QTL for canopy temperature response related to yield in both heat and drought environments

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ABSTRACT

The effects of drought due to insufficient soil water supply frequently occur concurrently with high air temperature. These combinations of environmental conditions are likely to increase in frequency if climate change predictions are realised. While there have been studies of the effects of heat shocks and high temperatures at various stages of wheat reproductive growth, there are no published reports on genomic regions associated with responses to heat and drought conditions in the field. Experiments in north-west Mexico were grown as managed droughts (i.e. growing into full moisture profile) or were planted three months after the normal planting time and irrigated. Maximum daily temperatures in the heat trials were 7 to 10°C higher (> 30°C) than in the drought trials. Yields of a set of 167 recombinant inbred lines from the Seri-Babax cross were highly correlated (>0.59) among the experiments (two of each treatment, averaging 303 and 253 gm^{-2} under drought and heat, respectively). Using composite interval mapping, cooler canopy temperatures and higher grain yields were associated with the Babax allele on linkage groups 1B, 3B and 4A under both drought and heat conditions. Cool canopy effects were also detected due to the Seri allele on linkage group 2B, but with no effect on yield. The effects of these QTL were to decrease canopy temperatures by 0.2 to 0.5°C in heat trials and by almost 1.5°C in one of the drought trials. The associated positive effects on grain yield ranged from 15 to 50 g m^{-2} and included a positive effect due to the presence of the 1BS chromosome segment of Babax instead of the 1RS rye segment present in Seri.

INTRODUCTION

Spring bread wheat has become adapted to a large range of environments in terms of soil and climatic conditions. Around the time of planting and early vegetative growth, the conditions are typically cool with little chance of heat or drought stress. In rain-fed production areas, drought due to shortage of water supply to roots may occur any time from about the middle period of vegetative growth right through to maturity. These drought effects may be accompanied and exacerbated by high daytime temperatures. In fact, irrigated wheat production in the low to mid-latitudes is also often affected by high temperatures (say > 30C), especially from flowering through to grain filling.

High temperatures affect plant production through several mechanisms. They accelerate phenology (reducing the potential production), and have direct effects on the physiology of photosynthesis and processes of the setting, fertilisation and filling of grains. An additional major effect of high temperatures on plants is via an increase in the vapour pressure deficit between leaves and the air. The increased evaporation via stomata reduces the effective transpiration efficiency of leaves (i.e. carbon assimilation per unit of transpiration). An indication of the degree of opening of the stomata can be shown by measuring the canopy temperature with an infra-red temperature 'gun'. Plants that keep stomata open will be relatively cooler. In an irrigated crop where the roots are able to access water, canopy temperature is then a potential indicator of the capacity of the roots to supply water under high evaporative demand. If stomata close, then this will reduce both transpiration and assimilation (useful if water supply is limiting), but potentially increases the risk of direct heat damage to leaf and photosynthetic structures; if stomata do not close, then the high transpiration may lead to an faster onset of direct effects of drought and dessication. For a canopy that is already suffering from lack of soil water supply, high temperatures can therefore affect the crop through both direct and indirect effects on growth and assimilation.

Given that climate change scenarios predict increases in temperature in many wheat-growing regions, it is instructive to begin to study the relationships among the genetic controls of response to heat and drought. In this paper, we outline preliminary results of an experiment comparing the canopy temperatures and yield performance of an elite bi-parental wheat cross when grown under drought conditions from the mid vegetative stage or under high temperature irrigated conditions from about the same stage until maturity. The objective was to determine (1) whether canopy temperature was a reliable predictor of yield and (2) if there were strong correlations between the performance of lines under drought and heat.

MATERIALS AND METHODS

Four trials of the Seri×Babax population were grown at the CIANO research station of CIMMYT located in Obregon, Sonoroa in north-west Mexico (27°25'N 109°54'W, 38masl). One drought trial (D02 emergence 08/12/01) of the 167 recombinant inbred lines was that studied before (Olivares-Villegas et al., 2007), and we planted another drought trial (D05 emerged 10/12/04). The drought trials were irrigated at sowing onto full soil water profiles and were then grown until maturity without further irrigation. Two heat trials were grown under irrigation and emerged in March (H05 16/03/05 and H06 03/03/06). Plot sizes were 5m x 4 rows (dual rows on 2 raised beds per plot). All of the trials had two replicates and were grown and analysed using GenStat as incomplete block designs with adjustment for spatial variation due to row and column effects, according to mixed model methods (Smith et al., 2001). Canopy temperatures during morning and afternoon were measured using an infra-red 'gun' (Mikron Instruments) during vegetative (not D05) and grain-filling periods. The experiments were plot harvested at physiological maturity and the grain threshed, dried and weighed, including for 1000 grain weight.

A molecular map was constructed for the population using a combination of SSRs and DArT markers, resulting in 401 markers across the genomes (see (Mathews et al., 2009) for additional information). WinQTLCartographer was used to undertake composite interval mapping analysis and estimate LOD scores for each trait and each environment. LOD effect sizes were illustrated as heatmaps using the R software package.

RESULTS AND DISCUSSION

For both the vegetative and reproductive (from Anthesis – 100°Cd) stages, temperatures were 7 to 10°C greater in the heat treatments than in the drought treatments (Table 1). In the heat treatments, the maximum temperatures during grain-filling were all > 30°C, while less than 30% of days were this hot in the grain-filling period of the drought treatments (data not shown).

Table 1 Mean daily maximum temperatures (°C) in the vegetative and reproductive stages

Treatment	Vegetative	Anthesis through grain filling
D02	25.2	28.0
D05	26.0	27.5
H05	32.0	35.2
H06	34.2	39.4

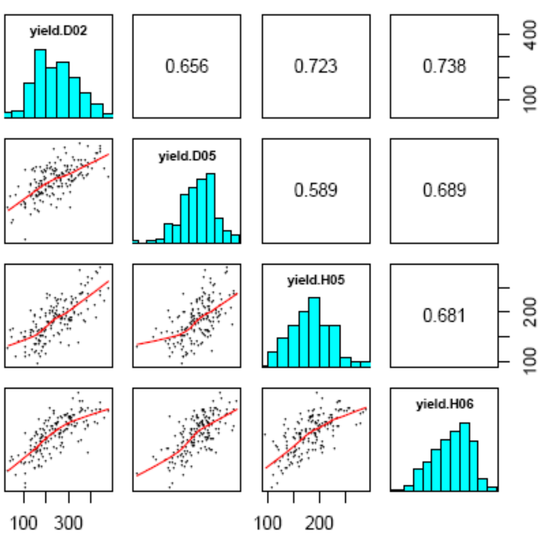

Figure 1 Histograms of line yields (g m^{-2}) and correlations among drought and heat treatments

Mean anthesis date in the drought trials was 86 (D02) and 76 (D05) days from emergence under drought and was significantly earlier under the late-planted heat treatment: 58 (H05) and 62 (H06) days. The drought crops reached maturity at about 114 days after emergence, while the heat treatment crops were mature after only 81 days. Mean grain yields were 243 (D02), 362 (D05), 184 (H05) and 321 (H06) g m^{-2}. Thousand grain weight was similar in the H05 (33.3g) and D02 (35.2g) and D06 (35.2g) treatments, such that differences among their grain yields were related to a reduction in the number of grains per unit ground area. In H06, there was a decrease in thousand-grain weight (28.9g) although grain number (11223 m^{-2}) was similar to that of the D05 treatment (10289 m^{-2}).

Yields were highly correlated across the treatments. Figure 1 shows that the ranking of lines was consistent across treatments with correlations ranging between 0.59 and 0.74. The negative genetic correlations between canopy temperature during the vegetative stage and yield were greatest for heat treatments (-0.60 in H05 and -0.87 in H06, data not shown), i.e. lines with canopies that were able to stay cooler (maintain water supply) under hot conditions were able to set a greater number of grains per m^2 and achieve greater yields. Thousand grain weight was not correlated to yield under heat conditions.

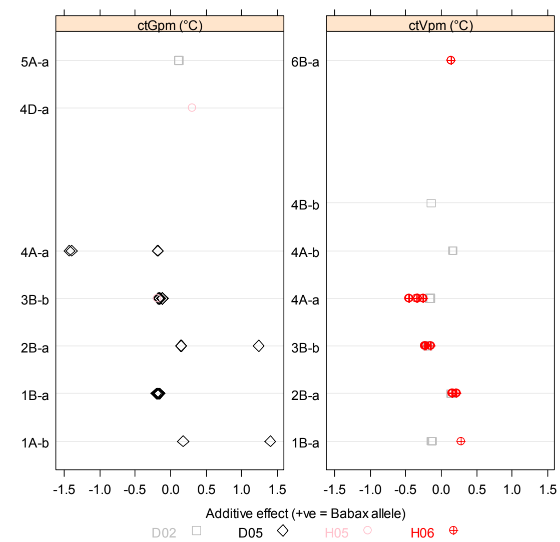

Figure 2 QTL effects (LOD > 2.5) for canopy temperature measured during grain filling (G) or vegetative (V) stages in drought and heat treatments

In the drought treatments, negative genetic correlations with yield were greatest for canopy temperature when measured during grain filling (-0.83 in D02 and -0.43 in D05, data not shown). Again, lines with cooler canopies had higher yields. Apparently, these lines were better able to fill their grains as there was a significant correlation between thousand grain weight and yield under drought (0.41 in D02 and 0.72 in D05). To maintain these cooler temperatures, these lines may have conserved water in the soil profile by extracting

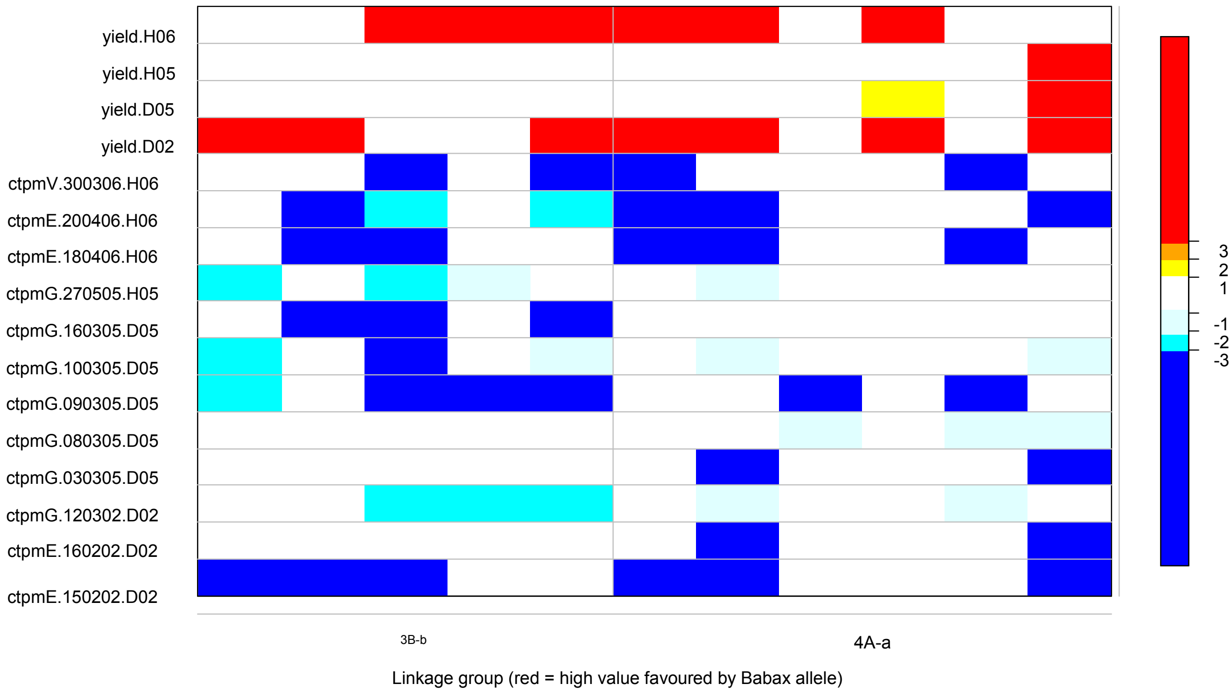

Figure 3 LOD score heatmap for two linkage groups from interval mapping analysis of vegetative (E or V) and grain filling (G) canopy temperatures and yield in drought and heat experiments

less during earlier growth, i.e. via slower leaf area development and/or higher transpiration efficiency of leaves. Alternatively, cooler lines may have developed deeper rooting systems and therefore had access to greater soil water supply during grain filling.

Positive effects for cooler afternoon canopy temperature in both drought and heat treatments were associated with the Babax allele on linkage groups 3B and 4A (Figure 2 and Figure 3). The effect on 1B under heat was also favourable for morning measurements (data not shown), but was unfavourable for measurements in the afternoon (data not shown). On linkage group 2B, a consistently favourable effect was associated with the Seri allele in both treatments. While effect sizes were generally about 0.2 to 0.5 °C, stronger effects (> 1°C) were noted for the Babax allele under drought for linkage group 4B and for the Seri allele on linkage groups 1A and 2B.

The favourable effects of the Babax allele were shown to be co-located with positive effects for yield in both drought and heat experiments (Figure 3). However, there was no co-location of favourable temperature and yield effects for the Seri alleles (data not shown).

These trials have demonstrated strong phenotypic and genetic correlations between heat and drought treatments for both canopy temperature and grain yield. QTL analyses confirm that part of these correlations are explained by genomic co-location of effects on canopy temperature and eventual grain yield. Further analyses of these data are being undertaken to examine the more complex relationships among component traits, including grain number and grain size, as well as relationships with other indirect measures of plant growth such as leaf nitrogen content (measured by Minolta SPAD meter), and NDVI. Our expectation is that the demonstration of such relationships using appropriate field data should inform genomic studies that aim to look for genes causing these effects (e.g. (Hays et al., 2007)), while providing candidate regions for evaluation and potentially selection in breeding programs.

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