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Molecular mapping of high temperature tolerance in bread wheat adapted to the Eastern Gangetic Plain region of India

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ABSTRACT

The inheritance of tolerance to high temperature stress during the grain filling period was investigated via a QTL analysis based on 138 doubled haploid progeny of a cross between the wheat cultivars Berkut and Krichauff. Performance data were collected from three seasons, in each of which the material was planted both at the conventional time and a month later. A heat sensitivity index (HSI) was also used to monitor the effect of high temperature on grain yield, thousand grain weight, grain filling duration and canopy temperature. Using composite interval mapping, seven stable QTL were identified for HSI of traits, mapping to chromosomes 1D, 6B, 2D and 7A. Three of the QTL related to HSI of grain filling duration, two to thousand grain weight and one each to grain yield and canopy temperature. A region of chromosome 1D harbored a QTL determining HSI of both thousand grain weight and canopy temperature. The QTL analysis for the direct traits GY, TGW, GFD and CT led to detection of 22 QTLs spread over to 17 chromosomal regions. Of these 13 QTLs were shown under normal sown, while 9 under the heat stress. A QTL for TGW on chromosome 6B under normal sown co-located with HSI(TGW) QTL *QHTgw.bhu-6BL*. QTL × environment interactions were not observed for any of the grain filling duration associated loci.

1. Introduction

Heat stress is a major production constraint for bread wheat grown in non-temperate environments (Fischer, 1986; Mason et al., 2010; Pinto et al., 2010). When experienced during the reproductive phase, high temperatures induce the loss of both grain weight and number (Hays et al., 2007a). The stress is thought to affect some 40% of irrigated wheat grown in less developed countries (Joshi et al., 2007b), representing some 13.5 Mha in India alone (Joshi et al., 2007a). Current predictions are that by the end of this century, mean daytime temperatures in South Asia will have risen by up to 4 °C (IPCC Climate and change, 2007), transforming as much as one half of the Indo-Gangetic plain into an environment which is sub-optimal for wheat production (Ortiz et al., 2008). Modeling has suggested that grain yield in this area will fall by 3–17% per 1 °C increase in mean air temperature. There is thus a growing priority for a breeding-led approach to adapting wheat to higher temperature environments (Reynolds et al., 2007; Singh et al., 2007).

Wheat is a cool season crop with an optimal daytime growing temperature of 15 °C during reproductive development and for every 1 °C above this optimum a reduction in yield of 3–4% has been observed (Wardlaw et al., 1989a,b). Several reports suggest that high temperature (>30° C) before and after anthesis in wheat can decrease the rate of grain filling and decrease the yield (Randall and Moss, 1990; Wardlaw and Moncur, 1995; Rane et al., 2007). In other studies, a yield reduction of 23% was reported in response to high temperature above 32 °C for as little as 4 days (Hawker and Jenner, 1993; Stone and Nicolas, 1994).

The genetic basis of high temperature tolerance in wheat is poorly understood; to date it has been assessed largely by monitoring the response of grain yield (Yang et al., 2002; Singh and Trethowan, 2007; Pinto et al., 2010), grain filling duration (Yang et al., 2002), grain size, canopy temperature depression (Reynolds et al., 1994; Ayeneh et al., 2002), a heat sensitivity index (Mohammadi et al., 2008; Mason et al., 2010; Paliwal et al., 2012) or various senescence-related traits (Vijayalakshmi et al., 2010) to exposure to high temperatures. A few cultivars able to maintain yield under stressful conditions have been identified (Yang et al., 2002; Hays et al., 2007a, 2007b), but the quantitative nature of the tolerance and the difficulty of assuring a correctly timed stress episode in the field has made it particularly difficult to effectively

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select for tolerance (Ortiz et al., 2008). To date, the level of success in identifying genetic markers associated with high temperature tolerance in wheat, and indeed other crop species, has been limited. Reliable marker-trait associations are a pre-requisite for an effective marker-assisted breeding program (Kato et al., 2000), and these are most effectively established via quantitative trait locus (QTL) mapping (Patterson, 1998).

A QTL mapping exercise focused on an abiotic stress tolerance needs to develop segregating populations where pheonological differences between the parental lines is minimized (Pinto et al., 2010). Ideally, these parental lines should both be elite varieties, rather than the more frequently made choice of highly diverse ones. Here, a doubled haploid (DH) population was created from a cross between the cultivars Berkut and Krichauff, which differ only marginally from one another with respect to their flowering time and mature plant height when grown in the Eastern Gangetic Plain (EGP) of India. The material was phenotyped following its sowing both at the conventional time and also a month later; the latter crops reached anthesis at a time when high temperature stress was highly likely to occur. Thus phenotyping was achieved in both normal and heat stressed environments, thereby attempting to identify QTLs of yield and other agronomic traits consistently associated with adaptation to a hot irrigated environment.

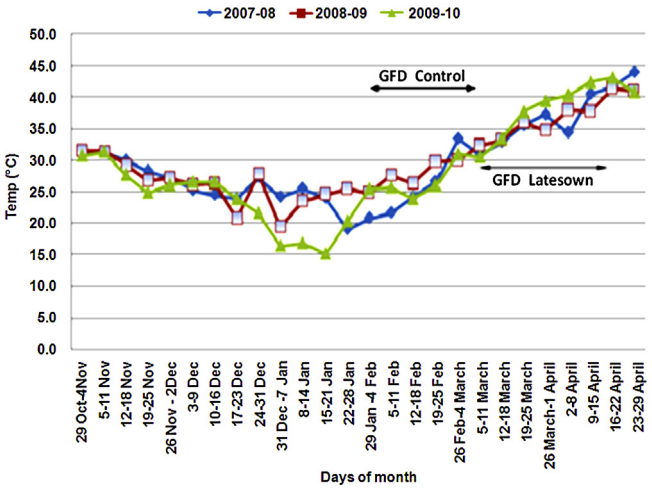

Fig. 1. Daily mean temperatures experienced during 2007–2008, 2008–2009 and 2009–2010 at Varanasi, India.

2. Materials and methods

2.1. Plant material

The DH population comprised 138 segregants from the cross cv Berkut × cv. Krichauff. Berkut is derived from the cross IRENE/BAV92//PASTOR while Krichauff from WARIQUAM//KLOKA/PITIC-62/3/WARIMEK/HALBERD/4/3-AG-3/AROONA. The former cultivar was developed at CIMMYT and is high temperature susceptible (2002), while the latter is an Australian cultivar showing a degree of high temperature tolerance (Balouchi, 2010). When the same population was previously exploited to map salinity tolerance (Genc et al., 2010), its range of plant height and flowering time was very narrow.

2.2. Crop management

The field experiments were established at the Agricultural Research Farm, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi (25.18°N, 83.03°E) over three consecutive seasons (2007–2008, 2008–2009 and 2009–2010). One complete set of material (the 138 DH lines along with the two parental cultivars) was planted at the conventional time (third week of November), and a second complete set was sown during the third week of December; the former planting date represented a control for the high temperature environment expected to be experienced at anthesis following the later sowing (Fig. 1). Each crop was irrigated four times, and the material was set out using a randomized complete block design, based on six row plots of length 3 m, with an inter-row spacing of 25 cm. Each of the three replications included comprised four blocks, each of which included 35 entries plus a local check variety (HUW 468) planted after every fifth entry. The mean performance of each contiguous pair of check plots was used as a covariate for the entries sown between them. Fertilizer application followed local commercial practice (120 kg N, 60 kg P_2O_5, 40 kg K_2O per ha); the P_2O_5 and K_2O were applied in one shot during sowing, but the N application was split such that one third was given at sowing, and a further one third after each of the first and the second irrigations. The crop was protected from infection by spot blotch and leaf rust by spraying with 625 g a.i./ha Tilt (propiconazole) at growth stages GS 54 and GS69 (Zadoks et al., 1974), and was maintained weed-free by applying 1 kg/ha pendimethalin three days after sowing, followed by 25 g/ha sulfosulfuron 25 days after sowing.

2.3. Data collection

The following traits were monitored: mature grain yield (GY), thousand grain weight (TGW), canopy temperature (CT), and the dates of anthesis (when anther extrusion had occurred on the leading tiller of 50% of the plants within a plot) and physiological maturity (75% of the plants within a plot were mature). The grain filling duration (GFD) was derived by subtracting the number of days to anthesis from the number of days to physiological maturity. CT values were recorded at three growth stages (GS55, GS65 and GS83) on bright sunny days between 1200 h and 1400 h, using a hand held infra red thermometer (Mikron Infrared Inc. NJ, USA) held at an angle of 30° to the horizontal at a distance of 1 m from the edge of the plot and ~50 cm above the canopy. An HSI was calculated for each trait based on the suggestion of Fischer and Maurer (1978); for example, for GY, the HSI was given by $[(1 - GY_{heat\ stress})/GY_{control}]/D$, where $GY_{heat\ stress}$ and $GY_{control}$ were, respectively, the GYs obtained from the conventional and the late sown crop, while D was given by the expression $[1 - (\underline{GY}_{heat\ stress}/\underline{GY}_{control})]$, where $\underline{GY}_{heat\ stress}$ and $\underline{GY}_{control}$ were, respectively, the mean GYs of the full set of DH lines.

2.4. DNA extraction and genotyping

DNA was extracted from each DH line and from the two parental cultivars following Williams et al. (2006), as modified by Genc et al. (2010). SSR typing also followed the methods given by Genc et al. (2010). The SSRs included a sample of *barc* (Song et al., 2002, 2005), *cfa* (Sourdille et al., 2003), *cfd* (Guyomarc'h et al., 2002), *gdm* (Pestsova et al., 2000), *gwm* (Röder et al., 1998) and *wmc* (Gupta et al., 2002) assays. Multiplex PCR amplicons were separated on an ABI3730 device (Applied Biosystems, Warrington, UK), as described by Hayden et al. (2008). Homoeolog-specific primers were used to amplify the *Vrn1* genes following Fu et al. (2005). The material was also subjected to DArT genotyping, performed by Triticarte Pty Ltd. (http://www.tritcarte.com.au). These markers have been prefixed '*wPt*'.