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# Yield and photosynthetic rate of wheat under continuously high temperature

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**Abstract.** In tropical regions high temperature occurs throughout wheat growth cycle and is a major factor influencing growth and yield in this area. The aim of this work is to describe the responses to continuously-high temperatures on growth, photosynthesis and yield of wheat, under controlled conditions. Nias and Dewata (Indonesian wheat varieties) and Axe and Gadius (Australian varieties) were tested in growth room experiment with temperature and photoperiod chosen to simulate conditions on Lombok Island, at lowland (32/23°C) and highland (28/20°C) sites. The third temperature (25/15°C) was selected to represent temperature in a more temperate wheat-producing area. High temperature reduced yield and dry matter accumulation which was associated with a reduction in photosynthetic rate and stomata conductance and an increase in respiration rate. The reduction in photosynthetic rate at high temperature was not only due to lower stomatal conductance but also non-stomatal effects as mesophyll conductance and quantum yield were lower. Genetic variability in response to heat stress was evident with the Indonesian varieties being more tolerant to high temperatures than Australian varieties. Nias and Dewata produced higher yield and biomass and maintaining higher rates of photosynthesis. Maintaining high photosynthetic rate and high stomata conductance, are important characters in adapting wheat into tropical environment such as Lombok Island.

## 1. Introduction

Biomass production is influenced by the development of leaf area and the rate of photosynthesis, both of which are sensitive to high temperatures. Leaf area can be reduced at high temperatures and high temperature also affects photosynthesis and other physiological processes such as respiration, stomata conductance ( $g_s$ ) and water relations, which in turn may affect crop biomass and yield [1-3]. Reduction of net photosynthesis and an increase in respiration under high temperature may be an important factor limiting productivity of wheat in tropical environments. For example, the adaptability of plants to high temperatures has been found to be associated with the ability to maintain photosynthetic capacity [4].

Research on heat stress in wheat is extensive, but the majority of the work has examined the effects of temperature at specific growth stages, and much of the work has focussed on the effects of terminal heat stress on grain set and grain filling [5-6]. Moreover, many of the experiments on heat stress under



controlled conditions have used short term heat stress events [7-8]. There are few studies on plant growth and development in a continuous high temperature environment typical of the temperatures experienced in tropical regions and consequently the response to, and effect of this continuous high temperature on wheat yield are not well documented, or only few studies conducted.

The major limitations to wheat growth in the tropics are related to temperature, moisture and poor nutrition but heat stress is one of the common abiotic factors responsible for limiting production [9]. Yield reductions of wheat by high temperature are caused by several factors such as accelerated growth, increase in transpiration [10] and reduction in net photosynthesis [11]. High temperatures are a pervasive feature of the environment of tropical regions such as Lombok Island and although the effect can be alleviated by altitude, heat stress will be an important limitation to the productivity of wheat in this environment

## 2. Materials and methods

### 2.1. Plant material

Plant material consisted of 2 Australian (Axe and Gladius) and 2 Indonesian (Nias and Dewata) bread wheat varieties (*Triticum aestivum* L.). They were chosen as they showed the most promising results in field experiments on Lombok and they represented a range in maturity types from early to midseason.

### 2.2. Experimental details

The experiment was conducted at the Waite Campus of the University of Adelaide, Australia. Plants were grown in pots (22 cm in height and 25 cm in diameter) filled with 6.0 kg of a standard fertile potting mix (coco peat soil). The plants were grown in 3 different temperature regimes, 32/23°C, 28/20°C, and 25/15°C day/night with 12 hours' daylight, in 3 growth chambers, with 4 replications. Temperatures and photoperiod were selected to simulate conditions at sites on Lombok at a low (32/23°C) and high (28/20°C) altitudes on the island. The lowest temperature (25/15°C) was selected to represent a temperature more typical of a wheat producing area in a temperate environment and was used as a low temperature control treatment. The temperatures and daylight treatments were maintained from germination to harvest. Light intensity in the growth rooms was 500-800  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ .

Six seeds were sown and thinned to 4 plants per pot once the seedlings had established. Pots were watered to their field capacity weight 2 or 3 times a week throughout the experiment, with more frequent watering in the highest temperature treatment, to avoid the occurrence of drought stress. The amount of water added was recorded.

### 2.3. Gas exchange measurements

A week after anthesis photosynthesis was measured on the flag leaf using a LI-6400 portable gas exchange system (LI-COR Inc., Lincoln NE, USA). This time was selected as representing a critical phase of crop development when grain set is determined and grain growth is commencing. Measurements were made between 9 am and 1 pm. Two sets of measurements were made: a light response curve and a CO<sub>2</sub> response curve. Light intensity was set at 800  $\mu\text{mol m}^{-2} \text{s}^{-1}$  with a red/blue light source for the CO<sub>2</sub> response curve and the CO<sub>2</sub> concentration was set at 400  $\mu\text{mol mol}^{-1}$  for the light response curve. Leaf to air VPD was maintained at 1.1 kPa. The effect of temperature on non-stomatal control of photosynthetic capacity was analysed in two ways: by measuring CO<sub>2</sub> assimilation-intercellular CO<sub>2</sub> (*A:C<sub>i</sub>*) response curves and by measuring light response curves. *A:C<sub>i</sub>* response curves for individual leaves were obtained with a series of measurements, where *A* was initially measured after 10–15 min at ambient CO<sub>2</sub> (400  $\mu\text{mol mol}^{-1}$ ). To determine the initial slope of the *A:C<sub>i</sub>* curve, the CO<sub>2</sub> concentration was gradually decreased to 0  $\mu\text{mol mol}^{-1}$  (300, 200, 100, 30 and 0  $\mu\text{mol mol}^{-1}$ ). The CO<sub>2</sub> concentration was then returned to 300  $\mu\text{mol mol}^{-1}$  before progressively increasing it to 800  $\mu\text{mol mol}^{-1}$  (300, 500, 600, 800  $\mu\text{mol mol}^{-1}$ ) to complete the

curve. The light response curve was used to estimate the rate of mitochondrial respiration and the quantum efficiency of the plants at each temperature. The response curve was derived by measuring photosynthesis rates sequentially at light intensities of 2,000, 1,500, 1,000, 500, 200, 100, 50, 25 and 0  $\mu\text{mol m}^{-2} \text{s}^{-1}$  after 2 mins equilibration at the new light intensity. The photosynthetic rate under zero light intensity was used as an estimate of mitochondrial respiration rate and the quantum efficiency was derived from the slope of the photosynthetic response between 0 and 100  $\mu\text{mol m}^{-2} \text{s}^{-1}$ .

### 3. Results and discussion

#### 3.1. Gas exchange measurements

Leaf temperatures were close to the air temperature with Nias showing a consistently lower temperature. At the two higher temperatures difference between air and leaf temperature was associated with a higher transpiration rate and stomatal conductance in this variety. Maximum photosynthetic rates declined with increased temperatures with the largest difference occurring between 28/20°C and 32/23°C (table 1).

**Table 1.** Leaf temperature ( $T_{\text{leaf}}$ ; °C), maximum rate of photosynthesis (A;  $\mu\text{mol m}^{-2} \text{s}^{-2}$ ), stomatal conductance ( $g_s$ ;  $\text{mol m}^{-2} \text{s}^{-2}$ ), apparent mesophyll resistance ( $g_m$ ), ratio of internal and external partial pressures of  $\text{CO}_2$  ( $C_i:C_a$ ), and dark respiration rate (R;  $\mu\text{mol m}^{-2} \text{s}^{-2}$ ) in four wheat varieties grown at three temperatures. Measurements were made on the flag leaf at anthesis.

| Treat            | Variety  | $T_{\text{leaf}}$ | A      | $g_s$  | $g_m$  | $C_i:C_a$ | R      |
|------------------|----------|-------------------|--------|--------|--------|-----------|--------|
| 25/15            | Axe      | 25.2              | 22.6   | 0.37   | 0.081  | 0.71      | 1.9    |
|                  | Gladius  | 26.3              | 14.2   | 0.25   | 0.049  | 0.74      | 0.8    |
|                  | Nias     | 24.9              | 25.1   | 0.65   | 0.080  | 0.81      | 1.8    |
|                  | Dewata   | 25.1              | 22.7   | 0.41   | 0.079  | 0.74      | 2.2    |
|                  | Mean     | 25.4              | 21.2   | 0.42   | 0.072  | 0.75      | 1.6    |
| 28/20            | Axe      | 29.7              | 21.1   | 0.17   | 0.121  | 0.45      | 1.8    |
|                  | Gladius  | 31.1              | 15.9   | 0.14   | 0.081  | 0.50      | 1.6    |
|                  | Nias     | 28.8              | 21.9   | 0.33   | 0.081  | 0.70      | 1.3    |
|                  | Dewata   | 29.4              | 18.9   | 0.42   | 0.064  | 0.77      | 1.9    |
|                  | Mean     | 29.7              | 19.5   | 0.27   | 0.087  | 0.61      | 1.6    |
| 32/23            | Axe      | 33.4              | 11.9   | 0.13   | 0.053  | 0.57      | 2.2    |
|                  | Gladius  | 34.3              | 13.1   | 0.14   | 0.059  | 0.56      | 2.0    |
|                  | Nias     | 28.2              | 16.9   | 0.32   | 0.065  | 0.73      | 1.7    |
|                  | Dewata   | 33.4              | 8.1    | 0.22   | 0.025  | 0.81      | 2.4    |
|                  | Mean     | 32.3              | 12.5   | 0.21   | 0.049  | 0.67      | 2.1    |
| SED <sup>A</sup> |          |                   |        |        |        |           |        |
|                  | Temp     | 0.24              | 1.08   | 0.027  | 0.0048 | 0.015     | 0.17   |
|                  | Temp.Var | 0.47              | 2.16   | 0.054  | 0.0096 | 0.030     | 0.33   |
| F Prob           |          |                   |        |        |        |           |        |
|                  | Temp     | <0.001            | <0.001 | <0.001 | <0.001 | <0.001    | 0.052  |
|                  | Temp.Var | <0.001            | <0.001 | <0.001 | <0.001 | <0.001    | <0.001 |

<sup>A</sup> Standard error of the difference among temperatures and among varieties within each temperature.

Stomatal conductance decreased with an increase in temperature and there were significant differences among varieties at each temperature. The Indonesian varieties maintained higher stomatal conductance at each temperature compared to Axe and Gladius, but this was most evident at the two highest temperatures. This was reflected in higher values of  $C_i:Ca$  at 28/20°C and 32/23°C. Estimates of dark respiration showed small differences among the three temperatures and among varieties at each temperature, but at 28/20°C and 32/23°C Nias tended to have a slightly lower respiration rate compared to the other varieties (table 1).

Quantum efficiency of photosynthesis declined with increasing temperatures in all the varieties except Gladius which showed little change, although its value was lower than the others at 25/15°C which contributed to its stability (table 2). Axe and Dewata, which showed the lowest photosynthetic rates at 32/23°C, had quantum efficiencies significantly lower than Gladius and Nias. Temperature affected the  $A:C_i$  curves (figure 1). The initial slope of the  $A:C_i$  curve estimates the RuBP-carboxylase-limited  $CO_2$  fixation capacity of plants [12,13]. At 32/23°C the lowest value was estimated for Dewata with no significant difference among the other varieties. Interestingly there was a consistent increase in  $CO_2$  fixation at 28/20°C in all varieties except Dewata (table 2).

The reduction in photosynthetic rate with increasing temperatures was most strongly correlated with declines in stomatal conductance ( $r= 0.71$ ), apparent mesophyll resistance ( $r= 0.76$ ) and quantum efficiency ( $r= 0.83$ ). The reduction in mesophyll resistance was also associated with a lower initial slope of the  $CO_2$  response curve. The effects of temperature on photosynthesis and leaf conductance were also reflective of the variation in whole plant growth. Dry matter production at maturity was correlated with quantum efficiency ( $r= 0.73$ ) and weakly, but significantly, with mesophyll resistance ( $r= 0.59$ ) while grain yield was significantly correlated with photosynthetic rate ( $r= 0.73$ ), stomatal conductance ( $r= 0.58$ ) and quantum yield ( $r= 0.74$ ).

### 3.2. *Photosynthesis and whole plant growth*

It is known that high temperature may induce stomatal closure and reduce photosynthesis [14]. Measurements of the photosynthetic rates of flag leaves at anthesis showed a substantial decline at 32/23°C compared to 25/15°C, but relatively little reduction at 28/20°C. Tolerance to moderate to high temperatures has been reported in other temperate crops; for example, it was found that photosynthetic rates of mature pea leaves changed by less than 10% when exposed to temperatures between 25°C and 35°C [15]. The reduction in photosynthetic rate at 32/23°C was due to stomatal and non-stomatal effects because the stomatal conductance, mesophyll resistance and quantum yield were lower (table 1).

The higher the temperature the yield decreases both the dry matter and grain yield and also the harvest index (HI). The decrease in HI shows the grain yield is more affected than dry matter. However, this temperature increase did not affect the quality of the seeds, which showed no difference in kernel weight (table 3).

While it is often difficult to demonstrate a direct effect of leaf photosynthetic rates on whole plant growth and yield, in this experiment differences in photosynthetic rates measured at anthesis were significantly correlated with observed difference in yield. Previous field studies in both warm and temperate environments have also found that differences in yield among varieties can be related to differences in photosynthetic rates and in stomatal conductance [16,17] and similar trends were observed in the current experiment, although the relationships were largely due to the growth environment rather than varieties. However, at 32/23°C it is notable that Nias maintained a high yield relatively to the other varieties which was associated with a high stomatal conductance and photosynthetic rate. High photosynthetic rates also contributed to the storage of WSC and ultimately to kernel weight.

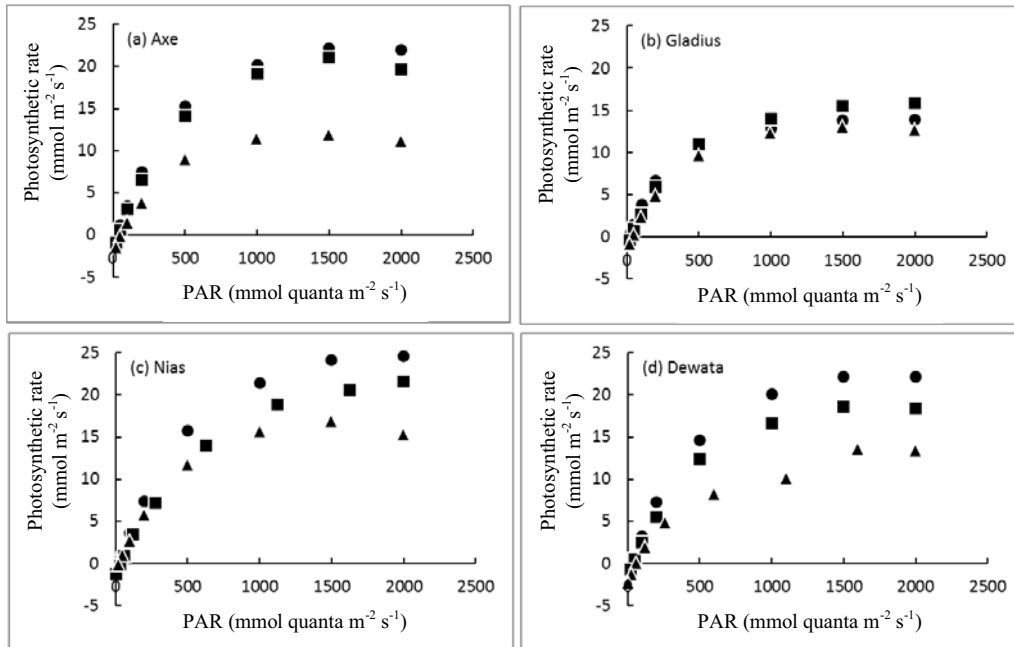
**Table 2.** The effects of temperature on the initial slope of the  $A:C_i$  curve and the light response curve for four varieties of wheat grown at three temperatures. The values are shown as the mean  $\pm$  s.e.m based on the regression at either external  $nCO_2$  concentrations of 50, 100, 150 and 200  $\mu mol mol^{-1}$  or light at 0, 25, 50 and 100  $\mu mol m^{-2} s^{-1}$ . All regressions were significant ( $P < 0.001$ ).

| Variety                                    | Temperature ( $^{\circ}C$ ) |                  |                  |
|--|-----------------------------|------------------|------------------|
|  | 25/15 $^{\circ}$            | 28/20 $^{\circ}$ | 32/23 $^{\circ}$ |
| CO <sub>2</sub> response ( $\times 10^2$ ) |                             |                  |                  |
| Axe  | 11.7 $\pm$ 0.04             | 28.4 $\pm$ 1.20  | 8.8 $\pm$ 0.74   |
| Gladius                                    | 6.1 $\pm$ 0.30              | 15.0 $\pm$ 0.59  | 9.4 $\pm$ 0.47   |
| Nias                                       | 9.1 $\pm$ 0.62              | 11.8 $\pm$ 1.00  | 8.5 $\pm$ 0.69   |
| Dewata                                     | 10.8 $\pm$ 0.70             | 7.8 $\pm$ 0.41   | 5.7 $\pm$ 0.08   |
| Light response ( $\times 10^3$ )           |                             |                  |                  |
| Axe  | 5.2 $\pm$ 0.20              | 5.0 $\pm$ 0.21   | 3.6 $\pm$ 0.23   |
| Gladius                                    | 4.4 $\pm$ 0.07              | 4.3 $\pm$ 0.21   | 4.2 $\pm$ 0.08   |
| Nias                                       | 5.4 $\pm$ 0.16              | 4.0 $\pm$ 0.07   | 4.2 $\pm$ 0.44   |
| Dewata                                     | 5.4 $\pm$ 0.03              | 4.4 $\pm$ 0.15   | 3.6 $\pm$ 0.21   |

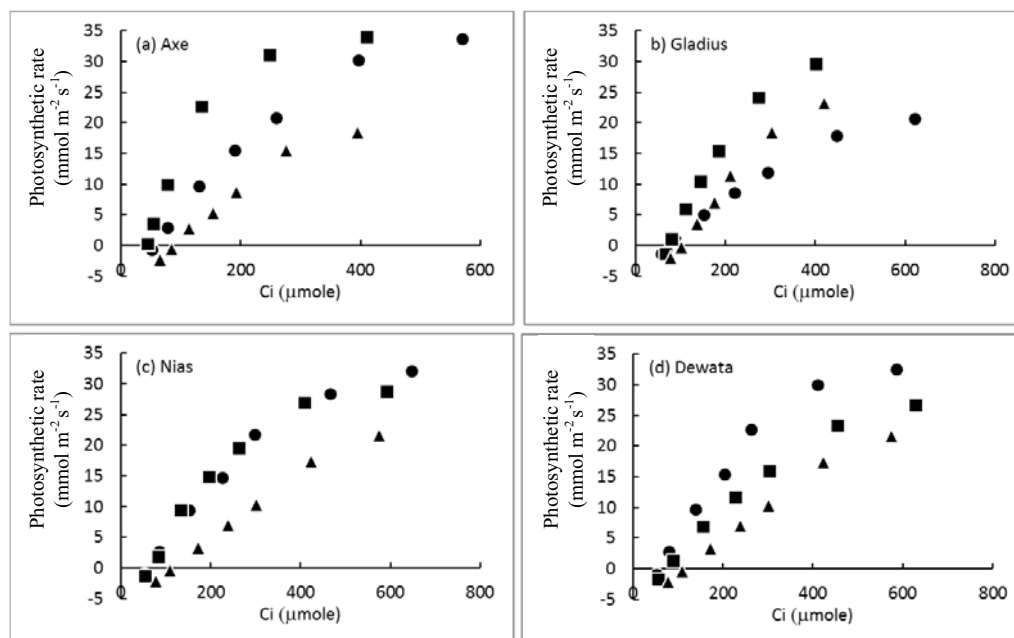
**Table 3.** Plant yield and yield components of four wheat varieties grown under three temperature regimes.

| Temperature | Variety          | Total dry matter | Grain yield | Kernel weight | HI     |
|-------------|------------------|------------------|-------------|---------------|--------|
|             |                  | (g per plant)    |             | (mg)          | (%)    |
| 25/15       | Axe              | 37.9             | 16.2        | 29.1          | 42.9   |
|             | Gladius          | 48.0             | 16.7        | 29.8          | 34.8   |
|             | Nias             | 39.4             | 17.2        | 33.1          | 43.6   |
|             | Dewata           | 40.9             | 16.0        | 36.7          | 39.2   |
|             | Mean             | 41.5             | 16.5        | 32.2          | 40.1   |
| 28/20       | Axe              | 26.2             | 11.3        | 28.1          | 42.7   |
|             | Gladius          | 42.6             | 14.6        | 27.2          | 34.3   |
|             | Nias             | 26.5             | 12.3        | 37.8          | 46.8   |
|             | Dewata           | 26.3             | 12.0        | 34.5          | 46.1   |
|             | Mean             | 30.4             | 12.6        | 31.9          | 42.5   |
| 32/23       | Axe              | 5.1              | 1.8         | 24.2          | 36.7   |
|             | Gladius          | 20.6             | 3.0         | 23.9          | 13.6   |
|             | Nias             | 13.9             | 5.7         | 38.2          | 41.1   |
|             | Dewata           | 17.1             | 3.8         | 30.1          | 22.9   |
|             | Mean             | 14.2             | 3.6         | 29.1          | 28.6   |
|             | SED <sup>A</sup> |                  |             |               |        |
|             | Temp             | 1.43             | 0.72        | 1.66          | 2.06   |
|             | Temp.Var         | 2.81             | 1.11        | 2.76          | 3.51   |
|             | F Prob           |                  |             |               |        |
|             | Temp             | <0.001           | <0.001      | ns            | <0.001 |
|             | Temp.Var         | <0.001           | 0.003       | <0.001        | <0.001 |

<sup>A</sup> Standard error of the difference among temperatures and among varieties within each temperature.



**Figure 1.** The light response curves for four wheat varieties grown at 25/15°C (●), 28/20°C (■) or 32/23°C (▲).



**Figure 2.** The CO<sub>2</sub> response curves for four wheat varieties grown at 25/15°C (●), 28/20°C (■) or 32/23°C (▲).

#### 4. Conclusions

High temperature reduced yield and dry matter accumulation of wheat which are caused by accelerated growth, reduced grain set, reduction in photosynthetic rate, and stomatal conductance. There was some evidence of genetic variability to heat stress. The difference in yield among varieties at high temperature was related to differences in photosynthetic rate and stomatal conductance. The Indonesian varieties were more tolerant to high temperature with higher photosynthetic rate at high temperature.

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