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A BIOMASS MODEL WITHOUT PHOTORESPIRATION FOR HUISACHE AT DIFFERENT CO₂ LEVELS.

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MUTTIAH R. S. and JOHNSON H. B. A BIOMASS MODEL WITHOUT PHOTORESPIRATION FOR HUISACHE AT DIFFERENT CO₂ LEVELS. BIOTRONICS 28, 23–31, 1999. This paper estimates daily biomass of Huisache (*Acacia farnesiana*) from leaf temperature dependent photosynthetic rates and a glucose to biomass storage calibration parameter (Φ_G^B). To test importance of photorespiration at different CO₂ treatments, a biomass model assuming no photorespiration in leaves was developed and then checked against measured allometric biomass. Leaf temperature of Huisache was determined from energy balance, and photosynthetic rates were calculated from light and leaf temperature dependent Michaelis–Menten reactions. The Φ_G^B parameter was calculated to be 0.33 based on ambient CO₂ experiments. Results of biomass modeling over the first year's growth of Huisache (October, 1992–July, 1993) agreed with observation in Root Mean Squared Error (RTMSE)/mean ratios of 34%, 11%, and 7% for ambient CO₂, double, and triple ambient CO₂ concentrations, respectively. Larger error for ambient CO₂ growth suggested biomass accumulation was more sensitive to photorespiration at higher temperatures under ambient CO₂ growth than at elevated CO₂ levels.

Key words: photosynthesis; energy balance; allometric measurements

INTRODUCTION

Polley *et al.* (10) have shown increased biomass in response to elevated CO₂ concentrations in the leguminous shrub Huisache (found in arid and semi-arid climates of south Texas and Mexico). Process-based biomass models use Radiation Use Efficiency (RUE) from field experiments to calibrate dependence of growth on CO₂ (11). Extrapolation of RUE to environmental conditions other than field observation requires use of regression methods since mechanistic physico-chemical steps of biomass accumulation are not considered. Application of biophysical principles in photosynthesis could provide generalized information about the importance of environmental variables on biomass changes in plants. We used a light and temperature biophysical model outlined by Gates (3) to estimate photosynthetic rates. The objective here was not to suggest replacement of existing photosynthesis models but rather to examine how much ignoring photorespiration would influence biomass predictions.

Hendrix *et al.* (4) in free air enrichment experiments on cotton, for example, found increased starch resources in stems and more soluble sugars in leaves at elevated CO₂ levels. The efficiency at which glucose is stored as permanent biomass (Φ_G^B) in Huisache has not been quantified. Specific objectives of the present study were to 1) develop a biomass model from photosynthetic rates of Huisache, and 2) predict the sensitivity of biomass accumulation in Huisache (a C₃ plant) to photorespiration at ambient (350 ppm [CO₂]), and elevated [CO₂] (700, and 1000 ppm).

MATERIALS AND METHODS

Huisache Growth Experiments

Huisache, *Acacia farnesiana*, (same as *A. Smallii* in Polley *et al.* (10)) a woody member of the nitrogen fixing legume plant family, was grown at different atmospheric CO₂ concentrations in three bays of an air-conditioned, CO₂ controlled glasshouse. Target CO₂ control levels for the three bays were ambient (350 ppm), 2× ambient (700 ppm), and 3× ambient (1000 ppm). The actual average growth CO₂ concentrations realized were 385, 690, and 980 ppm, respectively as monitored with an infrared gas analyzer (Model 6262, LI-COR Inc, Lincoln, Nebraska, USA). Air temperatures were monitored with unshielded, unspirated fine wire thermocouples. Temperature controls in the 1000 ppm bay were set to approximate outdoor temperatures, and the controls of the other two bays were set to follow the 1000 ppm bay. Air temperatures among the three bays tracked each other closely. The mean daytime air temperatures were 16.8°C in January and rose during the spring and summer to 27.5°C at harvest time in October 1993. Vapor pressure deficits were also monitored and followed the same seasonal trends. Sunlight was continuously monitored in each bay with a LI-COR Photosynthetically Active Radiation (PAR) sensor and averaged approximately 65% of outside intensity, each bay showing similar values. Two 80 cm diameter air-circulating fans mounted in each bay stirred the air constantly.

Huisache plants were grown in large 380 liter steel containers (0.65 m × 0.65 m and 0.90 m deep) mounted on wheels. Soil in the containers was unfertilized fine sandy loam packed to a density of approximately 1.6 g cm⁻³. Three Huisache seeds were planted in each container with three containers per CO₂ treatment to give nine Huisache plants per treatment. Huisache growth was monitored through weekly measurements of length and diameter of woody stems and branches. Soil water was monitored weekly and water needed to return soil to field capacity was added. Plants were grown from August 1992 to October 1993 when the tops were harvested and weighed, and below ground root growth was sampled. After harvesting, Huisache plants sprouted and restarted growth.

Biomass estimates were made from stem length and stem diameters at weekly intervals. These allometric measurements were calibrated empirically by independent measurements and harvests of developing Huisache plants. Allometric methods have been proven to be accurate for biomass estimation (1, 6).

Hourly measurements of PAR, air temperature, daylight hours, and CO₂ concentrations were cumulated to daily values for modeling purposes. Leaf absorbed radiation (Q_a) was estimated as a function of measured leaf area index and PAR using Beer's law (9). The measured leaf area index of Huisache was linear from 0 to 4 ($\text{m}^2 \text{m}^{-2}$) in the ambient CO₂ treatment, and linear from 0 to 8 ($\text{m}^2 \text{m}^{-2}$) in both the elevated CO₂ treatments.

Energy Balance of Huisache Leaf

Leaf energy balance was used to estimate leaf temperature which governs rate of photosynthesis according to a Michaelis-Menten model. Moisture stress was not considered in first year's growth since water use was similar in all three treatments (see Figure 1). The energy balance for a leaf was obtained by equating absorbed radiation, Q_a (W m^{-2}), to emitted thermal radiation, convected heat transfer, and water vapor cooling (3):

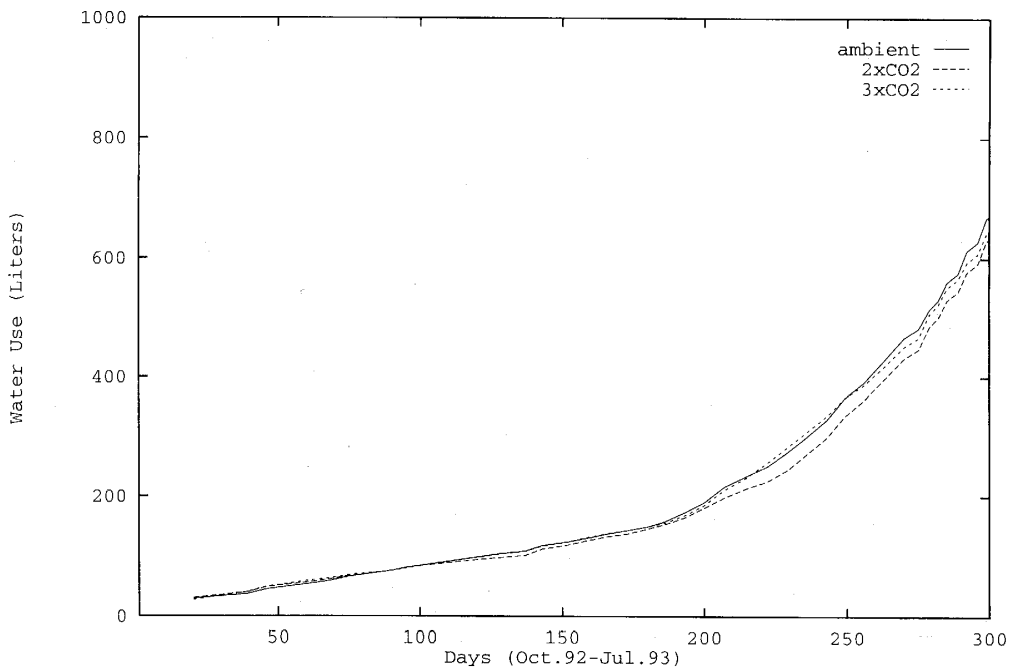


Fig. 1. Water use by Huisache for all three CO₂ treatments.

$$Q_a = \varepsilon \sigma (T_1 + 273)^4 + k_1 \sqrt{(V/D)} (T_1 - T_a) + \lambda E. \quad [1]$$

Where, T_1 = leaf temperature ($^{\circ}\text{C}$),

ε = Emissivity (set at 0.98),

σ = $5.670 \times 10^{-8} \text{ J m}^{-2} \text{ s}^{-1} \text{ K}^{-4}$, Stefan-Boltzman constant,

k_1 = Air convection constant, 9.14 (3),

V = Wind speed (m s^{-1}), 1.9 m s^{-1} from fan rate,

D = Dimension of leaf perpendicular to air flow, 1 mm,
(leaf shape is conic)

T_a = Air temperature ($^{\circ}\text{C}$),

λ = Heat of vaporization of water ($2.43 \times 10^6 \text{ J kg}^{-1}$).

The rate of transpiration, E ($\text{kg m}^{-2} \text{ s}^{-1}$) was taken as (3):

$$E = [d_1 - h d_a] / (r_1 + r_a). \quad [2]$$

Where, d_1 is the density of water in the leaf stomates (17.5 g m^{-3} at an average leaf temperature of 20.2°C), d_a is the density of air at water saturation (18.2 g m^{-3} at an average air temperature of 20.9°C), h is the relative humidity (average value of 0.6 from bay measurements), r_1 is the resistance to transpiration from inner part of leaf to stomates (assumed constant 1000 s m^{-1}), and r_a is the boundary air layer resistance (from (3): $r_a = 630.9 \sqrt{(D/V)}$). Since equation [1] is a fourth order polynomial in T_1 , we solved for T_1 by gradient descent iteration.

The rate of photosynthesis ($\text{mmole m}^{-2} \text{ s}^{-1}$) for a *non-photorespiring* leaf was calculated from the biophysical Michaelis-Menten equation for light and temperature dependence (3):

$$p(L, T) = P_{\text{Mit}} * G(T_1) / (1 + K_L/L). \quad [3]$$

Where, P_{Mit} is the gross rate of photosynthesis at optimum temperature, saturating light, and saturating CO_2 (taken as $0.05 \text{ mmole m}^{-2} \text{ s}^{-1}$ (3)), K_L for PAR wavelengths (400–700 nm) is the light intensity at which $p(L, T) = P_{\text{Mit}}/2$ (K_L was taken as 100 W m^{-2}), and L is the optimum light intensity (400 W m^{-2}), and $G(T_1)$ is a normally distributed calibration parameter that controls dependence of p on leaf temperature T_1 . Daily light interception by leaves plays a part in equation [3] through the leaf temperature from the energy balance equation [1]. The $G(T_1)$ mean and standard deviation were calibrated only for ambient CO_2 treatments by checking *final* biomass predicted on substitution of p from equation [3] into equation [4] below with final allometric biomass. For elevated CO_2 model runs no calibration of parameters was done. When equation [3] is substituted into Fick's law of air diffusion through stomatal openings in leaves, a quadratic equation in p results (see Appendix). Since the above Gates' model doesn't include photorespiration, biomass calculations from equation [3] leading to large discrepancies against observed biomass suggests importance of photorespiration to plant growth.

During glucose synthesis, 6 moles of CO_2 are fixed in the presence of light photons to produce 180 grams of glucose. Conversion efficiency of glucose to permanent structural and non-structural plant biomass was denoted by Φ_G^B . The net daily biomass accumulation B in the plant was therefore:

$$B (\text{g m}^{-2} \text{ day}^{-1}) = p (\text{mmole m}^{-2} \text{ s}^{-1}) \times 0.18 (\text{g mmole}^{-1}) \times 3600 (\text{s hour}^{-1}) \times \text{daylight hours/day} \times \Phi_G^B. \quad [4]$$

From calibration of final allometric biomass for end of July, 1993 values for ambient CO_2 , we found that best fit was at $\Phi_G^B = 0.33$. For computer simulation at the different CO_2 concentrations, leaf stomatal resistances of Huisache were set to bay measured averages of 250 s m^{-1} for ambient, 335 s m^{-1} for $2 \times [\text{CO}_2]$, and 350 s m^{-1} for $3 \times [\text{CO}_2]$.

RESULTS AND DISCUSSION

Figure 2 shows the GT calibration curve fit for final ambient CO_2 biomass. The best biomass match was obtained for GT with mean of $25^\circ C$, and standard deviation of $2.5^\circ C$. Figure 3 shows the photosynthetic rate as a function of leaf temperature predicted by Gates' model (equation A3 in Appendix). The curves are similar to what has been reported by others (7, 8). Table 1 shows the average photosynthetic rates from the model and those observed in the bay. Figure 4 shows the leaf and air temperatures under ambient CO_2 for simulation period from October, 1992 to July, 1993. Since the leaf diameter for Huisache is very small (1 mm), the leaf temperature closely follows air temperature. Figure 5 shows the observed and predicted biomass (B) using the proposed biomass model [4]. Since there was winter quiescence in the first hundred days after planting, results are shown thereafter. Table 2 summarizes the model results and observed values. Gates' photosynthesis model which assumed no leaf photorespiration, approximated biomass at the higher CO_2 levels relatively well. At ambient CO_2 , the model over predicted biomass. Some of the predicted photosynthetic rates for ambient CO_2 at higher temperatures later in the growing season (see figure 4 leaf temperatures for days 175–225) suggested lower biomass production relative to sub-optimal leaf temperatures. This discrepancy was presumably due to photorespiration. The temperature dependence of photorespiration has been experimentally confirmed by Jordan and Ogren (5) who observed increased temperature at low CO_2 favors oxygenation by decreasing the specificity of Rubisco for CO_2 relative to O_2 . Measurements by Polley *et al.* (10)

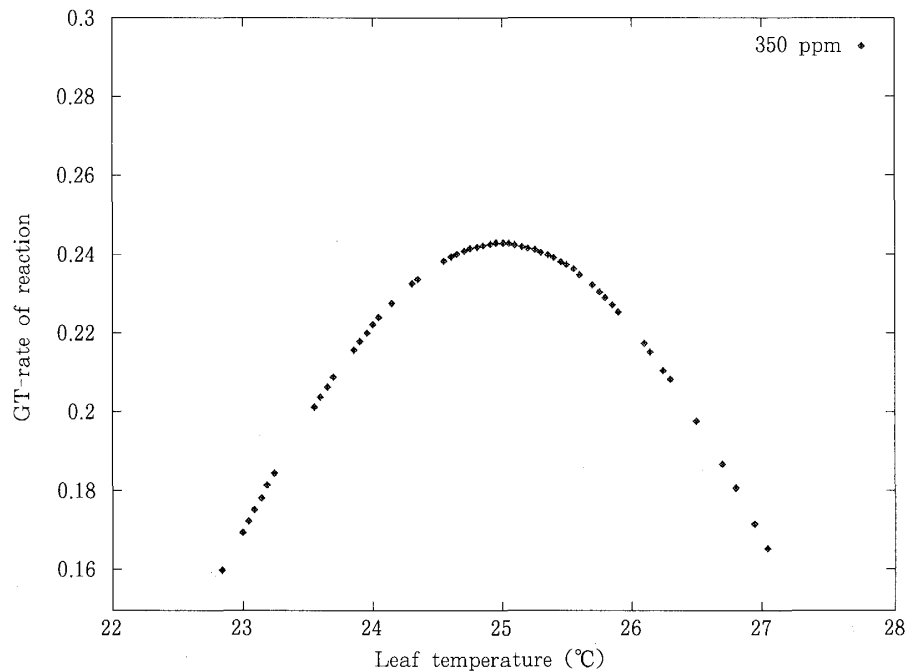


Fig. 2. The GT calibration curve fit for the final biomass at end of July, 1993 for ambient CO_2 .

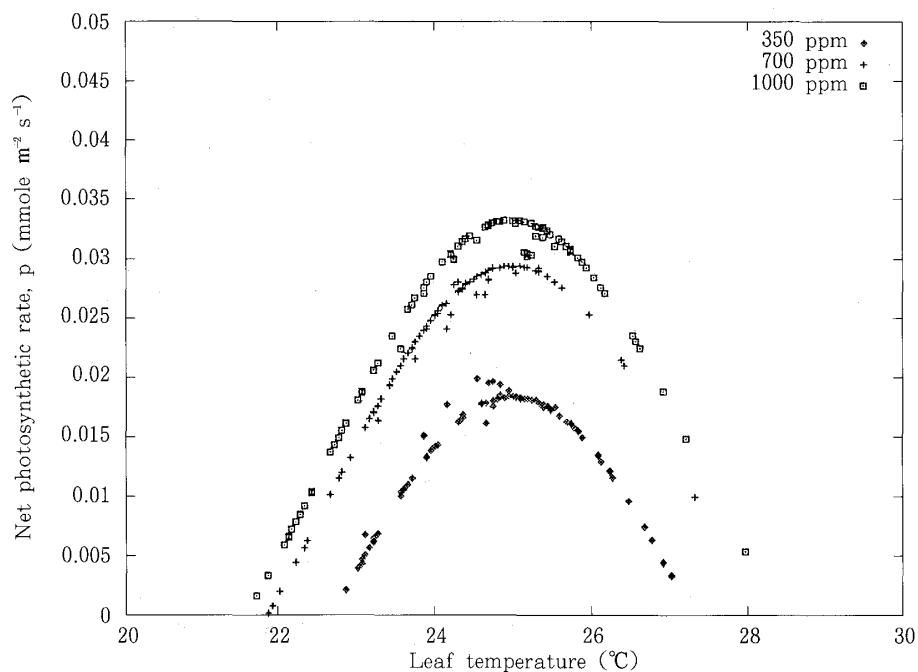


Fig. 3. Photosynthetic rate (p) as a function of leaf temperature using the Michaelis-Menten reaction equation proposed by Gates. The T_{opt} in the figure is the optimal temperature for photosynthesis.

Table 1. Average photosynthetic rates ($\text{mM m}^{-2} \text{s}^{-1}$) from model and observed bay values.

	Ambient	$2 \times [\text{CO}_2]$	$3 \times [\text{CO}_2]$
Model	0.0134	0.0232	0.026
Observed	0.0137	0.0163	0.021

Table 2. Summary of biomass at end of July, 1993.

	Ambient		$2 \times [\text{CO}_2]$		$3 \times [\text{CO}_2]$	
	Obs.	Pred.	Obs.	Pred.	Obs.	Pred.
Mean (g m^{-2})	1431	1714	3212	3051	3748	3715
RTMSE (g m^{-2})		488		361		280
RTMSE/Obs. Mean		34%		11%		7%

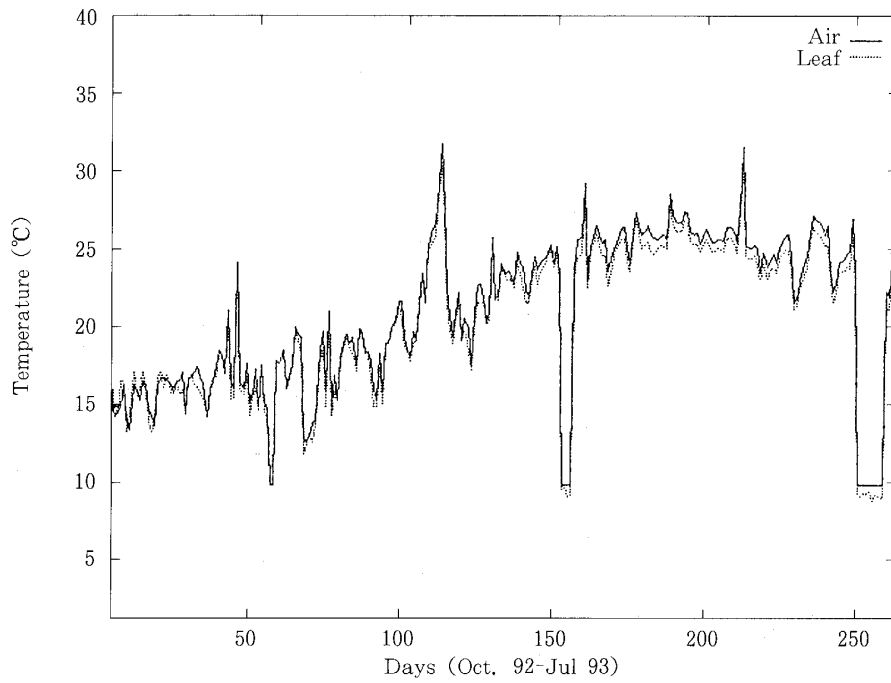


Fig. 4. Air and leaf temperature for Huisache at ambient CO₂.

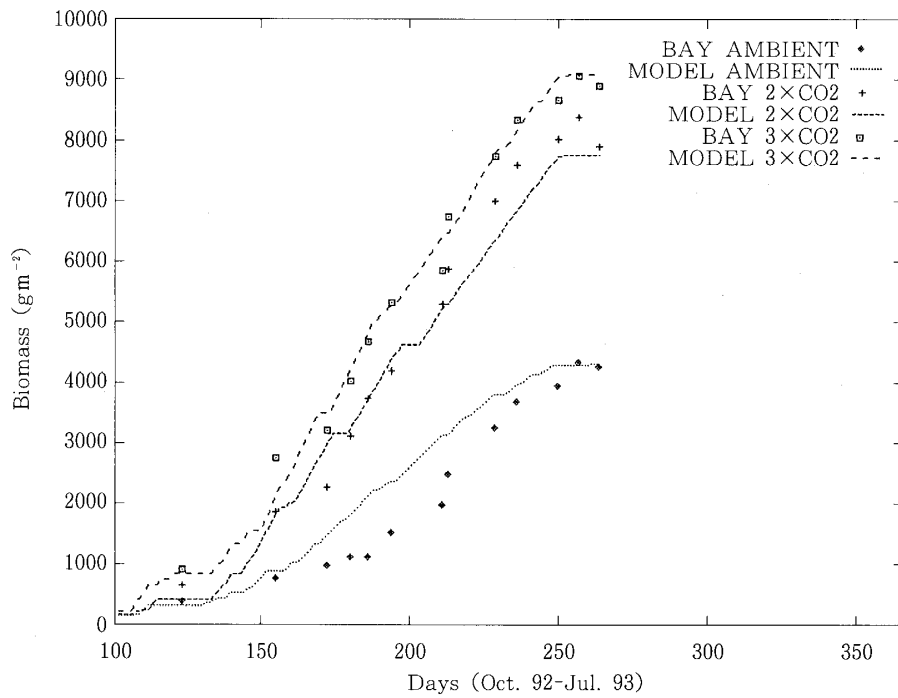


Fig. 5. Biomass estimation from energy balance model, and observed allometric biomass for all three CO₂ treatments.

on Huisache leaves for all three treatments showed that interstitial/air concentration of CO₂ stayed at a constant value of 0.75 ($P > 0.05$). Therefore, at elevated CO₂ there was more likelihood of carboxylation due to influences of leaf temperature on Rubisco. The model was unable to predict the decline in biomass during the last few days of the growing season because of leaf abscission.

Since the Gates' model is a biophysical photosynthetic model for light and temperature dependence, the model does not address any of the biochemical (nitrogen and enzyme dynamics) processes as Farquhar's model does (2). A reason that the proposed biomass model successfully predicted biomass accumulation was that nitrogen accretion in leaves was not a limiting factor because of symbiotic nitrogen fixation (10). Plant water use also stayed nearly constant for all three treatments. Since Huisache growth was not nitrogen or water limited for the first year, the biomass model showed sensitivity primarily to CO₂ concentrations and temperatures.

CONCLUSIONS

A biomass model using energy balance and efficiency of glucose to biomass storage (ϕ_G^B) assuming non-photorespiring Huisache leaves was used to discern environmental influences on Huisache biomass accumulation. The larger disagreement between predicted and observed biomass at 350 ppm CO₂ suggested that ignoring photorespiration at ambient CO₂ (especially at high temperatures) leads to sizeable over prediction of biomass. At elevated 700 ppm and 1000 ppm CO₂, neglecting photorespiration does not affect biomass predictions.

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APPENDIX

We reproduce the quadratic equation in p derived in Gates (3). The diffusion of CO₂ from air into a leaf is given by Fick's law of diffusion:

$$p = (C_a - C_c) / R \quad [A1].$$

Where C_a is CO₂ in air, and C_c is CO₂ in chloroplasts, and R is resistance to CO₂ diffusion (s m⁻¹). The Mihaelis–Menten reaction equation is given by:

$$p = p_{\max} / (1 + K / C_c). \quad [A2].$$

Where p_{\max} is the maximum rate of photosynthesis, K is a constant equal to the chloroplast concentration of CO₂ at which $p = p_{\max} / 2$. Solving (A1) for C_c , and substituting in (A2) gives:

$$Rp^2 - (C_a + K + Rp_{\max})p + C_a p_{\max} = 0. \quad [A3].$$

When there is light and temperature dependence in the chemical reaction, we set $K = K_L$, and $p_{\max} = p_{\text{mlt}}$.