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CHROMOSOMAL LOCATIONS OF GENES FOR HEAT TOLERANCE IN TETRAPLOID WHEAT

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SUMMARY

D-genome disomic substitution lines of durum wheat (Triticum turgidium L. var. durum) and their parental cultivars Langdon (recipient) and Chinese Spring (D-genome donor) were evaluated for their relative heat tolerance as measured by membrane thermostability to determine the chromosomal locations of genes controlling this trait. Results indicate that homoelogues 3 and 4 are most closely associated with heat tolerance. Chromosomes 3A, 3B, 4A, 4B, and 6A were found to be associated with heat tolerance of Langdon, while chromosomes 1B, 2A, 6B, and 7B were not related to heat tolerance.

INTRODUCTION

High temperature is a limiting factor of crop productivity in many agricultural regions of the world (Christiansen et al., 1982). High temperature over 30^0C is frequent in many wheat production areas, particularly during the grain-filling period, causing a reduction in kernel weight and a loss of grain yield (Wardlaw et al., 1989; Shpiler and Blum, 1986). Genetic variation in heat tolerance has been found to exist among wheat cultivars and lines (Shanahan et al., 1990; Saadalla et al., 1990a; Moffatt et al., 1990b; Blum and Ebercon, 1981). Therefore, genetic improvement of the trait by breeding is possible.

Electrolyte leakage or membrane thermostability (MT) has been found to be a good indicator of heat tolerance in crop plants (Sullivan and Ross, 1979; Saadalla et al., 1990a; Blum and Ebercon, 1981), and is a quantitatively inherited trait (Blum, 1988). Studies have also shown that membrane thermostability is correlated with the performance of crops under field conditions (Shanahan et al., 1990; Saadalla et al., 1990b). Shanahan et al. (1990) demonstrated that the MT in spring wheat is correlated with grain yield and test weight under heat stress conditions, and concluded that the MT test can be a useful screening procedure for selecting spring wheat genotypes that tolerate high temperature stress. Similar results were obtained in winter wheat (Saadalla et al., 1990a).

In hexaploid wheat, chromosome substitution lines have been extensively used to identify chromosomal location of genes for qualitative and quantitative traits (Law et al., 1987). A unique set of substitutions, Langdon durum D-genome disomic substitution lines in which a pair of A- or B-genome chromosomes in Langdon were replaced with a pair of homoeologous D-genome chromosomes from Chinese Spring wheat, has been developed to facilitate genetic studies in tetraploid wheat (Joppa and Williams, 1988). The substitution lines have been used to determine the chromosomal location of a gene for chocolate chaff in durum wheat (Konzak and Joppa, 1988), and the chromosomal location of genes for grain protein content in wild tetraploid wheat (Joppa and Cantrell, 1990).

There have been few studies regarding gene action and combining ability of heat tolerance in wheat (Porter et al., 1989a; Moffatt et al., 1990b). Recently, Porter et al. (1989b) reported the chromosomal location of genes controlling heat shock proteins in hexaploid wheat using Chinese Spring and its ditelosomoic series. However, little information is available with respect to the chromosomal location of genes for heat tolerance in terms of membrane thermostability in wheat. We found that Langdon durum wheat was heat tolerant, and Chinese Spring heat susceptible in preliminary studies (unpublished). The objective of this study was to determine the chromosomal association with heat tolerance using the Langdon D-genome disomic substitution lines.

MATERIALS AND METHODS

Fourteen substitution lines, Langdon, Chinese Spring, 'TAM 105', and 'Nugaines' were tested in the seedling stage for heat tolerance, using a procedure similar to that described by Saadalla et al., 1990a. Seeds of Langdon and substitution lines were kindly provided by L.R. Joppa and N.D. Williams, USDA-ARS, Fargo, ND, USA. TAM 105 and Nugaines, extremely heat tolerant and extremely susceptible, respectively, were included as standard cultivars since they were used as routine controls in our previous tests. Forty seeds of each genotype were wrapped in moistened germination paper and allowed to germinate in an incubator at 15^{0}C without light. When the first leaf reached 4 to 5 cm above the coleoptile tip, they were moved to a water bath set at 34^{0}C with roots immersed in water (2 cm deep) for 48 h under continuous light for heat hardening. The water bath was covered with transparent plastic to stabilize temperature and maintain high humidity.

After the heat hardening treatment, 10 seedlings were selected to comprise a sample (experimental unit), and four replicates per genotype were collected. The seedlings were cut into two segments (2 cm in length); the upper portion was used for heat treatment and the lower for the control. The leaf segments were rinsed twice in 10 mL deionized water in test tubes to remove electrolytes adhering

to and released from the cutting of leaves. After final rinsing, 5 mL deionized water was added to each tube, and tubes were covered with aluminum foil. The treatment tubes (T) were incubated in a water bath at 50°C for 1 h, while control tubes (C) were kept at 22°C during the same time period. After heat treatment, both treated and control tubes were held at 10°C for 20 h to allow diffusion of electrolytes from the leaf segments. The tubes were then brought to 22°C and shaken to mix the contents. Initial conductances (C1 and T1) were determined with an electrical conductivity meter (Electroanalyzer 4400, Markson Science Inc., Del Mar, CA). After the first measurement, the tubes were autoclaved for 12 min at 0.10 Mpa pressure to completely kill leaf tissue and release all of the electrolytes. Subsequently, tubes were cooled to 22°C, shaken, and the second measurements of conductivity (C2 and T2) made. The level of injury (MT) was determined as relative injury (RI) from the following formulae:

$$\text{Relative Injury (\%)} = (1-(1-T1/T2)/(1-C1/C2)) \times 100$$

RESULTS AND DISCUSSION

Analysis of variance (Table 1) shows that there were highly significant differences among the lines tested for heat tolerance. The recipient cultivar Langdon was heat tolerant, and the donor cultivar Chinese Spring was heat susceptible, with relative injuries of 43.2 and 78.3%, respectively (Table 2). This difference between donor and recipient permitted the use of Langdon D-genome substitution lines to determine gene-chromosome associations for heat tolerance.

Significant genetic variation existed among the 14 substitution lines and the relative injury ranged from 15.4 for 5D(5B) to 74.1% for 6D(6A) (Table 2). Chromosomes 3D and 4D of Chinese Spring, when substituting for the homoeologues 3A, 3B, 4A, and 4B of Langdon, caused a significant increase in the relative injury (reduced the heat tolerance). This suggests that chromosomes 3A, 3B, 4A, and 4B of Langdon are associated with its heat tolerance, and that chromosomes 3D and 4D of Chinese Spring are absent of genes for heat tolerance. Chromosome 6D, when substituting for 6A of Langdon, significantly reduced heat tolerance of the recipient, but had no effect when substituting for 6B. This suggests that chromosome 6A is associated with heat tolerance, but 6B is not. Chromosome 6D is unlikely to carry gene(s) for heat susceptibility. Substitution lines of 1D(1B), 2D(2A), 6D(6B), and 7D(7B) demonstrated no differences with the recipient for heat tolerance, which suggests that chromosomes 1B, 2A, 6B, and 7B of Langdon were not associated with heat tolerance.

It is interesting to note that substitution lines of 1D(1A), 2D(2B), 5D(5A), 5D(5B), and 7D(7A) had significantly lower relative injury than the recipient, i.e., they became more heat tolerant

Table 1. Analysis of variance for membrane thermostability in 18 wheat lines.

Source	df	Mean squares	F
Replication	3	58	0.92
Line	17	1847	29.39 **
Error	51	62	

** Significant at the 0.01 probability level.

Table 2. Relative injury of Langdon and its substitution lines, Chinese Spring, TAM 105, and Nugaines.

Line	Rel. injury	Line	Rel. injury
	-- % --		-- % --
1D(1A)	19.2 **	1D(1B)	41.0
2D(2A)	48.8	2D(2B)	30.9*
3D(3A)	70.9 **	3D(3B)	70.2**
4D(4A)	60.5 **	4D(4B)	64.8**
5D(5A)	20.7 **	5D(5B)	15.4**
6D(6A)	74.1 **	6D(6B)	47.5
7D(7A)	23.3 **	7D(7B)	46.1
Langdon	43.2	TAM 105	28.8*
Chinese Spring	78.3 **	Nugaines	76.5**
LSD 0.05	11.3		
LSD 0.01	15.0		

*,** Significantly different from Langdon at the 0.05 and 0.01 levels, respectively.

than the recipient, and even more tolerant than TAM 105 which was considered one of our extreme heat tolerant cultivars (Table 2). This might be due to an interaction between a substituted D-genome chromosome and the recipient background. While studying chromosomal association with milling and baking quality in spring wheat, Kosmolak et al., (1980) divided the effects of chromosome substitution into two classes, (i) those chromosomes that changed the substitution line in the direction of the donor parent, and (ii) those that changed it in the direction of the recipient parent. Their explanation for the second class was that it may be due to the loss of genes on the replaced chromosome of the recipient parent and the absence of these on the homoeologue of the donor, or may be a gene that has no apparent effect in the donor parent itself because of lack of complementary genes, but it may enhance the character in the recipient where complementary genes were already present. Al-Qaudhy et al. (1988) attributed the transgressive value of straw strength exceeding the recipient in Cheyenne-Wichita reciprocal substitution lines to a complementary interaction between genes on the substituted chromosome and those in the recipient background. Zemetra and Morris (1988) reported that there is a gene for spring habit on chromosome 3B of Wichita which was expressed only in Cheyenne background, not in Wichita itself. They proposed that there was another gene(s) in Wichita that suppresses the expression of the 3B gene. The mechanism(s) which apply to our heat tolerance case is not yet known. Since five chromosomes were associated with heat tolerance, the genetic system for the trait is expected to be more complicated.

There is evidence that heat shock protein (HSP) plays an important role in the development of thermostability (Lin et al., 1984; Nagao et al., 1986; Krishnan et al., 1989). Porter et al. (1989b) reported that there were genes controlling HSP synthesis located mostly on homoeologues 3, 4, and 7 in Chinese Spring. In our study with tetraploid wheat, we also found that homoeologues 3 and 4 were associated with heat tolerance. Since homoeologous groups tend to carry genes that affect the same character (Kosmolak et al., 1980), it might be expected that homoeologues 3 and 4 in hexaploid wheat carry genes for heat tolerance. Chinese Spring was found to be highly heat susceptible in terms of membrane thermostability in our study, although Porter et al. (1989b) found that it still had the ability to induce synthesis of 13 LMW HSPs.

Further studies are needed to determine how many genes are on the related chromosomes, and what kind of mechanisms are involved in the transgressive heat tolerance in those substitution lines.

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