

## PREDICTION OF THE EFFECTS OF ELEVATED CO<sub>2</sub> AND TEMPERATURE ON IRRIGATED RICE YIELDS IN THE LOW-COUNTRY DRY ZONE OF SRI LANKA USING A PROCESS-BASED SIMULATION MODEL

W.A.J.M. DE COSTA\*

*Department of Crop Science, Faculty of Agriculture, University of Peradeniya, Peradeniya 20400*

*(Received: 18 March 1999 ; accepted: 06 September 2000)*

**Abstract:** Atmospheric CO<sub>2</sub> concentration has been increasing at a rate of 1.2-1.4 ppm per year and is expected to be doubled before the end of next century. As CO<sub>2</sub> is the main substrate for photosynthesis in all plants, an increase in the ambient CO<sub>2</sub> level would have a direct effect on biomass production and yields of all agricultural crops. Increased concentrations of CO<sub>2</sub> and other 'greenhouse' gases lead to greater absorption of infra-red wavelengths in the outgoing radiation causing global warming. The estimated increases of ambient temperatures with a doubling of ambient CO<sub>2</sub> range from 1°C to 3.5°C. As all plant physiological processes are dependent on temperature, a rise in temperature would also have an impact on yield formation processes and consequently on crop yields.

The present study was undertaken to predict the yield response of rice to elevated CO<sub>2</sub> and temperature using a process-based, mechanistic simulation model. The model quantifies the effects of CO<sub>2</sub> and temperature on crop duration, radiation interception, photosynthesis, respiration and partitioning of assimilates to grains. The model was validated by running it for the existing atmospheric conditions at Maha-Illuppallama representing the low-country dry zone of Sri Lanka. The validated model was used to predict yield variations in response to a doubling of atmospheric CO<sub>2</sub> (i.e. from 350 to 700 ppm). The model predicted that rice yield per unit area would increase by 50% in response to the above change in CO<sub>2</sub>. In contrast, rice yield would decrease by 39-47% due to a temperature increase of 4°C. Simulation of the combined effects of elevated CO<sub>2</sub> and temperature showed that the positive effects of elevated CO<sub>2</sub> are almost totally negated by elevated temperatures with only slight increases (upto 17%) of yield from the current levels. The recommended remedial measures are increasing breeding efforts for producing crop varieties with greater tolerance to high temperature and drought, introduction of rice-based multiple cropping systems, increasing irrigation efficiency and promoting research to increase understanding of plant functioning under future climates.

**Keywords:** Elevated CO<sub>2</sub>, Global warming, Rice, Simulation model, Sri Lanka

### INTRODUCTION

Atmospheric CO<sub>2</sub> levels have been increasing significantly during the 20th century mainly due to increased burning of fossil fuel in various human activities. Based on the current levels of emissions, the global CO<sub>2</sub> concentration is expected to rise from the present level of 350  $\mu\text{mol mol}^{-1}$  (ppm) to 530 ppm in 2050 and to 700 ppm in

---

\* Corresponding author

2100.<sup>2</sup> When combined with increased emissions of other greenhouse gases such as  $\text{CH}_4$  and  $\text{N}_2\text{O}$ , elevated  $\text{CO}_2$  levels have caused significant global warming due to the greenhouse effect. The mean global air temperature is predicted to increase by ca.  $3^\circ\text{C}$  by 2050 and by ca.  $4^\circ\text{C}$  by 2100<sup>1,2</sup> if greenhouse gas emissions continue at the present levels.

Both  $\text{CO}_2$  and temperature have direct effects in determining the yields of all agricultural crops. Crop yield formation is the integrated result of a series of physical and physiological processes starting from interception and absorption of incoming solar radiation, photosynthesis, respiration, initiation of grains and ultimately in partitioning of assimilates to grains. As  $\text{CO}_2$  is an essential component in the production of plant biomass through the interplay between photosynthesis and respiration<sup>3</sup>, increase of ambient  $\text{CO}_2$  concentration will have direct effects on the photosynthetic and respiratory processes. As the rates of all plant physiological and biochemical reactions are primarily determined by temperature<sup>4</sup>, rising global temperatures will also have a significant influence on all processes leading to crop yield formation. Therefore, the objective of the present work was to quantify and predict the effects of elevated  $\text{CO}_2$  and temperature on the grain yield of rice in the low-country dry zone of Sri Lanka.

Rice is the staple food in Sri Lanka and is the second most important crop in the world. The low-country dry zone contributes a significant proportion to the national rice production. Besides, rice-based agriculture is the major form of land use in the low-country dry zone. Therefore, prediction of the effects of climate change on rice production is important in future development planning and policy formulation of the low-country dry zone of Sri Lanka.

## METHODS AND MATERIALS

The method of simulation modelling was used in the present study to predict yield variation of rice in response to changes in  $\text{CO}_2$  and temperature. The relational diagram of the basic model is shown in Fig. 1.

*Overview of the model:* The model is primarily driven by incoming radiation which is intercepted by the leaf canopy and used in photosynthesis. The photosynthetic light response is determined by the prevailing  $\text{CO}_2$  and temperature levels. While photosynthesis proceeds, temperature drives the development of the crop through the different phenological stages. Hence, temperature determines the durations of the different developmental stages and the total crop duration. Both temperature and  $\text{CO}_2$  determine the total crop canopy leaf area and its variation during the course of the crop's duration. Part of the carbohydrates produced by photosynthesis is converted to plant biomass and the rest is used in respiration which provides the energy for synthesis of new biomass and the maintenance of existing biomass. Respiration rate is determined by the prevailing temperature and  $\text{CO}_2$  levels.

Synthesized biomass is finally partitioned into grains and straw with the proportions of partitioning varying according to the developmental stages as determined by temperature.

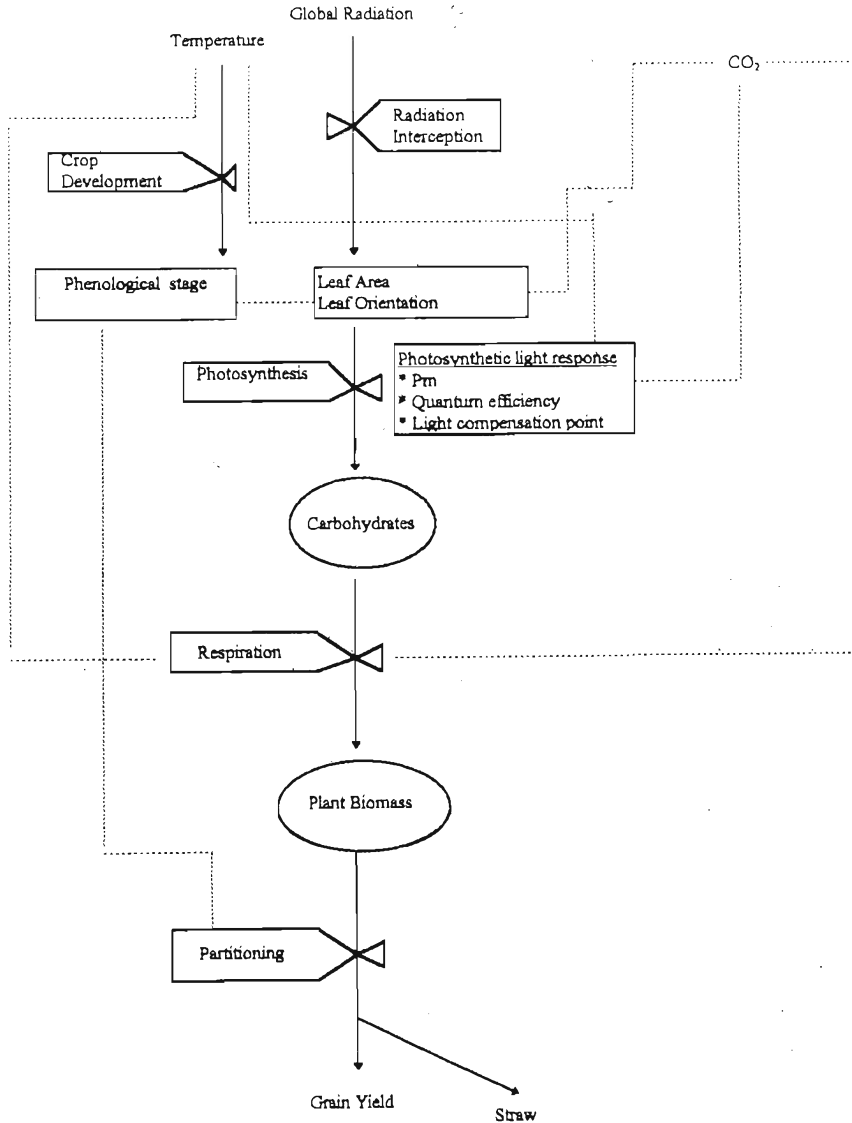


Figure 1: Relational diagram of the simulation model to predict rice yield under elevated CO<sub>2</sub> and temperature.

The model was run to simulate the growth, development and yield formation of rice crops under four different scenarios: (a) Present levels of CO<sub>2</sub> (350 ppm) and ambient temperatures; (b) Doubled CO<sub>2</sub> (700 ppm) and present ambient temperatures; (c) Air temperatures increased by 4°C at present CO<sub>2</sub> levels (350 ppm); (d) Air temperatures increased by 4°C and doubled CO<sub>2</sub> levels (700 ppm). In all four simulations, it was assumed that the rice crops are provided with adequate irrigation so that the crops do not experience water stress at any stage of their life cycle. It was further assumed that the crops were provided with adequate nutrients so that their growth and yield formation were not constrained by nutrient deficiencies. The simulations were carried out for a 12-year period from maha, 1984/85 to yala, 1996.

#### *Model components at present levels of CO<sub>2</sub> and temperature*

(a) *Total crop durations:* Following common farmer practice in the low-country dry zone, a 4-month rice variety was used for simulation during the maha season (i.e. November to March) and a 3½-month variety was used for the yala season (i.e. April to July). The sowing dates for maha and yala seasons were 15, November and 10, April, respectively.

(b) *Developmental stages and their durations:* A rice crop consists of three developmental stages, namely, vegetative, reproductive and grain filling. The vegetative stage is defined as the duration from germination to panicle initiation. The period from panicle initiation to heading is the reproductive stage and that from heading to maturity is the grain filling stage. Durations of developmental stages are determined by daily variations in temperature and photoperiod in photoperiod-sensitive varieties. However, in day-neutral varieties, crop phenology is determined only by temperature. The new, improved varieties that are grown by farmers in the low-country dry zone are day-neutral. Therefore, in the present model, crop phenology was determined on the basis of its response to temperature. A fixed amount of thermal duration ( $\Theta$ ) has to be fulfilled for completion of each successive developmental stage.<sup>5</sup>  $\Theta_i$  for a given stage can be defined as:

$$\Theta_i = \sum^d (T_a - T_b) \quad (\text{eq. 1})$$

where:  $d$  is the duration of the stage;  $T_a$  is the air temperature; and  $T_b$  is the threshold temperature at which the rate of development is zero (i.e. base temperature). A  $T_b$  value of 10°C which is representative of tropical rice<sup>5,6</sup> was used in the present study. Eq. 1 is applicable up to an optimum temperature ( $T_o$ ) at which the rate of development is maximum. For rice varieties growing in the low-country dry zone of Sri Lanka, an optimum temperature of 35°C was fixed in the present model. This was in accordance with the range of  $T_o$  values given by Squire<sup>5</sup> for crops adapted to high temperature environments. The required thermal durations for the three phenological stages (i.e. vegetative, reproductive and grain-filling) of

representative rice varieties of 4-month and 3½-month durations (Table 1) were estimated on the basis of an experiment done under controlled environmental conditions using Sri Lankan rice varieties.<sup>7</sup>

**Table 1: Estimated thermal duration (Θ) in °C days for different phenological stages of rice.**

Variety	Vegitative	Reproductive	Grain-filling
4-month	1015	492	520
3½-month	880	545	558

(c) *Incoming radiation*: The daily global radiation levels (in MJm<sup>-2</sup>d<sup>-1</sup>) for the simulation period (i.e. from October, 1984 to August, 1996) were computed from the measured daily values of sunshine duration (hours) by using a set of meteorological equations<sup>8</sup> and an empirical equation.<sup>9</sup> As the incident radiation values were calculated from measured values of daily sunshine duration, the effect of cloudiness on the incident radiation has been taken into account during the calculation. Cloudiness has also been accounted for in determining the parameters of the empirical equation<sup>9</sup> which was used in the calculation of incident radiation.

It was assumed that the daily total of global radiation energy is distributed according to a sine curve over the length of each day. The total day length was divided into 0.05 hour (3 minute) time steps and the irradiance (I), in terms of PAR, for a given time step was calculated as:

$$I = (\pi S/2T) \cdot \text{SIN}(\pi t/T) \quad (\text{eq. 2})$$

where: S is the daily global radiation in MJm<sup>-2</sup>d<sup>-1</sup>; T is day length; and t is the time after sunrise. It was assumed that 50% of the energy content in global radiation was contained within the PAR wavelength range.<sup>10</sup>

(d) *Interception of incoming radiation*: Interception of incoming radiation by a crop canopy and the distribution of intercepted radiation among the canopy leaf area determine the amount of energy available for photosynthesis and yield formation. Radiation interception by the rice canopy was quantified by the Monsi & Saeki's<sup>11</sup> application of the Beer's law for penetration of radiation into plant canopies given as follows:

$$I_L = I e^{-kL} \quad (\text{eq. 3})$$

where: I is the intensity of radiation (i.e. irradiance) incident on top of the canopy; I<sub>L</sub> is the irradiance on a horizontal plane of the canopy below a leaf area index of L; and k is the canopy light extinction coefficient which is mainly determined by the

orientation of leaves relative to the direction of incident radiation. Therefore, the amount of incident radiation intercepted by a canopy with a leaf area index of  $L$  and extinction coefficient  $k$  would be:

$$I - I_t = I(1 - e^{-kL}) \quad (\text{eq. 4})$$

(e) *Distribution of intercepted radiation*: The distribution of the above amount of intercepted radiation over the canopy leaf area needs to be quantified in order to compute canopy photosynthesis. Out of several different methods available, the approach used by Monteith<sup>12</sup> was used in the present study. Here, the canopy is divided into two categories as: (i) 'Sunlit' foliage which is the area of leaves directly-illuminated by incoming radiation penetrating into the canopy; and (ii) 'Indirectly-lit' foliage which is the area of leaves receiving radiation which has been intercepted once by the 'sunlit' foliage and subsequently transmitted to the lower leaf layers. Monteith and Unsworth<sup>13</sup> showed that the sunlit leaf area ( $L_0$ ) and indirectly-lit leaf area ( $L_1$ ) can be computed by the following equations:

$$L_0 = (1 - e^{-kL}) / k \quad (\text{eq. 5})$$

and

$$L_1 = L_0 - (L \cdot e^{-kL}) \quad (\text{eq. 6})$$

It can be shown that for large canopies with high  $L$ , both  $L_0$  and  $L_1$  tend to a limiting value of  $1/k$ .

(f) *Leaf area index and light extinction coefficient of rice canopies*: The variation of leaf area index ( $L$ ) of a crop, from germination upto the point of reaching maximum  $L$ , can be quantified by the logistic function.<sup>14</sup> Therefore, under the present levels of  $\text{CO}_2$  and temperature, the variation of  $L$  upto the point of maximum  $L$  of the simulated rice crops were specified by the following equations:

For the 4-month variety:

$$L = 7.57 [(1 + e^{4.39 - 0.116d})^{-1}] \quad (\text{eq. 7})$$

For the  $3\frac{1}{2}$ -month variety:

$$L = 7.03 [(1 + e^{5.11 - 0.170d})^{-1}] \quad (\text{eq. 8})$$

where,  $d$  is the number of days after sowing. The times of achieving maximum  $L$  were specified as 75 and 60 days after sowing (DAS) respectively for the 4-month and  $3\frac{1}{2}$ -month varieties. In both varieties, the maximum  $L$  values were maintained for the next 45-day period after which  $L$  decreased down to a value of 2

at maturity according to the following linear equations:

For 4-month variety:

$$L = 68.84 - 0.557 d \tag{eq. 9}$$

and for 3½-month variety:

$$L = 54.82 - 0.503 d \tag{eq. 10}$$

The variation patterns specified by equations 7-10, agreed with the observed patterns of L for rice crops grown in the low-country dry zone (De Costa, Unpublished).

Until the point of reaching maximum L, the light extinction coefficient (k) of both rice varieties were specified as 0.4 which is representative of the new high-yielding varieties with dwarf stature and erect leaves.<sup>6</sup> Thereafter, k was specified as 0.6 to take in to account the change in leaf angle that occurs in mature leaves.<sup>15</sup>

(g) *Photosynthetic light response*: The instantaneous gross photosynthetic rate (P) of a unit area of leaf in the canopy is primarily determined by the irradiance per unit leaf area (i). The variation of P with i (Fig. 2) can be described by an asymptotic exponential equation as following:

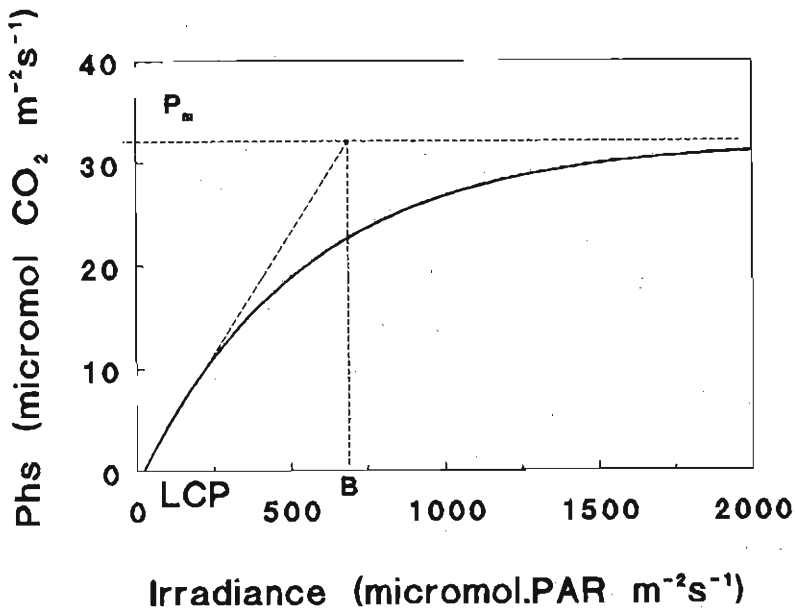


Figure 2: Photosynthetic light response curve at current CO<sub>2</sub> and temperature. Pgs- Gross photosynthetic rate. See text for explanation of symbols.

$$P = P_m (1 - e^{-(i-c)/B}) \quad (\text{eq. 11})$$

where:  $P_m$  is maximum light-saturated gross photosynthetic rate per unit leaf area;  $B$  is the irradiance per unit leaf area ( $i$ ) at which  $P_m$  is reached at initial, maximum quantum efficiency ( $\alpha$ ); and  $c$  is the light compensation point (i.e. the light intensity at which photosynthesis becomes zero). The  $P_m$  of rice at current  $\text{CO}_2$  and temperature levels was specified at  $32 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ .<sup>6</sup> It was assumed that the crops receive adequate levels of fertilizer, especially nitrogen, so that  $P_m$  is not reduced due to nitrogen deficiency. The value of  $B$  is determined by  $P_m$ ,  $\alpha$  and the light compensation point (LCP) as:

$$B = (P_m + \alpha \text{ LCP}) / \alpha \quad (\text{eq. 12})$$

For current  $\text{CO}_2$  and temperature levels, a  $B$  value of  $579.33 \mu\text{mol PAR m}^{-2} \text{ s}^{-1}$  was calculated based on the values of  $0.042 \text{ mol CO}_2 (\text{mol PAR})^{-1}$ <sup>16</sup> for  $\alpha$  and  $7.58 \mu\text{mol PAR m}^{-2} \text{ s}^{-1}$ <sup>6</sup> for LCP of rice.

Therefore, the gross photosynthetic rates per unit leaf area of sunlit ( $P_0$ ) and indirectly-lit ( $P_1$ ) foliage can be computed using eq. 11 as:

For sunlit leaves:

$$P_0 = P_m (1 - e^{-(kI/B)}) \quad (\text{eq. 13})$$

For indirectly-lit leaves:

$$P_1 = P_m (1 - e^{-(0.14 kI/B)}) \quad (\text{eq. 14})$$

As the respective areas of both sunlit- and indirectly-lit leaves tend to a limiting value of  $1/k$  at high  $L$  (eqs. 4 and 5), the irradiance per unit leaf area ( $i$ ) becomes  $kI$  and  $0.14 kI$  respectively. The constant 0.14 is the transmission coefficient<sup>13</sup> which represents the fraction of intercepted radiation transmitted through a sunlit leaf layer to be subsequently intercepted by an indirectly-lit leaf area.

(h) *Canopy photosynthesis*: The instantaneous canopy gross photosynthesis ( $P_c$ ) for a given time step of 0.05 hours (3 minutes) was computed as the sum of gross photosynthesis of sunlit and indirectly-lit foliage:

$$P_c = (P_0 \cdot L_0) + (P_1 \cdot L_1) \quad (\text{eq. 15})$$

The  $P_c$  values computed in  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  were converted to assimilated carbohydrates ( $P_{\text{CHO}}$ ) in  $\text{g [CH}_2\text{O] m}^{-2} \text{ s}^{-1}$  as:

$$P_{\text{CHO}} = P_c \times 30 \quad (\text{eq. 16})$$



indicating that each mole of CO<sub>2</sub> used in photosynthesis would produce 30 g of carbohydrates as assimilates.

(i) *Respiration*: Part of the carbohydrates assimilated by gross photosynthesis would be used in producing plant biomass consisting of various biochemical compounds (i.e. sugars, cellulose, proteins, lipids etc.). The rest would be utilized as a substrate for respiration to generate the energy required for synthesis of new plant biomass (i.e. growth respiration) and for maintaining the structure and functioning of the existing biomass (i.e. maintenance respiration). In rice, the fraction of growth respiration in total respiration is high during the vegetative and reproductive stages. On the other hand, during the grain filling period, the growth respiration decreases and the maintenance component of total respiration increases.<sup>6, 17</sup> However, despite the above variation of the relative contributions of growth and maintenance components, Yamaguchi<sup>18</sup> observed that total respiration is a relatively-constant fraction of gross photosynthesis. Monteith<sup>12, 19</sup> also concluded that despite the complex nature of the respiration process, a constant fraction of gross photosynthesis can be used to obtain an estimate of total respiration. Therefore, in the present study, for current CO<sub>2</sub> and temperature levels, a value of 0.3 was specified as the fraction of gross photosynthesis used for total respiration (R) during the vegetative and reproductive stages. A corresponding value of 0.4 was used for R during the grain filling period. These values were based on a survey of values used by other workers.<sup>12, 16</sup>

(j) *Net Photosynthesis and biomass accumulation*: The net increase of biomass (i.e. net photosynthesis · P<sub>n</sub>) for a given time step can be computed as:

$$P_n = (1 - R) P_{CHO} \quad (\text{eq. 17})$$

The computed P<sub>n</sub> values of each 0.05 hour time steps were integrated over the total day length to compute the daily accumulation of crop biomass.

(k) *Partitioning of biomass into grains*: Carbohydrates are partitioned into rice grains from two sources. The first source is current photosynthesis during the grain-filling stage. All carbohydrates synthesized from photosynthesis during grain-filling stage are translocated to grains.<sup>6, 20</sup> The second source of carbohydrates to the filling grains is the translocated assimilates which had been produced during the vegetative and reproductive stages and stored in vegetative parts, i.e. 'pre-heading storage'. According to Cock and Yoshida<sup>21</sup>, 68% of the biomass accumulated before the onset of grain filling is translocated to grains. However, when rice crops are grown with adequate supplies of water and nutrients and without experiencing extremely high or low temperatures, the percentage of pre-heading storage translocated to grains is generally lower than 68%.<sup>6</sup> Therefore, in the present simulations, it was assumed that 30% of carbohydrates assimilated during each day of vegetative and reproductive stages are ultimately translocated to grains.

This value of 30% is a weighted average of the maximum (i.e. 68%) and minimum (i.e. 0%) values for the contribution of pre-heading storage. The weighting factors were the daily gross photosynthesis and the daily total biomass of the crop up to the beginning of the grain-filling period.

Hence, the final grain yield is the sum of carbohydrates from current photosynthesis and pre-heading storage. This final grain yield was adjusted to a moisture content of 14% which is representative of the level of moisture in grains at harvest.

*Modification of model parameters for doubled CO<sub>2</sub> concentrations (700 ppm) at present temperatures*

(a) *Crop durations and radiation interception:* Increasing CO<sub>2</sub> levels without a simultaneous increase in ambient temperatures do not cause any modifications in the durations of the different developmental stages or the total duration of rice crops. Although the levels of incoming radiation do not vary, radiation interception at elevated CO<sub>2</sub> levels will be different from those at the present CO<sub>2</sub> levels because elevated CO<sub>2</sub> increases the canopy leaf area index.<sup>22</sup> Several workers including Lawlor and Mitchell<sup>22</sup> and Acock<sup>23</sup> have reported significant increases in leaf area under elevated CO<sub>2</sub>. This is not surprising as part of the increased amount of biomass produced under elevated CO<sub>2</sub>, is certain to be partitioned to leaves. Specifically, for rice, the latest research results from India<sup>24</sup> show that the leaf area per plant increased by 32% at a CO<sub>2</sub> concentration of 600 ppm. This increase of leaf area has occurred due to an increase of both the number of leaves per plant and area per leaf.<sup>24</sup> In the present simulations, doubled CO<sub>2</sub> was assumed to increase the leaf area index by 25% of the values at present CO<sub>2</sub> levels. In view of the results from Indian studies, the 25% increase in canopy leaf area index in the present simulations is reasonable as a slight reduction in the increase of leaf area index (i.e. from 32% to 25%) is possible due to self-thinning. The light extinction coefficient did not change with varying CO<sub>2</sub>.

(b) *Photosynthetic light response:* All parameters of the photosynthetic light response curve (eq. 11) would be changed at doubled CO<sub>2</sub>. Based on the predictions of Long<sup>25</sup>, doubled CO<sub>2</sub> at a temperature around 30°C increased P<sub>m</sub> by 73% (i.e. from 32 to 55.36 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>). As mentioned earlier, it was assumed throughout the model that the crops were supplied with adequate nitrogen so that P<sub>m</sub> was not constrained by a nitrogen limitation. α also would be increased by a doubling of CO<sub>2</sub>.<sup>16</sup> Based on the ratios calculated by Long<sup>25</sup>, α was increased from 0.042 mol CO<sub>2</sub> (mol PAR)<sup>-1</sup> to 0.051 mol CO<sub>2</sub> (mol PAR)<sup>-1</sup> at doubled CO<sub>2</sub>. The light compensation point decreased from 7.58 μmol PAR m<sup>-2</sup> s<sup>-1</sup> to 4.86 μmol PAR m<sup>-2</sup> s<sup>-1</sup> at doubled CO<sub>2</sub> (based on Long<sup>25</sup>). As a result of the above changes, the value of B (eq. 12) increased to 1086 μmol PAR m<sup>-2</sup> s<sup>-1</sup> at doubled CO<sub>2</sub>.

(c) *Respiration*: As rice has the C<sub>3</sub> photosynthetic pathway, elevated CO<sub>2</sub> levels would decrease photorespiration (by increasing the ratio of carboxylation to oxygenation of RUBP in the Calvin cycle) and thereby decrease total respiration.<sup>26</sup> Under ambient CO<sub>2</sub> concentrations and saturating light intensities, photorespiration in rice accounts for 40% of its gross photosynthesis.<sup>6</sup> However, it is difficult to separate the crop dry matter loss due to photorespiration from that due to dark respiration.<sup>26, 27</sup> In the present simulations, for doubled CO<sub>2</sub>, the fraction of gross photosynthesis used for total respiration (R) was decreased by 25% of its levels at present CO<sub>2</sub>. As total respiration is calculated as 30 - 40% of gross photosynthesis (shown earlier), the above-mentioned 25% reduction in total respiration would, in effect, add a fractional biomass of 7.5 - 10% (i.e.  $[30 \times 0.25] - [40 \times 0.25]$ ) of its gross photosynthesis. At the biochemical level, under ambient CO<sub>2</sub> concentrations, the enzyme RUBISCO is utilized for carboxylation (i.e. photosynthesis) and oxygenation (i.e. photorespiration) at a ratio of 3:1 (i.e. 75% : 25%).<sup>28</sup> However, even at doubled CO<sub>2</sub> concentrations, photorespiration is not totally eliminated in C<sub>3</sub> crops.<sup>23</sup> Therefore, the effective addition of 7.5 - 10% of gross photosynthesis takes in to account the amount of biomass saved due to the partial reduction of photorespiration due to elevated CO<sub>2</sub>.

(d) *Partitioning of biomass into grains*: Elevated CO<sub>2</sub> levels do not cause variations in the ratios of partitioning of assimilated carbohydrates to different organs.<sup>22</sup> Therefore, the same proportional contributions from current photosynthesis and pre-heading storage to grain yield of rice were used for simulations at both present and doubled CO<sub>2</sub> levels. Uprety<sup>24</sup> has observed a 17% increase in the number of panicles per plant and a 65% increase in the number of grains per panicle in rice growing under elevated CO<sub>2</sub>. Therefore, sink limitation under elevated CO<sub>2</sub> can be ruled out as a yield-limiting factor.

*Modification of model parameters for increased air temperatures (by 4°C) at current CO<sub>2</sub> concentrations (350 ppm)*

(a) *Phenological development of the crop*: The development of a crop through its successive phenological stages was determined on the basis of eq. 1 described earlier. Elevated temperatures shortened the durations all developmental stages because the required thermal durations were fulfilled within shorter durations. Table 2 gives the respective mean durations of different stages of rice when grown under air temperatures elevated by 4°C from the current levels. These values were computed using 12-year (1984-1996) averages of daily mean temperatures at Maha-Illuppallama for the three developmental stages of the two rice varieties used in the simulation.

(b) *Leaf area development and radiation interception*: The rate of leaf expansion is increased by elevated temperatures.<sup>5</sup> Hence, the pattern of variation of leaf area index (L) will be the same as that under current temperatures. However, it will be

confined within the shortened durations of the crops as following:

For the 4-month variety:

$$L = 7.61 [(1 + e^{4.47 - 0.139d})^{-1}] \quad (\text{eq. 18})$$

For the  $3\frac{1}{2}$ -month variety:

$$L = 7.01 [(1 + e^{5.08 - 0.199d})^{-1}] \quad (\text{eq. 19})$$

**Table 2: Mean durations (days) of developmental stages of rice at temperatures elevated by 4 °C from the current levels**

Variety	Vegetative	Reproductive	Grain-filling	Total
4-month	51	25	27	103
$3\frac{1}{2}$ -month	39	25	26	90

Note: Based on daily mean temperatures at Maha-Illuppallama during a 12-year period from 1984 to 1996

where,  $d$  is the number of days after sowing. The times of achieving maximum  $L$ , calculated on the basis of thermal durations, were 62 and 50 days after sowing (DAS) respectively for the 4-month and  $3\frac{1}{2}$ -month varieties. In both varieties, the maximum  $L$  values were estimated to be maintained for the next 30-day period after which  $L$  decreased down to a value of 2 at maturity according to the following linear equations:

For 4-month variety:

$$L = 61.28 - 0.61 d \quad (\text{eq. 20})$$

and for  $3\frac{1}{2}$ -month variety:

$$L = 50.33 - 0.56 d \quad (\text{eq. 21})$$

Radiation interception by the rice canopies at elevated temperatures would be determined according to eqs. 3 - 6. The light extinction coefficient does not change with rise in temperature.

(c) *Photosynthetic light response:* Within the range of prevailing ambient temperatures in the low-country dry zone of Sri Lanka, a temperature increase of 4°C will not cause a change in  $P_m$ <sup>16, 25</sup> However,  $\alpha$  decreases and the light compensation point (LCP) increases with increasing temperature because of increased

photorespiration. Based on calculations of Penning de Vries et al.<sup>16</sup> and Long<sup>25</sup>,  $\alpha$  was decreased from 0.042 mol CO<sub>2</sub> (mol PAR)<sup>-1</sup> at current temperature to 0.036 mol CO<sub>2</sub> (mol PAR)<sup>-1</sup> at a temperature elevated by 4°C. On the other hand, the LCP increased from 7.58  $\mu\text{mol PAR m}^{-2} \text{s}^{-1}$  to 11.52  $\mu\text{mol PAR m}^{-2} \text{s}^{-1}$ . As a result, according to eq. 12, B increased upto 891.15  $\mu\text{mol PAR m}^{-2} \text{s}^{-1}$ .

(d) *Respiration*: An increase in temperature increases respiration.<sup>26</sup> The extent of respiration increase due to elevated temperature was estimated by eq. 22<sup>4</sup> using a Q<sup>10</sup> value of 2.<sup>6</sup>

$$Q_{10} = (R_e/R)^{(10/\Delta T)} \quad (\text{eq. 22})$$

where: R<sub>e</sub> and R are the respiration rates at elevated and current temperatures respectively; and  $\Delta T$  is the temperature rise (i.e. 4°C). Therefore, according to eq. 22, the respiration rate would be increased by a factor of 1.32 with a 4°C rise in temperature.

(e) *Partitioning of biomass into grains*: The proportion of partitioning of biomass into grains is not altered by a temperature increase, either for pre-heading storage or for current photosynthesis. Although the number of sterile grains could increase with increasing temperature<sup>6</sup>, the amount of biomass partitioned in to grains could remain constant because the fertile grains could absorb the biomass that was to be filled in to the sterile grains.

*Modification of model parameters for doubled CO<sub>2</sub> concentrations (700 ppm) and for increased air temperatures (by 4°C)*: The above-discussed effects of elevated CO<sub>2</sub> and temperature would be combined here.

(a) *Crop durations and radiation interception*: The crop durations would be shortened by elevated temperatures and, as described earlier, the leaf area index would be increased by 25% by doubled CO<sub>2</sub>. The light extinction coefficient would not change and radiation interception by a rice canopy would occur according to eqs. 2-5.

(b) *Photosynthetic light response*: As P<sub>m</sub> is not affected by elevated temperature within the range considered, the value of 55.36  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  is used.  $\alpha$  is increased by elevated CO<sub>2</sub> and decreased by elevated temperature. The net result of these two opposing effects was estimated according to Long<sup>25</sup> and a value of 0.05 mol CO<sub>2</sub> (mol PAR)<sup>-1</sup> was computed. Likewise, the light compensation point is decreased by elevated CO<sub>2</sub> and increased by elevated temperature. The net effect was estimated based on Long<sup>25</sup> and a value of 8.49  $\mu\text{mol PAR m}^{-2} \text{ s}^{-1}$  was used. According to eq. 12, the computed B was 1107.53  $\mu\text{mol PAR m}^{-2} \text{ s}^{-1}$ .

(c) *Respiration*: The respiration rates which would be reduced by 25% (as described earlier, relative to current levels of  $\text{CO}_2$  and temperature) due to doubled  $\text{CO}_2$  were adjusted for elevated temperatures according to eq. 22. Hence, a factor of 0.99 was used to compute respiration rate at elevated  $\text{CO}_2$  and temperature relative to the current levels.

All models were run with a time step of 0.05 hours (i.e. 3 minutes) on the SAS statistical software and the results were integrated over the respective crop durations to obtain the final grain yields of the simulated rice crops. The 3-minute time step was selected in order to simulate the diurnal variation of canopy photosynthesis. This is essential in the computation of daily total photosynthesis and the resulting increase of crop biomass. Although the incident radiation data were on a daily basis, these were also partitioned in to 3-minute time intervals for the purpose of computing the diurnal variation of canopy photosynthesis.

## RESULTS AND DISCUSSION

### Comparison of predicted rice yields at current $\text{CO}_2$ and temperature with actual yields

Fig. 3 shows the actual rice yields obtained in Kalawewa (representing irrigated rice crops in Mahaweli 'H' area in Anuradhapura district) during the period between maha, 1984/85 and maha, 1995/96 as compared to the yields predicted from the model using meteorological data at Maha-Illuppallama and the relevant crop parameters. The actual yield data were obtained from the Socio-Economics and Planning Centre of the Department of Agriculture, Peradeniya and are based on the yields of a large number of farmer fields in the area. There was satisfactory agreement between predicted and actual rice yields.

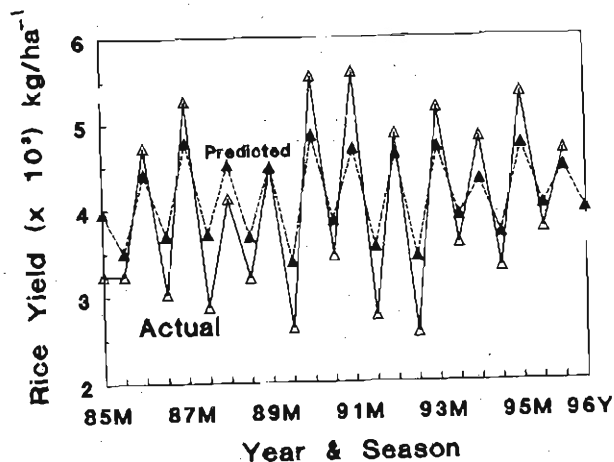


Figure 3: Irrigated rice yields predicted by the model as compared to the actual yields in the Kalawewa area.

However, the model slightly underestimated the maha yields and slightly overestimated the yala yields. The underestimation of maha yields has occurred most probably because of the fact that some farmers cultivate rice varieties of a longer duration (i.e.  $4\frac{1}{2}$ -month) than the 4-month variety used for the simulations. Under proper management, especially irrigation, a  $4\frac{1}{2}$ -month variety would have a higher yield than a 4-month variety and would cause the predicted yield to be slightly lower than the actual yield. The most probable reason for the slight overestimation of yala rice yields is the probable occurrence of soil water deficits in farmer fields and the higher atmospheric vapour pressure deficits (ranging from 1 kPa upto 4 kPa) which would cause a yield reduction. The model assumed that the yala crops are fully-irrigated and hence do not experience water deficits either in the soil or air. However, despite these unavoidable errors, the model is accurate enough to be used to make predictions about rice yields at elevated CO<sub>2</sub> and temperature levels.

### Predicted change in rice yield due to doubled CO<sub>2</sub>

Fig. 4 shows that a doubling of CO<sub>2</sub> would increase rice yields significantly. The percentage increase is around 50% relative to the current yields. This value agrees closely with the actually-observed yield increase of 47% in rice crops grown in open-top chambers in the field at doubled CO<sub>2</sub>.<sup>22, 23</sup> The yield increase of 50% predicted by the present model also agreed very closely with the 53% yield increase for rice under elevated CO<sub>2</sub> observed in the most recent Indian studies.<sup>24</sup> The yield increase is mainly due to increased leaf area, light-saturated photosynthesis ( $P_m$ ), quantum efficiency ( $\alpha$ ) and decreased respiration.

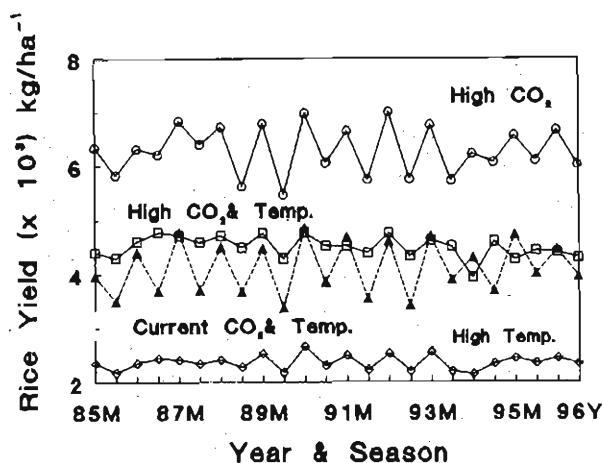


Figure 4: Predicted irrigated rice yields under different scenarios of future climate change as compared with predicted yields under current climatic conditions in the Anuradhapura district.

### **Predicted change in rice yield due to increased temperature by 4°C**

In contrast to the yield increases produced by doubled CO<sub>2</sub>, the elevated temperature causes a significant yield decrease (Fig. 4) ranging from 39-47%. This is mainly because of the shortened crop duration which would decrease radiation absorption and photosynthesis and increase respiration.

### **Predicted change in rice yield due to doubled CO<sub>2</sub> and a 4°C temperature increase**

Fig. 4 shows that the significant probable yield increases at doubled CO<sub>2</sub> would be considerably negated by a 4°C increase in temperature. In fact, in certain years, the maha yields under elevated CO<sub>2</sub> and temperature will be slightly lower than the current yields whereas, in all years, the yala yields will be slightly higher (by 3-17%). Therefore, it is clear that the negative effects of elevated temperature (i.e. shortened crop duration and increased respiration) almost totally negate the positive effects of elevated CO<sub>2</sub> (i.e. increased leaf area and photosynthesis and decreased respiration).

Much of the existing research information are in agreement with the above predictions from the present model. The most comprehensive research and modelling effort, so far, on the effects of climate change on rice was carried out at IRRI with collaboration from many South Asian countries which included Bangladesh, China, India, Indonesia, Japan, Malaysia, Myanmar, Philippines, South Korea, Taiwan and Thailand.<sup>30-32</sup> At all sites, increasing CO<sub>2</sub> alone increased simulated yields. The average yield increase was 23.6% at a CO<sub>2</sub> concentration of 510 ppm and 36.8% at 680 ppm.<sup>31</sup> However, increments in temperature decreased simulated yields. Regression analysis indicated yield declines of 6.7, 14.1 and 29.4% for temperature increases of 1, 2 and 4°C respectively (i.e. a yield decrease of 6.7 and 7.4% for each 1°C increase in temperature). The net result of the positive effect of increased CO<sub>2</sub> and the negative effect of increased temperature on the rice production in the tested countries was predicted to be an overall decrease of 3.8% under the climate of the next century.<sup>32</sup> These results showed close agreement with the predictions of the present model.

### **Implications of predicted changes in rice yield due to future climate change and recommended remedial measures**

It is clear that expected climate change in the future would not be favourable for achieving the required increases in rice production in Sri Lanka, particularly in view of the expected increases in population during the next century. Therefore, the following remedial measures are recommended:



(1) **Breeding of rice varieties with tolerance to high temperature:** As it is the effects of elevated temperature that negate the potential yield increases due to elevated CO<sub>2</sub>, varieties with greater tolerance in their physiology to temperature increases will perform better in a future climate. Therefore, the breeding efforts should be directed towards incorporating greater high-temperature tolerance to the existing high-yielding varieties.

(2) **Introduction of rice-based multiple cropping systems:** The shortened durations of the rice crops due to increased temperatures will mean that more time will be available between the two traditional rice-growing seasons. This time could be utilized either for a third rice crop or for other suitable short-duration crops. However, as availability of water will be a major factor here, crops of greater drought tolerance will have to be used. Therefore, considerable breeding effort has to be channelled to breeding drought-tolerant varieties of both rice and other field crops. Policy decisions may have to be taken to ensure that the additional *inputs (i.e. seeds, fertilizer, agrochemicals, harvesting and storage facilities)* required by the farmers for cultivation of a third crop are available in adequate quantities at the required time. It is true that the above inputs are limiting even at the present time where only two crops per year are grown. Therefore, a concerted effort to increase the availability of these inputs as a preparation for future climate change, is certain to bring about overall benefits to ensure future food security in Sri Lanka.

(3) *Increasing irrigation efficiency:* More efficient use of the available irrigation water during the two traditional growing seasons, would make a certain amount of water available for limited irrigation of a third inter-seasonal crop. Therefore, irrigation management has to be improved with a view of minimizing unproductive wastage of irrigation water and obtaining a greater yield in return for a unit of irrigation water utilized.

(4) *Promotion of research within Sri Lanka into crop responses to future climate change:* All research information for the present study had to be obtained from studies carried out in other countries because of lack relevant research in Sri Lanka. Therefore, research into plant physiological responses of rice and other important crops to elevated CO<sub>2</sub> and temperature should be promoted within Sri Lanka. This could even lead to identification of genotypes among local germplasm which have inherently greater yield potential at higher CO<sub>2</sub> and temperature levels. Furthermore, increased understanding of the internal functioning of crops under future climatic conditions will contribute significantly into breeding of crop varieties more suitable for future climates.

## Acknowledgements

The author thanks the Department of Agriculture for providing data on rice yields and K. Karunagoda, K.N. Shanmugathan and K.G.D. Jayaweera for their help in the study.

## References

- 1 Watson R.T., Rodhe H., Oeschger H. & Siegenthaler U. (1990). Greenhouse gases and aerosols. In *Climate Change: The IPCC Scientific Assessment* (eds J.T. Houghton, G.J. Jenkins & J.J. Ephraums), pp. 1-40. Cambridge University Press, Cambridge.
- 2 Watson R.T., Zinyowera M.C., Moss R.H. & Dokken D.J. (1995). *Climate Change 1995: Impacts, Adaptations and Mitigation of Climate Change: Scientific-Technical Analyses. Contribution of Working Group II to the Second Assessment Report of the Intergovernmental Panel on Climate Change*. Published for the Intergovernmental Panel on Climate Change. pp. 21-53. Cambridge University Press, Cambridge.
- 3 Penning de Vries F.W.T., Brunsting A.B. & Van Laar H.H. (1974). Products, requirements and efficiency of biological synthesis: a quantitative approach. *Journal of Theoretical Biology*, **45**: 339-337.
- 4 Jones H.G. (1992). *Plants and Microclimate: A Quantitative Approach to Environmental Plant Physiology*. Cambridge University Press, Cambridge. 428 pp.
- 5 Squire G.R. (1990). *The Physiology of Tropical Crop Production*. CAB International. 236 pp.
- 6 Yoshida S. (1981). *Fundamentals of Rice Crop Science*. IRRI, Los Banos, Philippines. 269 pp.
- 7 Piyasena H.D.A.S. (1998). Effects of temperature on development and growth characteristics of different rice varieties. B.Sc. Dissertation. Department of Crop Science, Faculty of Agriculture, University of Peradeniya (Unpublished).
- 8 List R.J. (1968). *Smithsonian Meteorological Tables*. Smithsonian Institute Press, Washington.
- 9 Samuel T.D.M.A. (1991). Estimation of global radiation in Sri Lanka. *Solar Energy*, **47**: 333-337.

- 10 Szeicz G. (1974). Solar radiation for plant growth. *Journal of Applied Ecology*, **11**: 617-636.
- 11 Monsi M. & Saeki T. (1953). The light factor in plant communities and its significance for dry-matter production. *Japanese Journal of Botany*, **14**: 22-52.
- 12 Monteith J.L. (1981). Does light limit crop production ? In *Physiological Processes Limiting Plant Productivity*. (Ed. C.B. Johnson). pp. 23-38. Butterworths, London.
- 13 Monteith J.L. & Unsworth M.H. (1990). *Principles of Environmental Physics*. 2<sup>nd</sup> Edition. Edward Arnold, London. 291 pp.
- 14 Hunt R. (1982). *Plant Growth Curves: The Functional Approach to Plant Growth Analysis*. Edward Arnold. 248 pp.
- 15 Kropff M.J., Matthews R.B., van Laar H.H. & ten Berge H.F.M. (1995). The rice model ORYZA1 and its testing. In *Modelling the Impact of Climate Change on Rice Production in Asia*. (Eds. R.B. Matthews, M.J. Kropff, D. Bachelet & H.H. van Laar). pp. 27-50. CABI/IRRI, Oxon, UK.
- 16 Penning de Vries F.W.T., Jansen D.M., ten Berge H.F.M. & Bakema A. (1989). *Simulation of ecophysiological processes of growth in several annual crops*. Simulation Monograph No. 29, Pudoc, Wageningen. 271 pp.
- 17 Tanaka A. & Yamaguchi J. (1968). The growth efficiency in relation to the growth of the rice plant. *Soil Science and Plant Nutrition*, **14**: 110-116.
- 18 Yamaguchi J. (1978). Respiration and growth efficiency in relation to crop productivity. *Journal of the Faculty of Agriculture, Hokkaido University*, **59**: 59-129.
- 19 Monteith J.L. (1981). Climatic variation and the growth of crops. *Quarterly Journal of the Royal Meteorological Society*, **107**: 749-774.
- 20 Murata Y. & Matsushima S. (1975). Rice. In *Crop Physiology*. (Ed. L.T. Evans). pp. 73-99. Cambridge University Press, Cambridge.
- 21 Cock J.H. & Yoshida S. (1972). Accumulation of <sup>14</sup>C-labelled carbohydrate before flowering and the subsequent redistribution and respiration in the rice plant. *Proceedings of the Crop Science Society, Japan*. **41**: 226-234.

- 22 Lawlor D.W. & Mitchell R.A.C. (1991). The effects of increasing CO<sub>2</sub> on crop photosynthesis and productivity: a review of field studies. *Plant, Cell and Environment*, 14 (8): 807-818.
- 23 Acock B. (1990). Effects of carbon dioxide on photosynthesis, plant growth and other processes. In *Impacts of Carbon Dioxide, Trace Gases and Climate Change on Global Agriculture*. (Eds. B.A. Kimball, N.J. Rosenberg & L.H. Allen). pp. 45-60. American Society of Agronomy, USA.
- 24 Uprety D.C. (2000). Response of rice varieties to elevated CO<sub>2</sub> using open top chamber CO<sub>2</sub> enrichment technology. In *Proceedings of the APN-SASCOM Workshop on CO<sub>2</sub> Enrichment Rice Research and Policy Interaction*. 18-20 February, 2000. Dhaka, Bangladesh (In Press).
- 25 Long S.P. (1991). Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO<sub>2</sub> concentrations: Has its importance been underestimated? *Plant, Cell and Environment*, 14 (8): 729-740.
- 26 Amthor J.S. (1991). Respiration in a future, higher CO<sub>2</sub> world. *Plant, Cell and Environment*, 14: 13-20.
- 27 Amthor J.S. (1989). *Respiration and Crop Productivity*. Springer-Verlag, Berlin.
- 28 Taiz L. & Zeiger E. (1991). *Plant Physiology*. Benjamin/Cummings Inc., California, USA.
- 29 Baker J.T., Allen J.H. & Boote K.J. (1990). Growth and yield responses of rice to carbon dioxide concentration. *Journal of Agricultural Science, Cambridge*, 115: 313-320.
- 30 Matthews R.B., Kropff M.J., Bachelet D. & van Laar L.H. (Eds.) (1995a). *Modelling the Impact of Climate Change on Rice Production in Asia*. IRRI/CAB International, 289 pp.
- 31 Matthews R.B., Kropff M.J., Bachelet D., Horie T., Lee M.H., Centeno H.G.S., Shin J.C., Mohandas S., Singh S. & Defeng Z. (1995b). Modelling the impact of climate change on rice production in Asia. In *Climate Change and Rice*. (Ed. S. Peng). pp. 314-325. Springer-Verlag, Berlin-Heidelberg.
- 32 Matthews R.B., Kropff M.J., Horie T. & Bachelet D. (1997). Simulating the impact of climate change on rice production in Asia and evaluating options for adaptation. *Agricultural Systems*, 54: 399-425.