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Analysis of Temperature and Atmospheric CO₂ Effects on Radiation Use Efficiency in Chickpea (*Cicer arietinum* L.)

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Abstract: In this study, a simple theoretical framework was extended to account for the effects of temperature and atmospheric CO₂ concentration on RUE. A general test of the model showed that simulated and observed daily biomass productions under average daily temperatures ranged from 11 to 28°C are similar. The calculated RUEs for 13-23°C were similar to measured ones and percentage increase in RUE for CO2 concentration of 640 ppm relative to 330 ppm was in agreement with the measured percentage increase in biomass production. By using the framework, RUE response functions to average daily temperature and CO₂ concentration were calculated for chickpea. RUE of chickpea at temperatures lower than 3°C and higher than 36°C is zero. RUE rapidly increased (9.5%°C⁻¹) with increasing temperature from 3 to 14°C. With further increase in temperature to 22°C, RUE slowly (1.4%°C⁻¹) decreased and temperature increase between 22 to 36°C resulted in sharp decrease (7.4%°C⁻¹) in RUE. Response of RUE to CO₂ concentration was curvilinear. At low concentrations of CO₂ (60 to 400 ppm), RUE was especially sensitive to increases in CO₂ concentration, but increases in CO₂ greater than 700 ppm were predicted to result in only small increases in RUE. The functions obtained can be used in simulation studies of chickpea crop response to projected climate change.

Key words: Radiation use efficiency, model, temperature, carbon dioxide, chickpea

Introduction

Chickpea (*Cicer arietinum* L.) is one of the major pulse crops in arid and semiarid environments of West Asia and North Africa (WANA) region and has considerable importance as food, feed and fodder. Due to the increasing need for legumes, chickpea is no longer considered a subsistence crop (Saxena *et al.*, 1996). Projected global climate change may have major influences on cropping aspects of this crop in the region. In order to ensure a balanced growth and development in agriculture in the region, a comprehensive assessment of the vulnerability of chickpea cropping due to projected climate change is required.

Radiation use efficiency (RUE, g MJ⁻¹) is the amount of biomass accumulated for each unit of total solar radiation intercepted by leaf canopy (Choudhury, 2000). Recently, a simple mechanistically based model was developed for chickpea in which the daily biomass production is calculated using RUE (Soltani *et al.*, 1999). In this model, the effect of supra-optimal temperatures and atmospheric CO_2 concentrations were not included and the effect of low temperature was only considered. The effect of temperature and CO_2 on RUE is especially important in climate change studies using RUE

based models. However, there is no report on the response functions of RUE to temperature and CO_2 concentration in chickpea.

Sinclair and Horie (1989), Sinclair (1991), Sinclair *et al.* (1992) and Hammer and Wright (1994) developed and extended a framework to analyze the effects of radiation, leaf nitrogen, fraction diffuse radiation and leaf light-saturated CO₂ assimilation rate on RUE. This framework provides a simple and effective method to analyses the variation of RUE between species and under different conditions. The framework, however, does not account for the effects of temperature and CO₂ concentration.

Our objectives of this study were: (1) to extend and test the theoretical framework to model the effects of average daily temperature and atmospheric CO_2 concentration on RUE and (2) to use the extended framework to produce the response functions of chickpea RUE to average daily temperature and atmospheric CO_2 .

Materials and Methods

The Theoretical Framework Used

Crop radiation use efficiency on any day is calculated as the ratio of crop biomass produced that day to total solar radiation intercepted by the canopy that day. Crop biomass increment is determined from canopy gross CO₂ assimilation rate, daily rate of maintenance respiration costs and the assimilate requirement for dry matter production (Goudriaan and van Laar, 1994; Choudhury, 2000). Growth respiration and the efficiency of conversion of glucose to plant tissue was computed using the procedure of Penning de Vries *et al.* (1989). The maintenance coefficients for chickpea were considered as 0.03 for leaves, 0.015 for stems, 0.015 for roots and 0.01 for storage organs based on Penning de Vries *et al.* (1989) and Goudriaan and van Laar (1994). When organs dry matter are not available, maintenance respiration is calculated as a fraction of the daily total hexose production. The fraction has a value of 0.15-0.2 (Sinclair and Horie, 1989).

Canopy gross assimilation is calculated by integrating the instantaneous assimilation rates of sun leaves and shade leaves over the day light periods. The instantaneous assimilation rates are calculated from the product of leaf area index of sunlit or shade leaves and the assimilation rate per unit leaf area (P). P is given by an asymptotic exponential equation of radiation flux density incident on either sun or shade leaves (KJ m⁻² sec⁻¹) (Boote and Loomis, 1991):

$$P = P_{\text{maxc}}[1 - \exp(-QE_c I / P_{\text{maxc}})]$$
 (1)

where P_{max} (mg CO_2 m⁻² sec⁻¹) is the assimilation rate per unit leaf area asymptote to leaf potential for CO_2 assimilation rate per unit leaf area corrected for temperature and CO_2 concentration and QE_c (mg CO_2 kJ⁻¹) is the light use efficiency at low light corrected for temperature and atmospheric CO_2 .

The leaf area index of sun or shade leaves is calculated by considering the sun angle elevation, the proportion of intercepted radiation and shadow projection function (Boote and Loomis, 1991). The radiation flux density, incident on either sun or shade leaves is calculated from the incident direct and diffuse radiation, the proportion of incident radiation intercepted by the leaf canopy and the leaf area index of sun or shade leaves in a manner similar to Sinclair *et al.* (1992). The direct and diffuse components of the total incident radiation at any time are calculated in a manner similar to that of Goudriaan and van Laar (1994).

P_{maxe} and QE_e required in Eq. 1 are calculated by:

$$P_{\text{maxc}} = P_{\text{max}} P_{\text{tmp}} P_{\text{CO}_2}$$
 (2)

$$QE_c = QE QE_{CO_2}$$
 (3)

where P_{max} is leaf light-saturated CO_2 assimilation rate (mg CO_2 m⁻² sec⁻¹), P_{tmp} is a correction factor (between 0 to 1) of P_{max} for temperature, P_{CO_2} is a correction factor of P_{max} for atmospheric CO_2 concentration, QE is the light use efficiency at low light which was set at 5 mg CO_2 KJ⁻¹ (Sinclair and Horie, 1989) and QE_{CO_2} is a correction factor of QE for CO_2 concentrations.

The correction of the P_{max} and QE for the effect of atmospheric CO_2 is modeled using Farquhar and von Cammerer (1982) procedure for limiting RuBP as used by Boote and Pickering (1994) and Yu *et al.* (2003):

$$P_{CO_2} = 6.5382 \left(C_i^{Pmax} - \Gamma^* \right) / \left(4 C_i^{Pmax} + 8 \Gamma^* \right)$$
 (4)

$$QE_{CO_2} = 5.7768 \left(C_i^{QE} - \Gamma^* \right) / \left(4 C_i^{QE} + 8 \Gamma^* \right)$$
 (5)

where C_i^{Pmsx} is internal CO_2 concentration for the computation of P_{CO_2} with a C_i/C_a ratio of 0.7, C_i^{QE} is internal CO_2 concentration for the computation of QE_{CO_2} with a C_i/C_a ratio of 1 and Γ^* is CO_2 compensation point in absence of dark respiration. The factors 6.5382 and 5.7768 scale P_{CO_2} and QE_{CO_2} to 1 at 25°C and 350 ppm CO_2 , respectively. C_i^{Pmsx} and C_i^{QE} are calculated as:

$$C_i^{\text{Pmax}} = \max (\Gamma^*, 0.7 \text{ CO}_2 + (1 - 0.7) \Gamma^*)$$
 (6)

$$C_i^{QE} = \max(\Gamma^*, CO_2) \tag{7}$$

where CO_2 is atmospheric CO_2 concentration (ppm). The Γ^* depends on the specificity factor (calculated according to Evans and Farquhar, 1991) and the O_2 concentration.

Photosynthesis response to temperature is modeled as Goudriaan and van Laar (1994). Considering a lack of data for chickpea, the P_{max} response function to temperature was borrowed from Penning de Veris *et al.* (1989) based on a fababean (a cool season legume crop like chickpea) photosynthesis response to temperature; P_{tmp} increases from 0 at 3°C to relative rate of 1 between 14°C and 22.5°C, declines with rising temperature above 22.5°C and reaches to 0 at 35°C. The average temperature during daytime is used to determine the relative response of P_{max} to temperature (P_{tmp}). QE was related to temperature using the function for P_{tmp} 0 plants cited in Penning de Veris *et al.* (1980)

A detailed description of the model equations and source codes of the model are obtainable from the authors.

Test of the Model

To conduct a general test of the model, P_{max} was firstly estimated as 0.85 mg $CO_2\,m^{-2}\,sec^{-1}$ for chickpea cultivars Jam and Kaka using crop growth rate data of K. Ghassemi-Golezani (unpubl. data). For testing of the model, crop growth rate data of Movahhedi (1996) was used. To do this, average daily crop growth rates (g m⁻² day⁻¹) were calculated using weekly samples of crop dry matter. In each case meteorological observations of maximum and minimum temperatures and sunshine hours were available and LAI for each day between samplings was estimated using linear interpolation. Then average simulated crop growth rates for different intervals were calculated and compared with observed ones.

For specific test of the model, calculated RUEs at temperatures between 13 and 23°C were compared to the measured values by Soltani *et al.* (2006) for the same average temperatures. Similarly, percentage increase in RUE calculated for CO₂ concentrations of 640 ppm relative to 330 ppm was

Table 1: Typical characteristics of a chickpea crop between flowering and beginning seed growth in Tabriz, NW Iran (K. Ghassemi-Golezani, unpubl. data of 2 years growth analysis of 9 chickpea cultivars at the University of Tabriz Tabriz Iran: Movahedi 1996)

Tabliz, Tabliz, Hall, Movaledi, 1990)	
Characteristic (unit)	Value
Planting density (No. m ⁻²)	30
Leaf area index (LAI, m ² m ⁻²)	2.6
Leaf dry weight/leaf area (g m ⁻²)	48.5
Leaf dry weight (g m ⁻²)	126
Stem dry weight (g m ⁻²)	104
Pod dry weight (g m ⁻²)	10
Root dry weight* (g m ⁻²)	47
Total dry weight (g m ⁻²)	287

^{*}Estimated using a root/shoot ratio of 0.2 (Gregory, 1988)

compared to percentage increase in biomass production measured by Khana-Chopra and Sinha (1987) in three chickpea cultivars at the same CO_2 concentrations.

Simulation for Chickpea

The model was run for chickpea crops at different latitudes and days of year with varying LAI and crop weight. Results showed that RUE is changed little with variation of latitude, day of year and LAI (data not shown), thus a typical chickpea crop between flowering and beginning seed growth stages in Tabriz (38 °N), NW Iran, with characteristics presented in Table 1 was considered. In this stage which occurs at day of year 177 (with a range of 170 to 190), vegetative organs are dominant. Long-term (1965-1997) averages of temperature and solar radiation at this time are 25 °C and 27.7 MJ m⁻² day⁻¹, respectively. The latitude was set at 38 °N, which corresponds to the chickpea growing area in NW Iran and the location of the crop presented in Table 1. To generate the response functions of RUE, daily average temperatures from 0 to 40 °C and ambient CO_2 concentrations from 20 to 1200 ppm were inputted to the model.

Results and Discussion

Figure 1 shows a plot of simulated versus observed crop growth rates. The crop growth rate data were observed under (and simulated for) average daily temperatures ranged from 11 to 28°C. Good

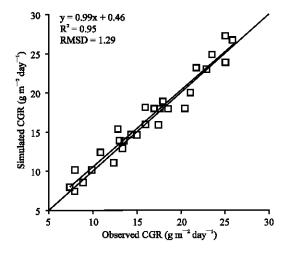


Fig. 1: Simulated versus observed Crop Growth Rates (CGR) for chickpea cultivars Jam and Kaka. The solid line is 1:1 line and the thick line is the regression line

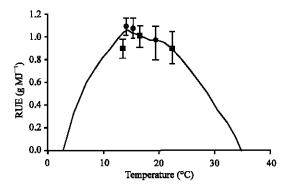


Fig. 2: Simulated curve of RUE response to temperature and experimental RUE values. Squares are RUE values from Exp. 1 and circles from Exp. 2 of Soltani *et al.* (2006)

agreement between simulated and observed crop growth rates was obtained. This test show the ability of the model to simulate daily biomass production under a range of temperatures. Of course, it should be noted that under field conditions temperature is normally associated positively with solar radiation and negatively with vapor pressure deficit.

The calculated RUEs for temperatures of 13 to 23 °C were similar to that measured by Soltani *et al.* (2006) in chickpea under the same temperature averages (Fig. 2). Soltani *et al.* (2006) measured RUE in 2 experiments each with 4 plant densities and 3 sowing dates at Gorgan in the west part of the Caspian Sea Coast of Iran. There was no significant difference between sowing densities, but sowing dates differed significantly. Variability of RUE between sowing dates was related to temperature. Khana-Chopra and Sinha (1987) found, in three chickpea genotypes, that with increase in CO₂ concentration from 330 to 640 ppm, biomass production increases by 20 to 33%. The model predicts a 25% increase in RUE for the same concentrations, midway between the reported values. From these tests we concluded that model performance is acceptable and can be used to produce response of RUE to temperature and CO₂ concentration.

With mean daily temperature of 25°C and radiation of 27.7 MJ m⁻² day⁻¹ the crop presented in Table 1 produced 23.8 g DM m⁻². RUE was 0.95 g MJ⁻¹ that was obtained with a P_{max} of 0.85 mg $CO_2 m^{-2} sec^{-1}$. This value of RUE is also equal to that reported for chickpea by Hughes *et al.* (1987).

Figure 2 shows the dependence of RUE to average daily temperature. At temperatures lower than 3°C and higher than 36°C RUE is zero. RUE is sharply increased (9.5%°C⁻¹) with increasing temperature from 3 to 14°C, where it has maximum of its value. With further increase in temperature to 22°C, RUE is slowly decreased (1.4%°C⁻¹). Rising temperature from 22 to 36°C is resulted in the sharp decrease (7.4%°C⁻¹) of RUE. This sharp decrease is a result of increasing respiration and declining photosynthesis with increase in temperature.

Figure 3 shows response to atmospheric CO_2 of RUE in chickpea. At CO_2 concentrations lower than 60 ppm, RUE is zero, a similar value presented by Wolfe (1994) for net photosynthesis response to CO_2 . With increasing CO_2 , RUE is increased by a diminishing rate and saturated at CO_2 greater than 700 ppm. This response also is very similar to that reported for C_3 plants (net photosynthesis) by Wolfe (1994). Figure 3 shows that a doubling atmospheric CO_2 (from 350 to 700 ppm) increases RUE of chickpea by 23%. Kimball *et al.* (2002) summarizing data from experimental studies, found a 25% increase in growth rate with a doubling of CO_2 concentration. Melkonian *et al.* (1998), using three formulations for estimating the impact of elevated CO_2 on daily net canopy carbon assimilation, found that with doubling CO_2 concentration 15-48% increase in net carbon assimilation is occurred.



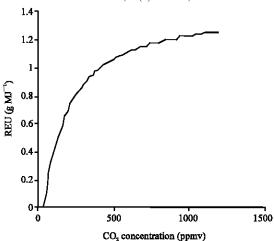


Fig. 3: Simulated Radiation Use Efficiency (RUE) of chickpea as a function of atmospheric CO₂ concentration

Overall, by integrating quantitative relationships that capture the physiological responses, a simple, suitable theoretical framework was extended to allow the effects of temperature and $\rm CO_2$ on RUE. By using the framework, response functions of RUE to temperature and atmospheric $\rm CO_2$ concentration were calculated for chickpea. The RUE response to temperature and $\rm CO_2$ concentration is consistent with the results obtained for some other $\rm C_3$ crops. These functions can be used for describing the response of RUE to temperature and $\rm CO_2$ concentration in climate change studies.

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