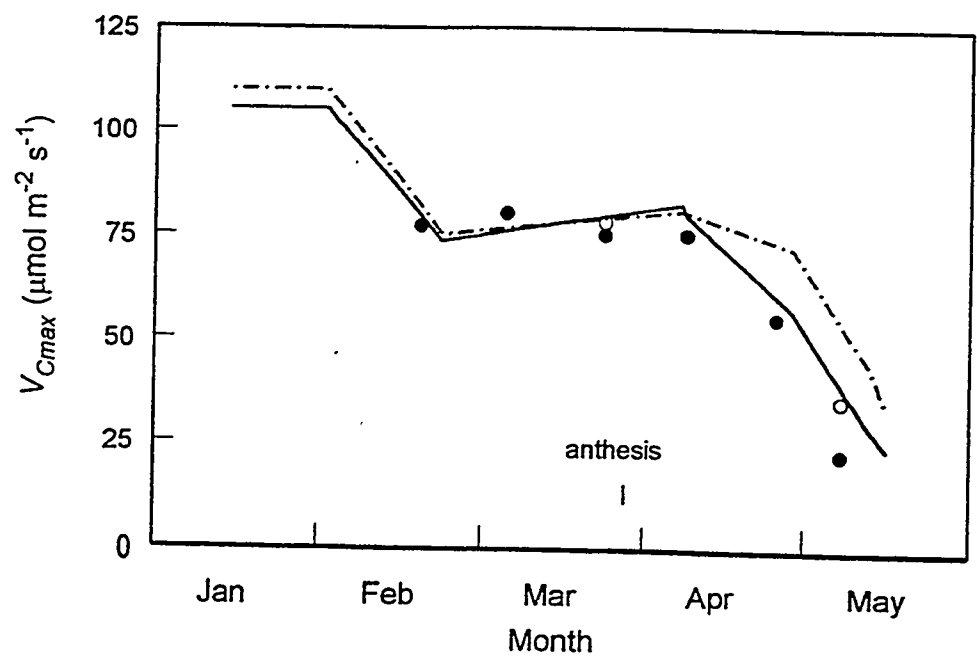


Figure 2 Grossman et al.

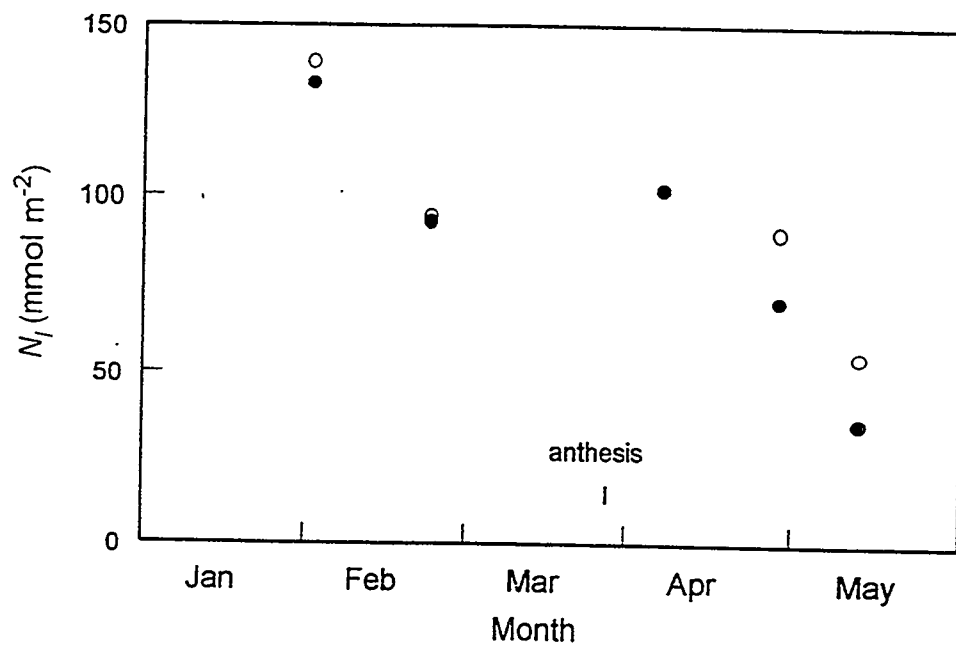


Figure 3 Grassman et al.

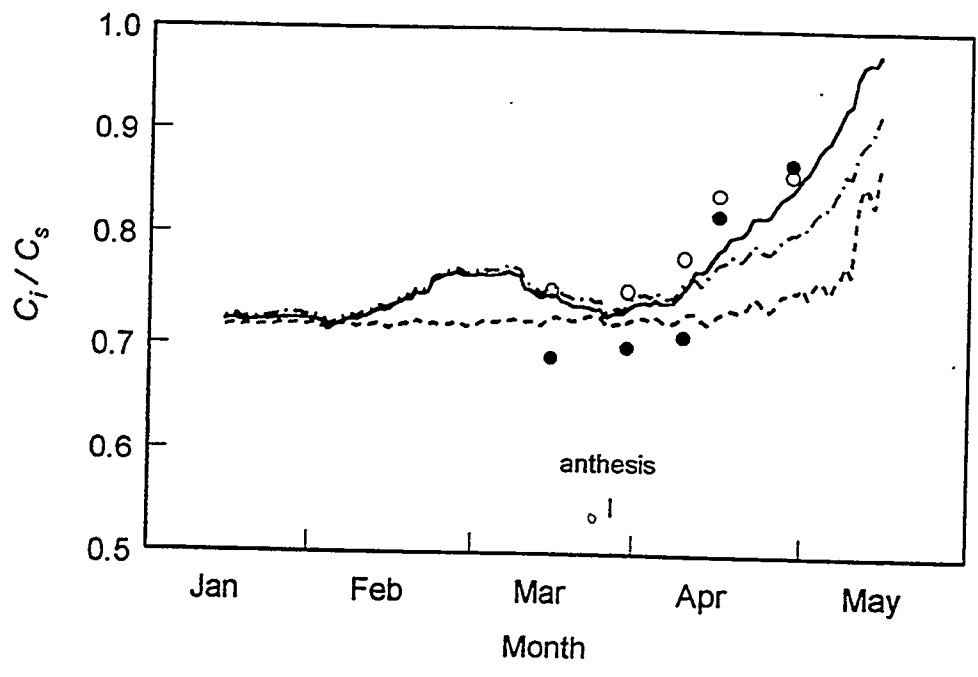
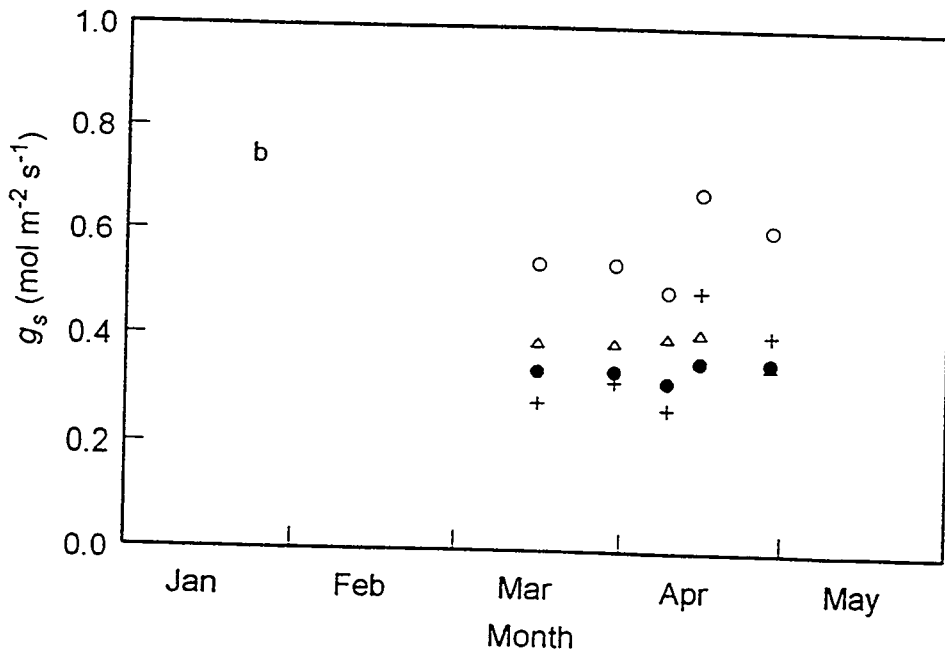
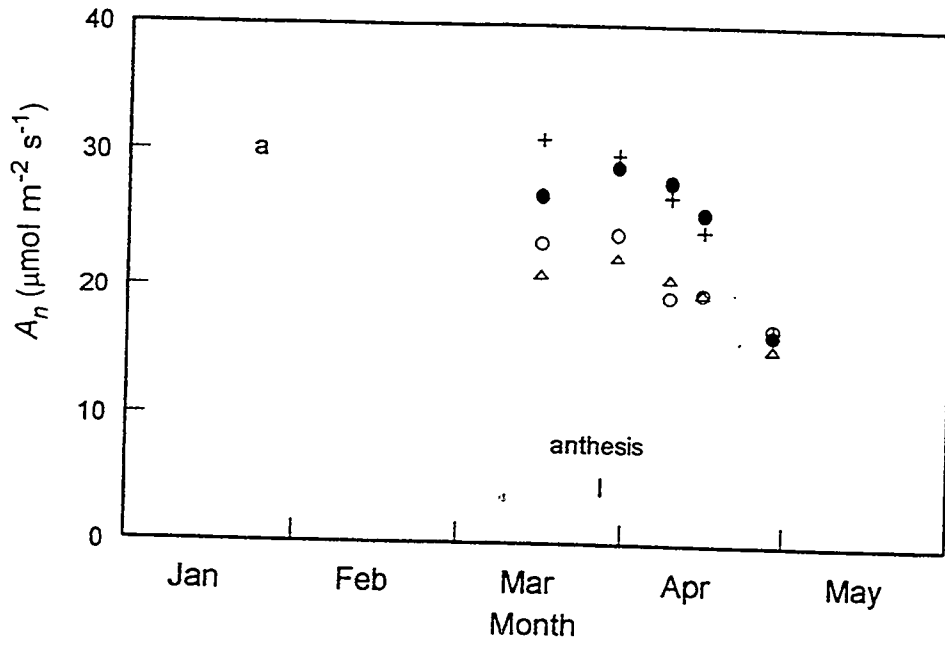


Figure 4 Grossman et al.



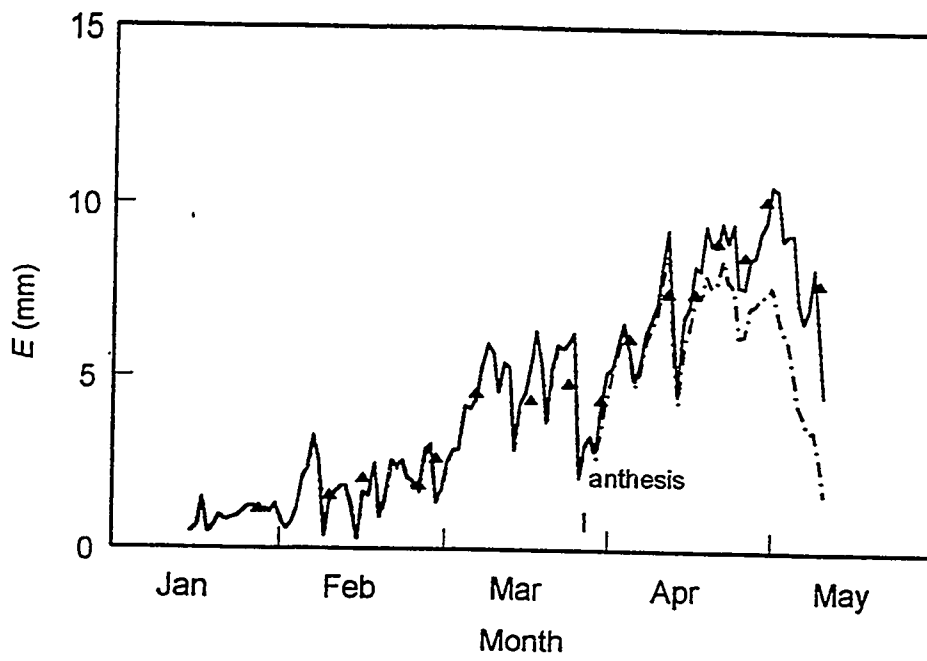


Figure 6 Grossman et al.

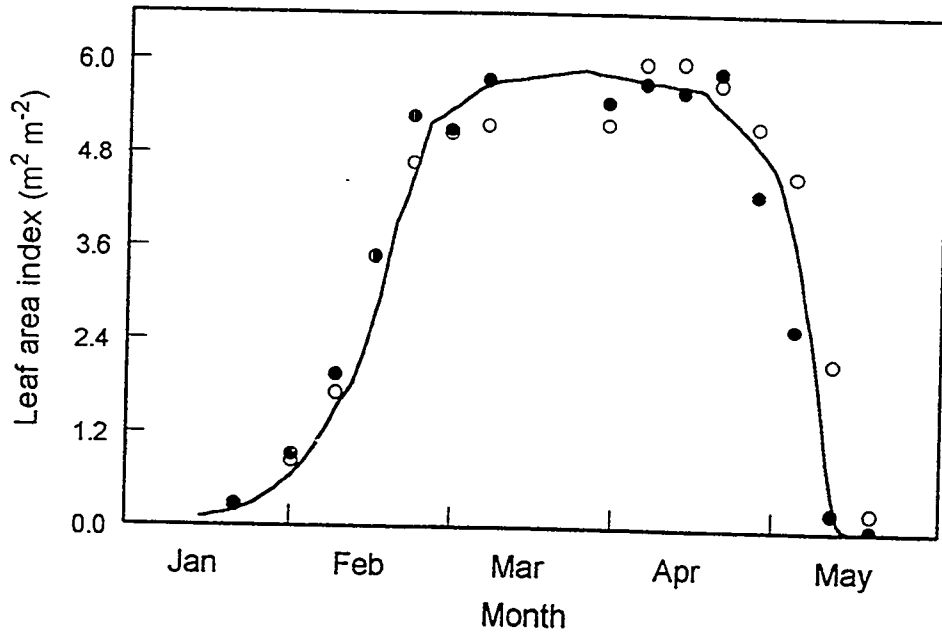


Figure 7 Grossman et al

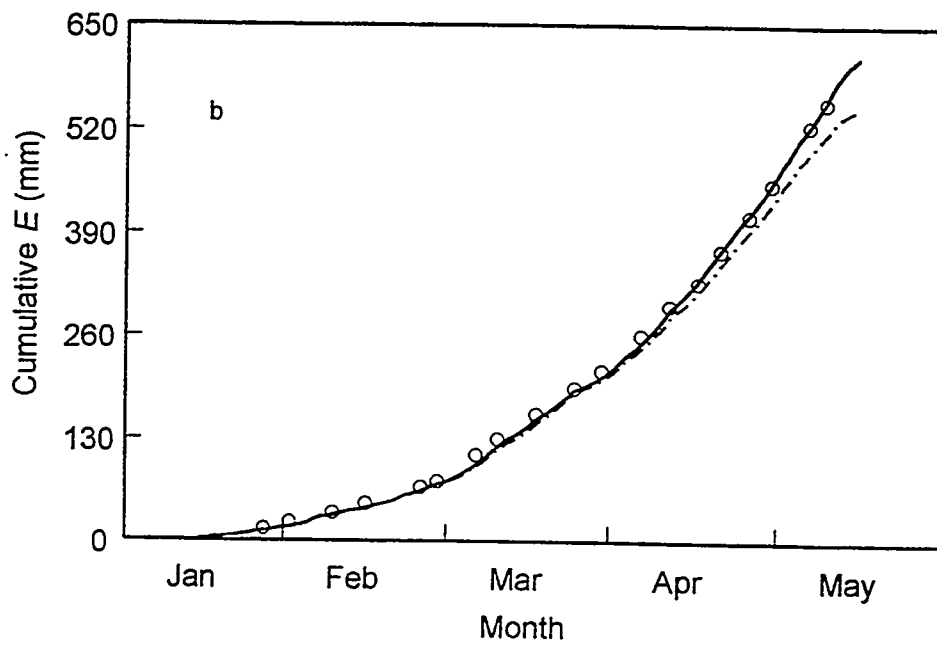
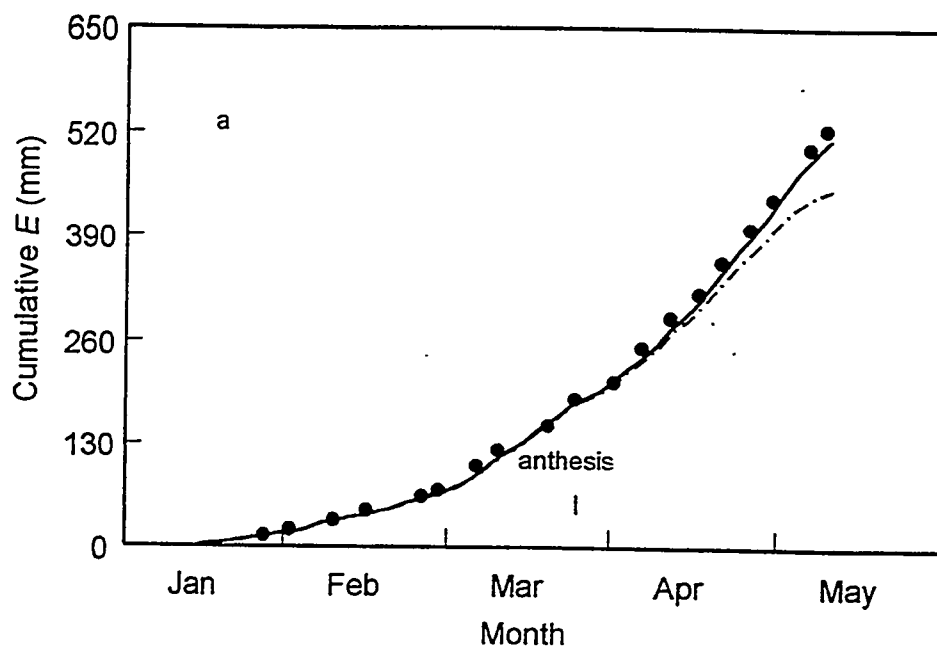


Figure 8 Grossman et al.

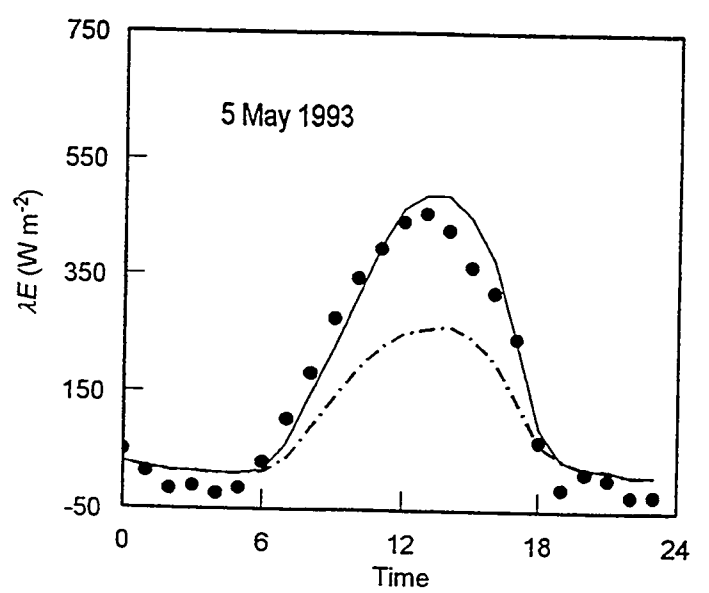
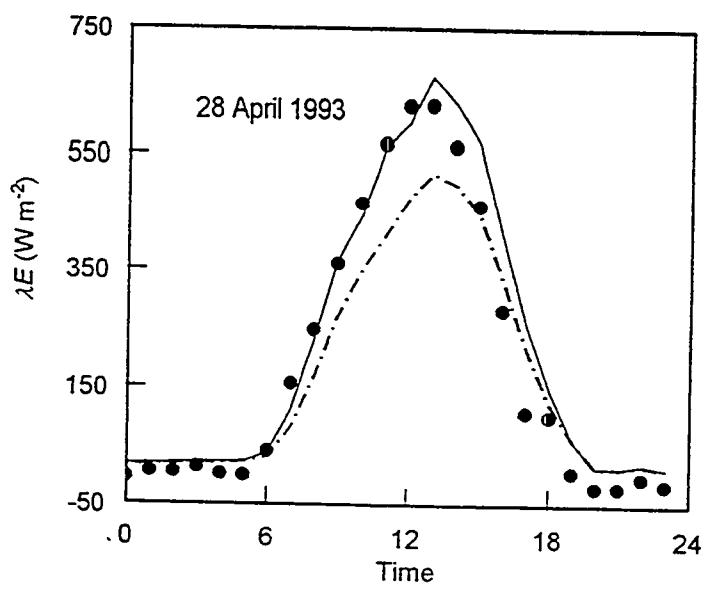
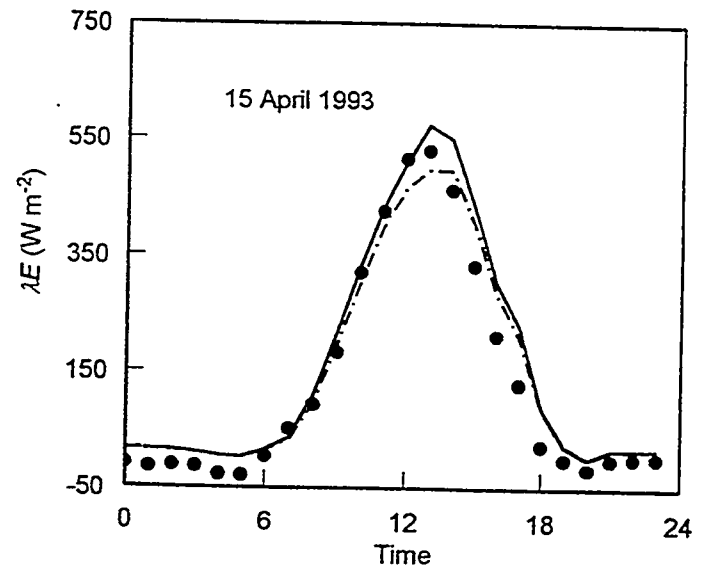
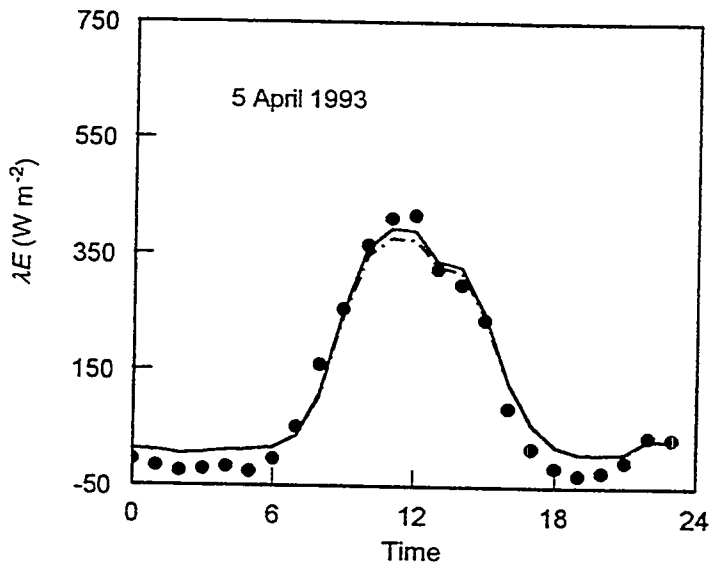


Figure 9 *Erismanni et al*