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Water use, water use efficiency, water soluble carbohydrate and yield of four varieties of wheat in continuously high temperatures

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Abstract. High temperatures are a common 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. The objectives of the experiment were to observe the responses of water use (WU), water use efficiency (WUE) and water soluble carbohydrate (WSC) to high temperatures on growth and yield of wheat under controlled conditions. In this experiment plants were grown under growth chambers at temperatures to simulate low and high elevation locations on Lombok Island. Water use, water use efficiency, WSC and yield of 4 wheat genotypes (2 Australian and 2 Indonesian varieties) grown at 3 temperatures (32°/23°C, 28°/20°C, and 25°/15°C day/night) were compared. Variation in water use, water use efficiency, and the concentration of water soluble carbohydrate was found. Indonesian wheat varieties, Nias and Dewata produced higher yield and biomass and maintaining higher rates of water use and remobilisation of water soluble carbohydrate from vegetative tissues to grain. The accumulation of water soluble carbohydrates was an important adaptive characteristic that was strongly associated with grain weight and grains per spikelet and maintained better yield.

1. Introduction

The feasibility of growing tropical wheat in parts of Indonesia is being investigated currently as a means of diversifying cropping systems in response to predicted changes in climate [1]. In tropical regions high temperatures may persist for long periods of time commencing early in the growing season.

Recent field studies with wheat in Lombok have demonstrated that yield is sensitive to the differences in growing season temperature associated with altitude: yields increased by approximately 500 kg ha⁻¹ for each 1°C fall in temperature associated with increases in altitude [2]. The field experiments in Lombok also found yield was more strongly related to grains/m² than to kernel weight, suggesting the effects of high temperature on pre-anthesis growth is more important to yield than post-anthesis growth. The major limitations to wheat growth in the tropics are related to temperature, moisture and poor nutrition [3, 4], but heat stress is one of the common abiotic factors responsible for limiting production [5]. Yield reductions of wheat by high temperature are caused by several factors such as accelerated growth, increase in transpiration [6] and reduction in net photosynthesis [7].



Photosynthesis and remobilisation of stored water-soluble carbohydrate (WSC) are the two major sources of carbon during grain filling period [8]. WSC can make a significant contribution to final grain yield of about 10–20% under relatively non-stressed conditions [9] but post-heading stress, when photosynthesis is reduced, increases the contribution of WSC to final yield to 50% or more [10–12]. Therefore, remobilisation of WSC stored temporarily in the wheat stem helps to maintain the supply of carbon to the grain when the rate of photosynthetic production has declined [10, 13]. However, a significant proportion of the WSC stored in the stems accumulates prior to flowering and prolonged heat stress may limit the amount of WSC stored in the stem, limiting the ability of these stored reserves to buffer against environmental stress. Ruuska *et al.* [14] demonstrated that genetic variation exists for WSC accumulation in the stems at anthesis. The ability to accumulate WSC may therefore help plants adapt to high temperatures. It can probably be anticipated that the reductions in photosynthesis and the increases in respiration that occur under high temperatures will restrict the accumulation of WSC. However, little is known about the effects of prolonged exposure to high temperature on the concentrations of WSC in wheat or whether the levels of genetic variation reported under cooler temperatures is expressed under high temperatures.

The objectives of the current experiment were to develop a better understanding of wheat plant responses to prolonged high temperatures as a means of reducing the effects of heat stress on the growth and yield and improving the adaptation of wheat in Lombok Island.

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.

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.

Yield was measured by weighing all the grains from all 4 plants in each pot. Water use efficiency based on total dry matter (WUE_{dm}) and grain yield (WUE_y) were calculated from total biomass and yield at maturity and the total water use over the course of the experiment.

2.3. Measurement of water soluble carbohydrate

Whole stem samples from anthesis and maturity were dried and grounded in a Wiley mill to pass a 1-mm sieve. Carbohydrates were extracted from 0.1 g (range 0.100 to 0.110) of stem material by extracting at 80°C with 8 ml of 80% ethanol (v/v) followed by extractions at 60°C with 8 ml of distilled water. Water extractions were repeated twice. Extraction time was 60 min for each, after which tubes were centrifuged at room temperature for 10 minutes at 3400 rpm. Extracts were then

combined. This procedure has been found to extract the soluble carbohydrates from plant tissue [10, 15]. Total carbohydrates in the extract were analysed by the anthrone method of Yemm and Willis [16] with fructose as a standard.

2.4. Experimental design and data analysis

At each temperature treatment (environment) the varieties were compared in a randomised complete block design with four replicates. The combined analysis treated Temperature as a fixed effect in the multi-environment analysis. The data were analysed with GenStat statistical package (VSN International Ltd, United Kingdom) by REML using the Multiple Experiments option. Temperature and Variety were considered as fixed effects.

3. Results and discussion

3.1. Biomass production and yield

Biomass accumulation was reduced when plants were grown at high temperatures. The average reduction as compared to the 25°/15°C control was 26% at 28°/20°C and 59% at 32°/23°C but varieties differed in their response. Dry matter at anthesis in the Australian varieties Axe and Gladius was affected more by high temperature than Nias and Dewata. When grown at 32°/23°C biomass of Axe was 78% lower and Gladius 70% lower than the control, whereas the reductions were 52% in Nias and 42% in Dewata. At mild heat stress (28°/20°C) there was no clear difference between the Australian and Indonesian varieties.

At maturity, Axe was the variety most affected by high temperatures with a decrease in dry matter at 32°/23°C of 87% compared to the control treatment, while the reduction among the other varieties ranged from 57% (Gladius and Dewata) to 65% (Nias) (Table 1).

Table 1. Plant yield, dry matter and harvest index of four wheat varieties grown under three temperature regimes.

Temperatures	Variety	Total dry matter (g/plant)	Grain yield (g/plant)	HI (%)
25/15	Axe	37.9	16.2	42.9
	Gladius	48.0	16.7	34.8
	Nias	39.4	17.2	43.6
	Dewata	40.9	16.0	39.2
	Mean	41.5	16.5	40.1
28/20	Axe	26.2	11.3	42.7
	Gladius	42.6	14.6	34.3
	Nias	26.5	12.3	46.8
	Dewata	26.3	12.0	46.1
	Mean	30.4	12.6	42.5
32/23	Axe	5.1	1.8	36.7
	Gladius	20.6	3.0	13.6
	Nias	13.9	5.7	41.1
	Dewata	17.1	3.8	22.9
	Mean	14.2	3.6	28.6
	SED ^A			
	Temp	1.43	0.72	2.06
	Temp.Var	2.81	1.11	3.51
	F Prob			
	Temp	<0.001	<0.001	<0.001
	Temp.Var	<0.001	0.003	<0.001

^A Standard error of the difference among Temperatures and among Varieties within each Temperature

All varieties produce similar yield when grown at the control temperature but yields were significantly lower at the two higher temperatures. At 28°/20°C yields were 24% lower on average while they were 78% lower when grown at 32°/23°C although there was evidence of significant differences among the varieties in their response to high temperature. At 32°/23°C the yield of Axe was reduced by 89% as compared to the control. Gladius and Dewata produced similar yields at 32°/23°C but compared to their yields at 25°/15°C, Gladius was affected more (81% reduction) than Nias (67%) and Dewata (76%) (Table 1).

Values of HI were similar at 25°/15°C and 28°/20°C suggesting growth and yield were affected similarly, but the HI at 32°/23°C was lower, indicating yield was affected more than dry matter production.

3.2. Plant water use and water use efficiency

Total water use (WU) increased with higher temperatures up to 28°/20°C, but at 32°/23°C, WU by Axe and Gladius decreased, especially in Axe. The larger reduction in WU by Axe was associated with a much reduced post-anthesis WU as the plants matured quickly. In contrast WU by the two Indonesian varieties did not decrease at the highest temperature (Figure 1). WUE_{dm} and WUE_y declined as temperature increased in all varieties (Figure 1). Among the four cultivars, Gladius used most water but there were no differences in WUE among the other varieties (Figure 1).

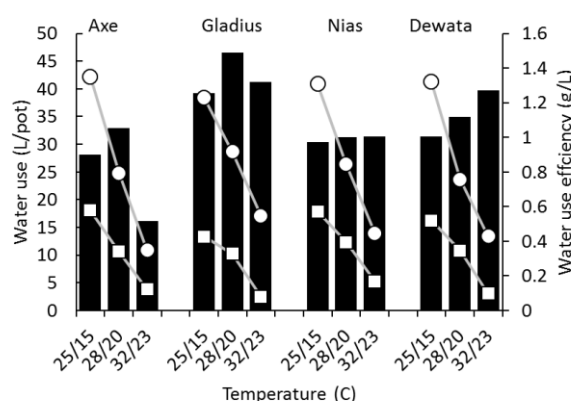


Figure 1. The effects of growth temperature on total water use (bars) and water use efficiency (lines) for dry matter production (○) and grain yield (□) for four varieties of wheat.

3.3. Water soluble carbohydrate

Concentrations of WSC at anthesis and maturity of plants grown at 25°/15°C were high compared to plants grown at the two higher temperatures (Figure 2). Within varieties, the two Indonesian varieties accumulated considerably more WSC at anthesis than the two Australian varieties.

WSC concentration fell markedly between anthesis and maturity with the relative reduction being higher at 28°/20°C except for Gladius. The two Australian varieties had a similar reduction in WSC (Axe: 45%; Gladius: 42%) which was less than that measured in the two Indonesian varieties (Nias: 76%; Dewata: 69%) (Figure 2).

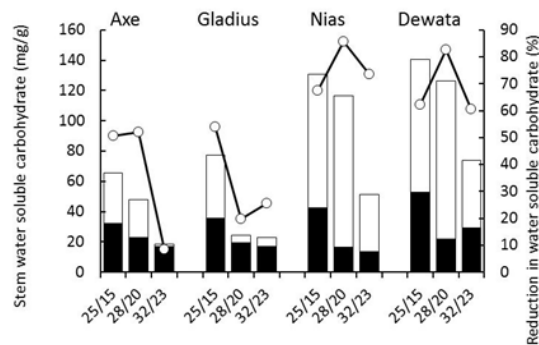


Figure 2. The concentrations of stem water soluble carbohydrate at anthesis (□) and maturity (■) and the percentage change between anthesis and maturity (lines) in four varieties of wheat grown at different temperatures.

3.4. Discussion

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. Water use increased, while water use efficiency decreased at higher temperatures and no variation found in varieties tested. 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, had higher concentrations and greater remobilisation of WSC. 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 and showed the greatest reduction of WSC between anthesis and maturity suggesting it transfers more soluble carbohydrate to the grains than the other varieties.

At 32°/23°C grain yield was affected more than dry matter, which caused HI to decline. Remobilisation of WSC stored temporarily in the wheat stem helps to maintain the supply of carbon to the grain when the rate of photosynthetic production has declined [8, 10, 13] and this was found to be an important trait in the present experiment: grain weight was related to the differences in WSC at anthesis and remobilisation during grain filling and this was reflected in the significant relationship between yield and WSC concentration at anthesis among the different temperatures. Variation in the concentration of WSC was more important in influencing grain weight than grain number, suggesting that the greater value of WSC was on post anthesis growth in these experiments (data not shown).

There was a wide variation in WSC among the four varieties with the two Indonesian varieties showing considerably higher concentrations than the Australian varieties. The ability to accumulate WSC in the stems appears to be an important adaptive characteristic of wheat varieties growing in temperatures typical of the tropical environment of Lombok to maintain grain set and especially grain growth. At 32°/23°C it is notable that Nias maintained a high yield relatively to the other varieties which was associated with higher reduction of the storage of WSC in stem, translocated to the grain.

4. Conclusion

There was some evidence of genetic variability to heat stress in this experiment. The differences in yield among varieties at high temperature was related to differences in remobilisation of WSC. The Indonesian varieties were more tolerant to high temperature than Australian varieties. Nias and Dewata produced higher yield and biomass and maintaining higher rates of remobilisation of WSC from vegetative tissues to grain. These traits could be used to select wheat varieties better adapted to high temperature at tropical environments such as Lombok.

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