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The effects of continuously high temperatures on apical development and yield of four varieties of wheat

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Abstract. The aim of the experiment was to examine how wheat responded to an extended period of high temperatures under controlled conditions to supplement field studies with these varieties on Lombok Island. Two Indonesian wheat varieties (Nias and Dewata) and two Australian varieties (Axe and Gladius) were examined in growth room experiments at 3 different temperature regimes 32/23°C, 28/20°C and 25/15°C day/night with 12 h daylight. Temperature and photoperiod were selected to simulate conditions on Lombok Island, at lowland (32/23°C) and highland (28/20°C) sites. A third temperature (25/15°C) was selected to represent the temperature in a more temperate wheat producing area. The rate of plant development increases with the rise of the temperatures up to an optimum temperature and slower after further increases. Despite being exposed to high temperatures from the establishment, the effect of high temperature was more severe during the reproductive stage as seen by the fact that yield was more affected than dry matter accumulation and yield was most strongly related to grain number. 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.

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1. Introduction

High temperature is a major environmental factor determining crop growth and yield. Many of the experiments on heat stress under controlled conditions have used short term heat stress events [1,2]. 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 the few studies conducted have shown varying results.

Heat stress is one of the common abiotic factors responsible for limiting production and the major limitations to wheat growth in the tropics is related to temperature, moisture and poor nutrition [3]. Yield reductions of wheat by high temperature are caused by several factors such as accelerated growth, increase in transpiration and reduction in net photosynthesis [4]. The effects of high temperature on growth and development of wheat have been widely reviewed [2]. An increase in average daily temperature above 20-25°C hastens phenological development such as timing of double ridge, terminal spikelet initiation, and duration of spikelet primordial initiation as well time to flowering of wheat [5,6,7], but further increases in temperature can delay development [8]. Heat stress at specific growth stages can reduce yields significantly with the period just prior to and during



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flowering being especially sensitive [5]. Increased sterility and reductions in kernel size can occur with even short exposures to the high temperature around flowering [9,10] and grain growth rates and final kernel weight are sensitive to temperatures above about 25°C [7].

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2. Materials and Methods

a. *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.

b. *Experimental details.* The experiment was conducted at the Waite Campus of the University of Adelaide, Australia. Plants were grown in pots (22cm in height and 25cm in diameter) filled with 6.0 kg of a standard fertile potting mix (coco peat soil). 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 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 $\mu\text{mol quanta/m}^2/\text{s}$.

c. *Measurement of plant development and growth; Plant dissection.* To monitor apical development of the varieties in each growth room, 30 seeds of each variety were sown in a tray filled with the same potting mix and plant samples taken regularly for apical dissection.

3. Results and Discussion

3.1. Plant development.

There were small effects of temperature on the time to DR and TSI but bigger differences were found in the time to flowering. Larger differences in rates of development generally occurred between 25°/15°C and 28°/20°C with relatively smaller differences between 32°/23°C and 28°/20°C. Plants grown at 25°/15°C were harvested 10-20 d later than those grown at 32°/23°C.

Times to DR and TSI in the two Australian varieties decreased (Axe) or were unaffected (Gladius) as temperature increased from 25°/15°C to 28°/20°C but in both varieties, time to DR stage was delayed at 32°/23°C. However, the early development of the 2 Indonesian varieties was less sensitive to high temperature as their time to DR and TSI showed no significant difference at 28°/20°C and 32°/23°C. Flowering times spanned 15-20 days among the varieties at each temperature with Axe being the earliest and Dewata the latest (Table 1). Time to flower became shorter with higher temperatures in all varieties.

Table 1. Time taken to reach specific growth stages in four varieties of wheat grown at three temperatures. Values are shown as the mean \pm standard error of the mean (n=4)

| | Temperature ($^{\circ}$ C) | | |
|-------------------------------------|-----------------------------|------------------|------------------|
| | 25/15 | 28/20 | 32/23 |
| Double ridge | | | |
| Axe | 17.2 \pm 0.7 | 15.8 \pm 0.2 | 17.5 \pm 0.9 |
| Gladius | 21.8 \pm 0.5 | 21.8 \pm 0.8 | 26.8 \pm 0.9 |
| Nias | 20.8 \pm 0.2 | 20.2 \pm 0.5 | 19.8 \pm 0.5 |
| Dewata | 30.4 \pm 0.4 | 30.2 \pm 0.2 | 31.4 \pm 0.2 |
| Terminal Spikelet Initiation | | | |
| Axe | 25.4 \pm 0.4 | 22.2 \pm 0.5 | 23.8 \pm 0.8 |
| Gladius | 32.0 \pm 0.0 | 31.2 \pm 0.5 | 38.6 \pm 0.4 |
| Nias | 34.4 \pm 0.2 | 30.8 \pm 0.5 | 29.6 \pm 0.2 |
| Dewata | 41.6 \pm 0.4 | 41.2 \pm 0.5 | 40.4 \pm 0.4 |
| Anthesis (ZGS 65) | | | |
| Axe | 56.0 \pm 0.71 | 45.5 \pm 0.50 | 44.3 \pm 0.85 |
| Gladius | 70.5 \pm 0.50 | 63.5 \pm 0.65 | 61.0 \pm 0.82 |
| Nias | 63.3 \pm 0.48 | 53.3 \pm 0.75 | 48.5 \pm 0.65 |
| Dewata | 75.5 \pm 0.29 | 71.8 \pm 0.25 | 68.5 \pm 0.50 |
| Maturity | | | |
| Axe | 115.3 \pm 0.48 | 92.5 \pm 0.29 | 93.8 \pm 0.48 |
| Gladius | 129.5 \pm 0.50 | 115.8 \pm 0.25 | 119.3 \pm 0.75 |
| Nias | 118.3 \pm 0.48 | 102.3 \pm 0.48 | 97.3 \pm 0.25 |
| Dewata | 127.5 \pm 0.50 | 113.3 \pm 3.61 | 107.5 \pm 0.29 |

8 The rate of plant development increases with high temperature up to an optimum temperature after which development slows with further increases in temperatures [8]. This effect was apparent in the present experimental though there were differences among varieties investigated. Times to DR and TSI were little affected or reduced when the growth temperature was raised to 28 $^{\circ}$ /20 $^{\circ}$ C but they were delayed by 1.5-5 d (DR) or by 1.5-7 d (TSI) at 32 $^{\circ}$ /23 $^{\circ}$ C in the two Australian varieties. Based on its greater responses in DR and TSI, the early development of Gladius seems to be relatively more sensitive to high temperature than the other varieties. The optimum temperature for early development is around 21 $^{\circ}$ C [7] and delays in DR and TSI with higher temperatures and genetic differences in sensitivity to high temperature have been reported previously [11]. It is notable that the rate of development of the Indonesian varieties, which presumably were developed for warm climates, appears to be less sensitive to high temperatures at these early stages. The response in flowering time differed from that observed with DR and TSI: time to flower became progressively shorter with higher temperatures in all varieties up to 32 $^{\circ}$ /23 $^{\circ}$ C and the Indonesian varieties were equally sensitive as the Australian varieties. It has been shown by Slafer and Rawson [7] that the optimum temperature for development increases in later growth stages and the fact that time to flower is not delayed at the highest temperature is consistent with a higher optimum temperature for development after the DR stage.

Table 2. Plant yield and yield components of four wheat varieties grown under three temperature regimes.

| Temp. | Variety | Total dry matter (g/plant) | Grain yield | Ears plant ⁻¹ | Spikelet ear ⁻¹ | Grains spikelet ⁻¹ | Grain number plant ⁻¹ | Kernel weight (mg) |
|------------------|----------|-------------------------------|-------------|--------------------------|----------------------------|-------------------------------|----------------------------------|-----------------------|
| 25/15 | Axe | 37.9 | 16.2 | 14.1 | 12.9 | 3.2 | 590 | 29.1 |
| | Gladius | 48.0 | 16.7 | 16.6 | 13.7 | 2.6 | 568 | 29.8 |
| | Nias | 39.4 | 17.2 | 11.5 | 15.7 | 2.9 | 525 | 33.1 |
| | Dewata | 40.9 | 16.0 | 9.8 | 18.4 | 2.5 | 447 | 36.7 |
| | Mean | 41.5 | 16.5 | 13.0 | 15.2 | 2.8 | 532 | 32.2 |
| 28/20 | Axe | 26.2 | 11.3 | 15.3 | 11.1 | 2.6 | 402 | 28.1 |
| | Gladius | 42.6 | 14.6 | 24.8 | 12.5 | 1.7 | 542 | 27.2 |
| | Nias | 26.5 | 12.3 | 10.2 | 13.9 | 2.3 | 329 | 37.8 |
| | Dewata | 26.3 | 12.0 | 8.9 | 15.3 | 2.6 | 348 | 34.5 |
| | Mean | 30.4 | 12.6 | 14.8 | 13.2 | 2.3 | 405 | 31.9 |
| 32/23 | Axe | 5.1 | 1.8 | 5.3 | 8.8 | 1.6 | 74 | 24.2 |
| | Gladius | 20.6 | 3.0 | 18.5 | 12.6 | 0.5 | 120 | 23.9 |
| | Nias | 13.9 | 5.7 | 9.2 | 11.3 | 1.4 | 150 | 38.2 |
| | Dewata | 17.1 | 3.8 | 8.5 | 13.0 | 1.2 | 125 | 30.1 |
| | Mean | 14.2 | 3.6 | 10.4 | 11.4 | 1.2 | 117 | 29.1 |
| SED ^A | | | | | | | | |
| | Temp | 1.43 | 0.72 | 0.84 | 0.62 | 0.16 | 29.5 | 1.66 |
| | Temp.Var | 2.81 | 1.11 | 1.67 | 1.22 | 0.32 | 53.1 | 2.76 |
| F Prob | | | | | | | | |
| | Temp | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | ns |
| | Temp.Var | <0.001 | 0.003 | <0.001 | <0.001 | 0.003 | 0.006 | <0.001 |

High temperature reduced the time to anthesis, which was related to a reduction in yield. The relationships for the two early varieties (Axe and Nias) and the two later varieties (Gladius and Dewata) differed. The reduced yield was also associated with a reduction in the time between TSI and anthesis. There was no association between yield and time to DR or TSI (data not shown). The time from TSI to anthesis includes the period of floret development and the relationship observed is consistent with the importance of grain number and grains per spikelet to yield observed in this experiment as well as in the field experiments. Therefore, extending the period of ear development, including time from TSI to anthesis could be used to increase grain yield. However this strategy may be limited at very high temperatures: the largest reduction in yield and grain number generally occurred between 28°/20°C and 32°/23°C, when there was a relatively small change in the duration of the TSI-anthesis period. While the rate of development is an important influence on yield, at very high temperatures heat stress appears to become an overriding factor.

3.2. Variation in response to high temperature among varieties

High temperature reduced most measures of growth and yield, but there was evidence of genetic variation in sensitivity to high temperature. All varieties showed a large reduction in yield when grown at 32°/23°C, but the two Indonesian varieties showed a smaller yield loss than the Australian varieties. The yields of Nias and Dewata at 32°/23°C were higher than those of Axe and Gladius and the reduction in yields were less: grain yields of Axe and Gladius were 89% and 82% lower respectively at 32°/23°C compared to the control temperature, while the yield losses of Nias and Dewata were 67% and 76% respectively. Compared to the Australian varieties, Nias and Dewata at 32°/23°C produced more biomass at flowering and showed smaller relative losses in biomass relative to the control, produced heavier kernels and maintained ear numbers better. These results suggest the two Indonesian varieties may possess inherently higher levels of heat tolerance compared to the two Australian varieties. Nias, in particular, possessed a number of traits that suggested it is more tolerant to high temperature compared to the other varieties. It produced higher biomass at high temperatures.

4. Conclusion

The rate of plant development increases with high temperatures up to an optimum temperature and slower after further increases. High temperature reduced yield and dry matter accumulation of wheat which are caused by accelerated growth, reduced grain set. The effect of high temperature is more severe during the reproductive stage as seen by the fact that yield is affected more than dry matter accumulation. Moreover, the number of grains/plant which reflects grain set was strongly correlated with yield and this was related to the duration of the period of spikelet development.

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