Identification of Wheat Genotypes Tolerant to the Effects of Heat Stress on Grain Quality

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ABSTRACT

High-temperature stress (>35°C) during the grain-filling period has the potential to modify grain quality. A consequent weakening of dough properties has been reported for many wheat genotypes. The experiment described in this article was designed to identify wheat genotypes that might be tolerant to the effects of heat stress on grain quality and to further assess the molecular basis of these changes. A diverse set of 45 wheat genotypes was exposed to 10 hr of 40°C on each of three consecutive days in a phytotron. Mean values for all genotypes (with unheated control samples, all in duplicate) showed highly significant changes ($P < 0.001$) in 1,000 kernel weight (–17% difference for heat stressed minus control), protein content (17% increase), dough mixing time in a 2-g Mixograph (–13%), and resistance breakdown (17%). The general weakening of dough due to heat was accompanied by a decrease in glutenin-to-gliadin ratio and in the percentage of very large glutenin polymers. Bound lipid content increased, and there was a general reduction (–9%) in the proportion of small (B-type) starch granules. For all these attributes, reactions for individual genotypes ranged from little change (tolerance to heat stress) to considerable change (susceptible to heat stress). A group of genotypes was thus identified that should be useful in breeding attempts to stabilize wheats against heat-related variations in grain quality. Markers identified as potentially useful in breeding for tolerance include the presence of the *Glu-D1d* allele (glutenin subunits 5 and 10), and increases in glutenin-to-gliadin ratio and in the percentage of very large glutenin polymers.

Our knowledge of the effects of growth environment on grain quality have not progressed so quickly as the genetic aspects of wheat quality. Nevertheless, in wheat-growing countries where the daily maximum temperature might rise above 35°C for a few days in succession before harvest time, heat stress during the grain-filling period is known to modify the genetic potential for dough properties (reviewed by Blumenthal et al 1993, Wrigley et al 1994). More recently, Ciaffi et al (1995) also reported a loss of dough strength following heat stress (>35°C) of four cultivars at four sites in Italy.

Concern about the effects of heat stress on grain yield and quality prompted the organization of a conference entitled *Heat Tolerance in Temperate Cereals* in February, 1994, in Hawaii (Wardlaw and Wrigley 1994; most papers published in Aust. J. Plant Physiol. 21, No. 6, 1994). At this conference, Wrigley et al (1994) reported a variety of changes in dough properties (as determined with the Mixograph) following a few days of heat stress at 40°C in growth cabinets for three cultivars, including considerable weakening for cv. Ella and little change in protein content or mixing properties for cv. Halberd. Other papers at the Hawaii conference focused on the ratio between gliadin and glutenin content as a potential indication of heat stress on dough properties. Stone and Nicholas (1994) reported on two extreme genotypes from a survey of a large number of wheats that had been heat-stressed in the glasshouse: cv. Osprey showed a dramatic decrease in glutenin-to-gliadin ratio, and little change for cv. Egret. Bernardin et al (1995) reported no significant differences in glutenin-to-gliadin ratio for five U.S. wheats as a result of many days of heat stress at 40°C. They did, however, detect considerable increases due to heat stress in proteins associated with the heat shock response.

These results suggest that there may be genetic sources of tolerance to the modification of dough properties by heat stress. We have, therefore, conducted a survey of 45 wheat genotypes with the primary aim of identifying genotypes that might be used as parents to confer greater consistency of wheat quality on commercially grown wheat. Choice of genotypes included the secondary aim of identifying heat-susceptible genotypes. Parallel aims were to further test the hypothesis set out by Blumenthal et al (1993) that for many genotypes, there is a weakening of dough properties due to heat stress associated with an increased proportion of gliadin. Beyond this, we had sought to determine changes in the size-distribution of glutenin aggregates due to heat stress; to determine how changes in mixing properties and gluten composition related to allelic composition for the *Glu-1* locus; and to examine changes in lipid composition and starch granule size distribution.

MATERIALS AND METHODS

Plant Selection and Growth Conditions

A set of 45 wheat cultivars (Fig. 1) was selected according to their potential to represent a range of responses to heat stress during grain filling, partly on the basis of anecdotal reputations, and partly on the basis of experimental evidence with respect to yield-associated attributes (Wardlaw 1994). Twenty-five of the cultivars chosen have been commercially grown in Australia, providing representatives of major pedigree groupings and representing significant Australian wheat grades as recommended in all states. The remaining 20 were chosen on the basis of reputation for heat tolerance or susceptibility as regards yield, such as a Gigas inclusion (Oligoculm) with a reputation for being heat sensitive, and Trigo I with a reputation for being heat tolerant. A selection of cultivars was also included from the Hot Climate Nursery at CIMMYT in Mexico.

These genotypes were grown in glasshouses in the phytotron at CSIRO, Division of Plant Industry, Canberra. The plants were grown in a vermiculite and pearlite mixture (1:1) in 25-cm pots (five plants per pot, three tillers per plant) and were rotated randomly to ensure that no effect from position occurred. Nutrient solution was applied each morning, and tap water each afternoon. Plants were grown at a 18°C day and 13°C night cycle. At 29 days after anthesis, half the pots were transferred to a growth cabinet where they were subjected to a three-day temperature

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regime of 10 hr at 40°C, with frequent watering, to ensure that no water stress occurred. Grain was harvested at physiological maturity (≈60 days after anthesis).

Flour Analyses

Duplicate sets of grain samples were harvested from mature plants yielding 50–100 g of grain. The grain was milled to flour in a Quadrumat Junior mill (Brabender, Germany). Protein content (N × 5.7) was determined on grain and flour by the Dumas method, using the Leco nitrogen analyzer, model FP-228. Flour samples were tested for dough properties in the 2-g Mixograph (Rath et al 1990) with replicated analyses and computer-based interpretation. Results were expressed as time to peak (mix time, sec), dough breakdown (% drop in resistance, 3 min after the peak), and as the height at peak resistance (in arbitrary units).

Protein Composition

The proportions of gliadin and glutenin were determined by size-exclusion high-performance liquid chromatography (SE-HPLC) by the method of Batey et al (1991). Protein was extracted from flour, without reducing agent, by sonication in phosphate buffer containing sodium dodecyl sulfate (SDS). The first major peak was defined as aggregated glutenin and the second major peak as monomeric gliadin, as described by Blumenthal et al (1994). Further characterization of the SDS-extracted protein fraction was performed using SDS multilayer gel electrophoresis of an unreduced sonicated SDS extract of flour samples according to the method of Wrigley et al (1993). The constitutions for the *Glu-1* A, B, and D loci for high molecular weight (HMW) glutenin subunits were obtained from published reports (where available) particularly from the GeneJar software of Cornish et al (1993), or by electrophoretic analysis (Gupta and MacRitchie 1991). In the few cases where a grain sample was polymorphic for a particular locus, the predominant allele was recorded.

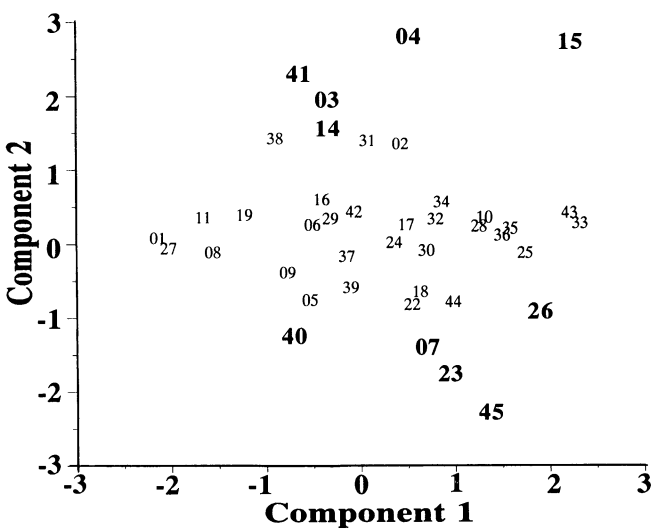

Fig. 1. Varimax rotation of principal component analysis of 45 wheat genotypes according to differences (heat stressed minus control) in the combination of the three dough-mixing attributes and protein content. Factor loadings for component 1 (horizontal axis) and component 2 (vertical axis) were (respectively): mix time (–0.053 and 0.942), resistance breakdown (0.378 and –0.821), peak resistance (0.932 and –0.078), and protein content (0.851 and –0.303). Genotypes with the most tolerance or susceptibility are shown as numbers in bold face at the top or bottom of the figure, respectively. Numbers refer to genotypes as follows: 01 (6385); 02 (6384); 03 (6372); 04 (6386); 05 (Aroona); 06 (Banks); 07 (Batavia); 08 (Condor); 09 (Croesus); 10 (Cunningham); 11 (Dagger); 12 (Dollarbird); 13 (Ella); 14 (Fang); 15 (Grebe); 16 (Halberd); 17 (Hartog); 18 (Janz); 19 (Kamilaroi); 20 (Kite); 21 (Kogat); 22 (Kulin); 23 (Lark); 24 (Lyallpur); 25 (Machete); 26 (Matong); 27 (ME71); 28 (Meering); 29 (Millewa); 30 (Miskle); 31 (Molineux); 32 (Oligoculm); 33 (Oxley); 34 (Scandia); 35 (Schomburgk); 36 (Sunco); 37 (Suneca); 38 (Tatiara); 39 (Tincurrin); 40 (Trigo I); 41 (Ulla); 42 (Veery); 43 (Vulcan); 44 (WW80); 45 (Wyuna).

Starch Size Distribution of Starch Granules

The size distribution of starch granules isolated from flour samples was determined by dispersing 100 mg of flour in 0.5*M* sodium chloride solution, resting it at 4°C for 45 min, and kneading it in the saline to separate the starch suspension from the gluten ball. The gluten was again kneaded in 0.5*M* sodium chloride solution to separate the starch from the gluten (repeated three times). The combined washings of starch were centrifuged, washed twice by suspension in 0.1*M* acetic acid solution, and finally suspended in water. Freeze-dried starch was analyzed for particle-size distribution in a Malvern laser analyzer.

Lipid Analysis

N-hexane extractable free lipids (FL) and water-saturated *n*-butanol bound lipids (BL) were isolated from 500-mg duplicate flour samples according to Bekes et al (1983).

Statistical Analyses

Results were analyzed for statistical significance using the MSUSTAT program (Lund 1986). Principal component analysis was performed using MINITAB software (Anon 1993).

RESULTS

The selection of genotypes was chosen to represent a wide range of quality types, as well as a range of reactions to heat stress. That a wide range of dough properties was obtained is indicated by the range of mix times (84–442 sec) shown in Figure 2 (top histogram) for the control samples (means of replicated analyses on duplicate growth sites). In Figure 2, genotypes are arranged from left to right in order of decreasing tolerance to the effects of heat stress on mixing time (see second histogram). We have used the term "tolerance" (suggesting no significant change after heat stress) for genotypes on the left of Figure 2. However, it is evident that the first few of these genotypes actually exhibited an increase in mix time, indicating a tendency towards strengthening after heat stress. Figure 2 (bottom histogram) also shows considerable variation in the percentage of large glutenin polymers for this set of genotypes before heat stress. There was a very highly significant correlation ($r = 0.60$, $P < 0.001$) between mix time and percentage of large glutenin polymers for the untreated control samples (Table I).

Overall Changes Due to Heat Stress

Comparison of mean values for all 45 wheat genotypes before and after heat stress (Table II) showed a significant change ($P < 0.001$) in the values of all attributes measured (except for free lipid content, not included in Table II) as a result of the heat stress. There were no significant differences between sites for any attributes (duplicate sets of pots for each treatment). Presumably, there was a general decrease in the synthesis of starch following the heat stress, leading to the general decrease in 1,000-kernel weight and the increase in relative protein content for heat-stressed samples, compared to that of the controls. In fact, comparison of the mean values in Table II indicates that 1,000 kernels contained 6.0 g of protein for control samples, and a similar amount of protein (5.8 g) for heat-stressed samples.

The relationship of this rise in protein content was compared with changes in all attributes, to see if they might be protein associated (Tables I and III). This association was highest for peak resistance in the Mixograph, an attribute generally acknowledged to be related to protein content (AACC 1983), and it is probably the statistical relationship of peak resistance to protein content that largely explains the modest increase (7%) in peak resistance

resulting from the heat treatment (Table II). On the other hand, the time to reach the peak of the Mixograph curve (mix time) particularly, and the degree of breakdown after the Mixograph peak, were virtually independent of protein content. The latter two attributes were thus used as measures of dough properties that were not merely reflections of changes in protein content. Based on the overall changes in these two measures of dough properties, the heat stress produced an overall dough weakening (shorter mix time and more rapid breakdown).

Principal component analysis (Fig. 1) was applied to the results to further examine relationships between the attributes determined both on an overall basis and with respect to individual genotypes. This showed close statistical relationships between protein content and peak height (high factor loadings for component 2) and also between mix time and breakdown (high factor loadings for component 1) on the other.

The extremes of change in Mixograph traces are shown in Figure 3 for the most tolerant (to weakening) (6386) and the most susceptible (to weakening) (Wyuna) genotypes, based on mix-time results. The traces for 6386 demonstrate the lack of (significant) change in breakdown and peak height, accompanied by an increase in time to peak, although there was little increase in protein content after treatment. In contrast, there were considerable changes for Wyuna in the time to the peak (shorter with heat) and in breakdown after the peak (steeper after heat); the increase in peak height accompanied the considerable increase in protein content. Although these few were selected to represent the extremes, it must be realized that they are not statistically identifiable as the most or least tolerant, as they are not statistically different from their neighbors in the ranking sequence of Figure 2.

There were overall decreases, as a result of heat stress, in the percentages of glutenin proteins (compared to gliadins) and of the very large glutenin polymers (as determined by multilayer SDS gel electrophoresis) (Table II). The proportion of bound lipids increased significantly, but the changes in free lipids did not fol-

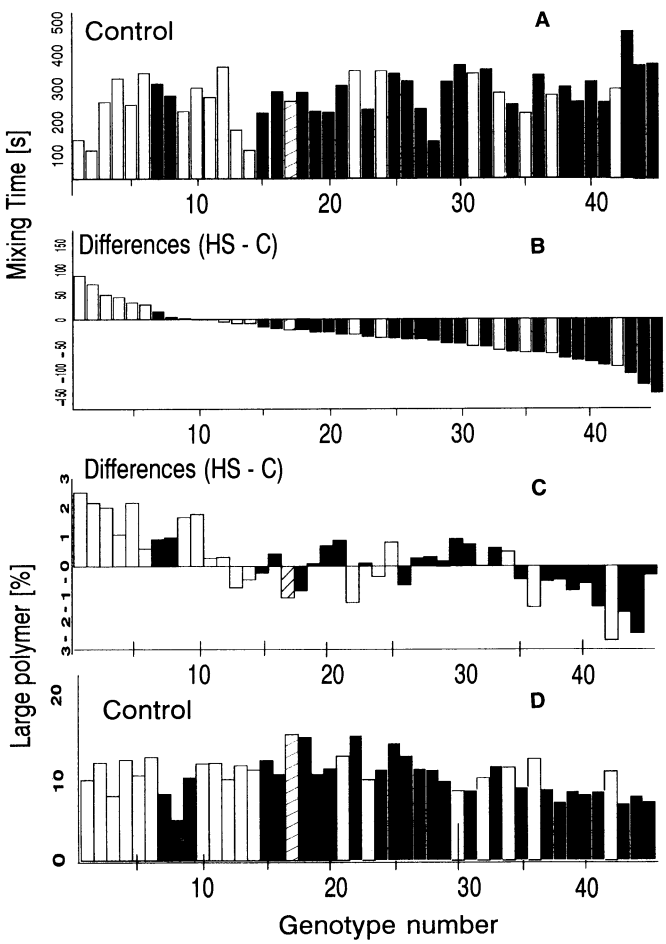

Fig. 2. Dough-mixing properties (time to peak, sec) and % large glutenin polymers for the set of 45 control samples (A and D) as mean values from replicated analyses for duplicate sites. Differences in these two attributes (B and C) (heat-stressed minus control [HS – C]). Genotypes arranged from left to right in order of decreasing differences in mix time. White and black columns indicate genotypes with high molecular weight glutenin subunits 5+10 or 2+12, (*Glu-D1d* or *Glu-D1a*), respectively. Hatched pattern indicates durum wheat cv. Kamilaroi. Average least significant differences (5% significance level, HS – C) are 57 sec for mix time and 0.9% for large glutenin polymers.

TABLE I
Correlation Matrix Relating Dough Properties (Mixograph) and Biochemical Attributes[a]

	Mix Time	Resistance Breakdown	Peak Resistance
Control			
Protein content	–0.153	0.322*	0.571***
Glu/Gli ratio	0.394**	–0.345*	–0.026
Large polymer	0.599***	–0.407***	0.109
Free lipid	0.224	–0.439***	0.274
Bound lipid	0.161	–0.320*	0.063
Heat stressed			
Protein content	–0.177	0.211	0.614***
Glu/Gli ratio	0.371**	–0.335*	–0.114
Large polymer	0.668***	–0.393**	0.213
Free lipid	0.172	–0.381**	0.303
Bound lipid	0.169	–0.270	0.049
Difference[b]			
Protein content	–0.347*	–0.266	0.679***
Glu/Gli	0.376*	–0.425**	–0.343*
Large polymer	0.607***	–0.417**	0.267
Free lipid	0.260	–0.183	0.187
Bound lipid	0.562***	–0.458**	0.128

[a] *, **, and *** = significant correlations at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.
[b] Heat stressed – control.

TABLE II
Mean Values for Attributes Significantly ($P < 0.001$) Changed by Heat Stress for 45 Wheat Genotypes

Attribute	Control (C)	Heat Stressed (HS)	% Change (HS–C)/C
1,000 kernel weight, g	48.2	39.8	–17
Protein content, %	12.5	14.6	17
Mixing time, sec	253	221	–13
Resistance breakdown, %	16.3	19.0	17
Peak resistance	333	358	7
Glu/Gli ratio	0.74	0.69	–7
Large polymer, %	17.63	17.08	–3
Bound lipid content, %	3.56	3.82	7
B starch granules, %	28.0	25.6	–9

TABLE III
Correlation Coefficients Relating Protein Content to Various Attributes for Heat Stress Treatment of 45 Wheat Genotypes[a,b]

Attribute	Raw Data	Difference[c]
1,000 kernel weight	–0.30	–0.16
Peak resistance	0.60	0.55
Mixing time	–0.26	0.25
Resistance breakdown	0.38	0.41
Glu/Gli ratio	–0.32	–0.47
Large polymer	–0.22	0.12
Free lipid	0.03	–0.16
Bound lipid	0.23	0
Starch particle size	–0.25	–0.36

[a] Considering means of replicated analyses but separately for duplicated samples of the same genotype or treatment.
[b] Underlined values are significantly different at $P < 0.05$.
[c] Heat stressed – control.

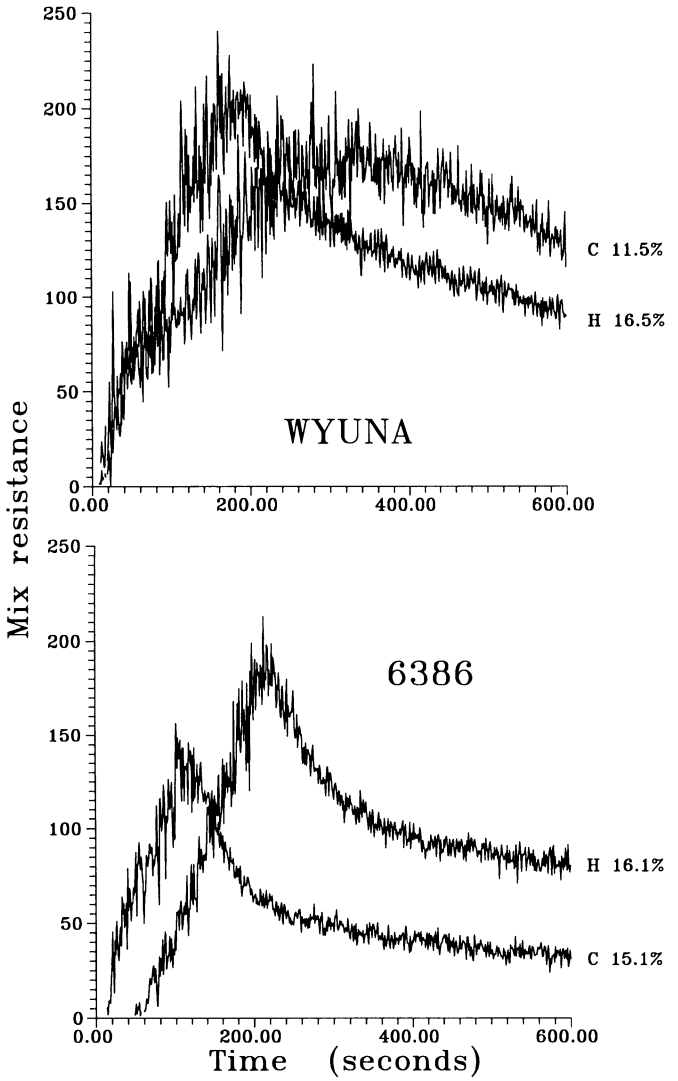

Fig. 3. Mixogram traces for tolerant (6386) and susceptible (Wyuna) cultivars (based on mix time). C = control; H = heat-stressed. Flour-protein content is indicated at the right of each trace.

low a significant trend (correlations not shown in Table II). There was a lower proportion of small (B-type) starch granules after heat stress. Lipid and starch results did not relate to changes in protein content; changes in the glutenin-to-gliadin ratio were significantly related ($P < 0.05$) to protein content (Table III).

Statistical relationships between dough and biochemical data are shown in greater detail in Table I, separately for the control samples, samples after stress, and for differences (heat-stressed minus control). The percentage of large glutenin polymers was the best biochemical indicator of changes in mix time, though it was not related to changes in peak resistance (Table I). In addition, glutenin-to-gliadin ratio was consistently correlated to mix time ($P < 0.05$). For differences due to heat, changes in bound lipids correlated significantly with mix time and resistance breakdown.

Relationships between mix time and percentage of large glutenin polymers (compared to glutenin-to-gliadin ratio) improved for both control samples and differences after heat treatment. Correlation between mix time and the percentage of large glutenin polymers improved slightly when glutenin-to-gliadin ratio was added in as a multiple correlation, improving from 0.60 (Table I) to 0.70. On the other hand, correlation of mix time difference to glutenin-to-gliadin ratio improved from 0.38 (Table I) to 0.70 with incorporation of the percentage of large polymers in the multiple correlation.

TABLE IV
Differences in Dough Properties and Gluten Composition[a,b] for Most Tolerant and Susceptible Genotypes

Genotype	Mix Time (sec)	Resistance Breakdown	Glu/Gli Ratio	Lg. Polymer (%)
Tolerant				
6386	89	2.5	0	2.55
Grebe	71	–0.5	–0.07	2.19
6372	51	–3	–0.01	2.03
Suneca	46	–3.5	–0.03	1.10
Fang	35	–2.5	0.03	2.20
Ulla	31	–8	0.01	0.61
Susceptible				
Matong	–70	–8.5	–0.12	–0.5
Lark	–82	14	–0.08	–0.82
Batavia	–93	12.5	–0.04	–1.36
Trigo 1	–132	5.5	–0.01	–2.28
Wyuna	–149	11.5	–0.09	–0.28

[a] Heat stress – control.
[b] Underlined values are significantly different at $P < 0.05$.

Heat-Related Changes for Individual Genotypes

Principal component analysis was used to obtain an indication of heat-related changes in combined protein content and in dough processing characteristics for the genotypes individually. This procedure provides another approach to selecting outstanding genotypes and to identifying those factors responsible for the differences between individuals. The results are shown in Figure 1 as a varimax rotation of the principal component analysis. The analysis pointed to the two sets of genotypes listed in Table IV as being the most extreme of the set of wheats, the more tolerant or susceptible ones appearing in bold at the top or bottom (respectively) of Figure 1. The two components (axes) selected by the principal component analysis accentuated mix time and breakdown in the vertical axis and peak resistance and protein content in the horizontal component.

Very few genotypes did not follow the general trend for a heat-stress-related decrease in the proportion of small (B-type) starch granules (Fig. 4). Table V lists specific results for the genotypes that were most tolerant or susceptible to the effects of heat with respect to the size distribution of the starch granules. Figure 4 also indicates a range of size distributions for the untreated set, adding to earlier data of this type (Blumenthal et al 1994) and indicating promising genotypes for breeding wheats that may provide a higher proportion of large starch granules for uses such as starch-gluten processing.

Grouping of Tolerant and Susceptible Genotypes According to Common Attributes

No significant relationship could be found for the heat-related reactions of the range of genotypes to various criteria such as grain hardness, national origin, or pedigree grouping, or even for many aspects of glutenin allelic composition. However, as previously reported (Blumenthal et al 1995), there was a very significant association between changes in dough properties and allelic constitution at the *Glu-D1* locus, coding for the alternative HMW glutenin subunit combinations 5+10 (allele *Glu-D1d*, more tolerant) or 2+12 (allele *Glu-D1a*, more susceptible to change due to heat). This relationship (Fig. 2 [2+12 and 5+10 genotypes designated by black and white columns, respectively]) is limited to 44 genotypes of the set studied, because one (Kamilaroi) is a durum wheat lacking the D genome.

DISCUSSION

Despite the overall weakening in dough properties evident in the above statistics, the range of reactions exhibited by the various genotypes indicated success in selecting wheats covering the spectrum from heat tolerance, with respect to dough properties

(left side of Fig. 2), to susceptibility (right side of Fig. 2). Individual results for other attributes also covered a range of values (Table IV). The percentage of large glutenin polymers received particular attention (Fig. 2) because of its close relationship to mix time (Table I). Comparison of the middle two histograms (differences) in Figure 2 shows that the ranking of this biochemical attribute followed the trends in mix time differences fairly closely, with a similar selection of genotypes showing positive or negative changes, especially for the most tolerant or the most susceptible genotypes.

Although a weakening of dough-mixing properties may be the general rule following heat stress (as reviewed by Blumenthal et al 1993), this reaction is apparently not universal. While observation of the changes in the many attributes provides some guide to the more general effects of heat stress on quality, quantitative figures depend on the particular selection of genotypes, presuming that their reactions are determined genetically. For example, different sets of wheats might be chosen that would give overall greater or lesser changes when compared to those reported in this experiment. Nevertheless, these results should be reasonably representative, given the size of this set and the distribution with respect to pedigree diversity and reputation for heat tolerance.

Even in this set of 45 genotypes, a considerable number of genotypes showed no significant loss of mixing strength, marking them as potentially useful in breeding programs to stabilize commercial cultivars against a major effect of environmental variation on grain quality. The relationships observed between changes in quality and changes in gluten composition (particularly molecular size distribution) points to a likely molecular explanation for the quality changes, as well as the possibility of using a chemical test (e.g., for gluten composition) to screen for tolerance or susceptibility. Such a screening test would still require the time-consuming task of growing and heat-stressing plants. The only genetic marker identified in this experiment that could be used to avoid this step is the *Glu-1* locus, the *d* allele (subunits 5 + 10) offering promise of identifying heat-tolerant genotypes, together with its value to predict other genetic (nonenvironmental) aspects of dough properties.

Despite the considerable size of the experiment described here, it provided only one time-sequence of heat stress: three 10-hr (day) exposures to 40°C, 29 days after anthesis. A late exposure to heat was chosen partly because it reflects the crop reality that episodes of high temperature are more likely to occur late in the grain-filling period as summer approaches. However, several reports suggest that the changes in grain quality associated with heat vary depending on the stage of grain development at which the stress is experienced (Randall and Moss 1990, Blumenthal et al 1991, Stone and Nicholas 1994). Thus, the results of a survey of genotypes might vary depending on the timing of the stress and even the rate of rise of temperature (Stone and Nicholas 1994).

The results open up some difficult to answer questions about the molecular basis of heat-stress-related modification of dough properties. The observed contrasts for 5+10 and 2+12 genotypes may indicate a degree of regulation at the glutenin gene level. Indeed, currently, the main hypothesis is that heat-stress elements may regulate the expression (or otherwise) of gluten proteins during heat shock (Blumenthal et al 1993). The close correlations to the percentage of very large glutenin polymers, indicates that the stage of polymerization of glutenin polypeptides (presumably disulfide bond formation) is critical to the establishment of dough properties, for normally grown grain as well as for heat-stressed grain. There is an additional possibility that heat shock proteins produced during stress (Blumenthal et al 1993) may contribute directly to variations in grain quality (Bernardin et al 1995). Further elucidation of these aspects will require closer study of the events following synthesis of the polypeptides.

Verification of the observations for individual genotypes described in this article may still be required by field trials and by test crossing. Further screening of an even wider range of genotypes would probably lead to the identification of additional tolerant (and susceptible) lines for potential use in cultivar improvement.

Finally, an accumulation of results describing the reactions of specific cultivars to heat is also likely to be valuable in formulating a model to help in predicting the effects of growth environment on grain quality, such as is already being formulated from historic and climatic data (Correll et al 1994).

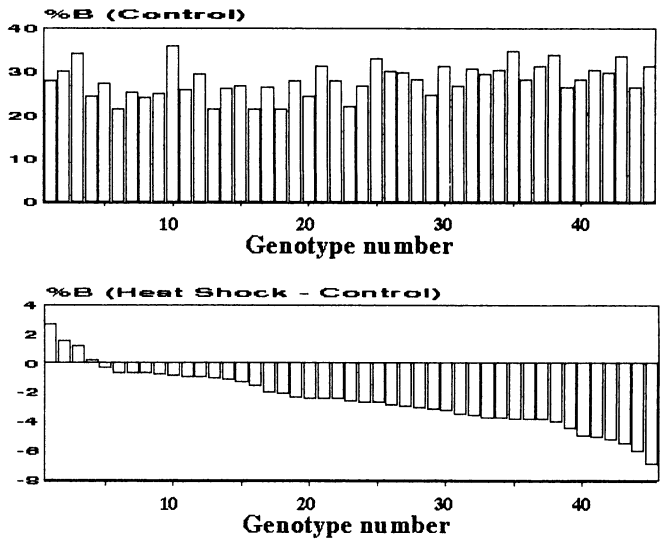

Fig. 4. Proportion of small (B-type) starch granules in control samples and differences due to heat stress (heat-stressed minus control), arranged from left to right. Average least significant difference is 2.3% of B-type granules (5% significance level, HS – C).

TABLE V
Starch Particle-Size Distribution Data (% B-type granules) for Genotypes Tolerant and Susceptible to Effects of Heat Stress[a]

Genotype	Control	Heat Stressed	% Change[b]
Tolerant			
6384	28.1	30.8	9.7
Ulla	30.1	31.7	5.3
6386	34.1	35.2	3.5
Trigo 1	24.4	24.6	0.8
Susceptible			
Grebe	29.6	24.4	–17.9
Oxley	33.6	28.1	–16.4
Wyuna	26.4	20.3	–23.1
Machete	31.2	24.4	–22.1

[a] Underlined values are significantly different at $P < 0.05$.
[b] Heat stressed – control.

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