

# Composition and Quality of Wheat Grown Under Different Shoot and Root Temperatures During Maturation

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## ABSTRACT

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Diminished quality of wheat (*Triticum aestivum* L.) from high temperature during maturation is usually attributed to direct effects of the stress on the shoots or grain. However, the upper soil temperature approaches the air temperature, and roots are highly sensitive and interact profoundly with other plant parts. The objective of this study was to determine the effect of differential shoot and root temperatures on quality of hard red spring wheat (cv. Len). Plants were grown in hydroponic containers at 15/10°C day/night until 10 days after anthesis, when shoot/root treatments of 15/15°C, 15/30°C, 30/15°C, and 30/30°C were imposed until the grain ripened. Both high shoot and high root temperature affected quality of the grain. Kernel size and weight were

diminished more by high root than by high shoot temperature, but flour yield was decreased significantly only by the 30/30°C treatment. The percentage of starch in B granules was reduced by high shoot temperature, and the diameter of A granules was decreased by all heat treatments. Amylose concentration was increased by high temperatures of both shoot and root, resulting in decreased pasting characteristics. Flour protein increased after all heat treatments, but high shoot temperature decreased the polymer-to-monomer ratio and unextractable polymeric protein and it affected dough mixing. We concluded that stress on roots directly affects properties of the grain that are important for milling and baking.

The quality of wheat grain for many end products is usually favored by high temperature during maturation (Randall and Moss 1990). However, extremely high temperature limits yield and quality of wheat grain in many regions of the world. Stress from high temperature during this critical developmental stage decreased grain yield by  $\approx 3\text{--}4\%$  for each 1°C rise above 15°C (Wardlaw and Wrigley 1994). Many kernel characteristics that affect end-use quality were altered at  $>30\text{--}35^\circ\text{C}$ . High temperatures caused shrinking, notching, splitting, and chalking of kernels (Tashiro and Wardlaw 1990) and low kernel weight, size, and test weight of the grain (Gibson et al 1998). Changes in kernel characteristics were most pronounced when plants were exposed to sustained temperatures of  $\geq 30^\circ\text{C}$  during early maturation (Gibson et al 1998).

The adverse relationship between kernel characteristics that are diminished by high temperature and milling quality was demonstrated in several studies. Low kernel weight that caused low yield of grain also reduced the yield of flour (Gibson et al 1998). Flour yield was correlated positively with kernel weight and kernel diameter (Bequette 1989; Gwirtz et al 1996), suggesting the likelihood of a similar association under high-temperature conditions. Shriveling of kernels from high temperature during maturation that reduced test weight also decreased the flour yield (Satumbaga et al 1995; Gwirtz et al 1996; Gibson et al 1998).

High temperature during maturation of wheat reduced flour yield by decreasing the content of starch, the major component of the endosperm (Jenner et al 1991). The number of starch B granules was reduced compared with A granules (Bhullar and Jenner 1985; Shi et al 1994; Tester et al 1995). Results conflicted on the effect of high temperature on amylose concentration. Stone and Nicolas (1994) reported no effect of temperature, whereas Shi et al (1994) and Tester et al (1995) showed that high temperature increased the proportion of amylose, which affected the physicochemical properties of starch. The increased quantity of amylose starch profoundly affected starch gelatinization and pasting properties (Zeng et al 1997).

Flour protein concentration and composition are primary determinants of flour quality (MacRitchie 1992). Several studies corre-

lated flour protein concentration or composition with environmental factors, particularly high temperature. Johnson et al (1972) found a slight positive correlation between increased temperatures during early maturation and protein concentration, but temperature during later stages had no effect. The protein concentration of soft white winter wheat was associated positively with maximum temperatures during grain filling; however, the relationship varied among locations (Rao et al 1993). The protein concentration of hard red winter wheat increased when high temperature was imposed 10 days after anthesis, but no effect was observed when plants were exposed after 15 and 20 days (Gibson et al 1998). Temperatures  $>35^\circ\text{C}$  during wheat maturation increased protein concentration (Blumenthal et al 1991).

High protein concentration was considered to enhance flour quality because of the positive relationship with loaf volume (Finney and Barmore 1948). However, extremely high temperature during maturation diminished the functional characteristics of dough without changing the protein concentration of flour (Finney and Fryer 1958; Randall and Moss 1990; Blumenthal et al 1991). Apparently, high temperature changed the protein biosynthetic pathways to increase the monomer-to-polymer (gliadin-to-glutenin) ratio, because accumulation of monomers was reduced less than polymers (Stone and Nicolas 1994; Blumenthal et al 1995).

Most studies on the effect of high temperature on kernel characteristics and flour quality of wheat subjected the whole plant to a brief or sustained period of stress at  $25\text{--}40^\circ\text{C}$  (Bhullar and Jenner 1985; Randall and Moss 1990; Blumenthal et al 1991, 1995; Shi et al 1994; Stone and Nicolas 1994; Tester et al 1995; Gibson et al 1998). However, exposing individual plant parts to high temperature also greatly influenced kernel characteristics. Warming vegetative parts at 20 or 25°C while keeping the spike at 15°C initially increased dry matter accumulation but decreased the final dry weight of the spike (Ford et al 1976). Increasing the temperature of the spike to 33°C for six days reduced kernel weight by 29.8% (Bhullar and Jenner 1983), whereas increasing it to 35°C for 1, 2, 4, or 7 days reduced the kernel weight only in the 7-day treatment (Jenner 1991). The decrease in kernel weight was attributed to decreased duration of kernel growth, which was only partially compensated for by an increase in the rate of starch synthesis (Jenner et al 1991).

Synthesis of starch, the major component of wheat grain, is catalyzed by sucrose synthase, UDP and ADP glucose pyrophosphorylase, starch synthase in its soluble and insoluble isoforms, and branching enzyme (Smith et al 1997). The reduction in starch synthesis under high temperature was linked to diminished activity of soluble starch synthase, suggesting that the effect originated in the grain itself (Hawker and Jenner 1993). However, applying

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differential shoot and root temperatures to maturing plants demonstrated that responses to high temperature came from the roots as well as the shoots. Grain yields of wheat were highest when both the shoots and the roots were at the lowest temperature (25°C), and high temperature (35°C) was more damaging when it was applied to the roots than the shoots (Kuroyanagi and Paulsen 1988). Increasing the shoots to 30°C and keeping the roots at 15°C decreased kernel weight by 40%, while holding the shoots at 15°C and increasing the roots to 30°C decreased kernel weight by 57% compared with maintaining the whole plant at 15°C (Guedira and Paulsen, *in press*). The decrease in kernel weight was accompanied by reductions in starch content and activities of the same enzymes in the starch synthesis pathway that were affected in previous studies when only the spike was heated (Hawker and Jenner 1993). The greater reduction in kernel properties from high root temperature than from high shoot temperature suggested that underground organs regulate some grain-filling activities and are highly susceptible to stress (Guedira and Paulsen, *in press*).

Soil temperatures near the root zone become nearly as high as the air temperature during maturation of wheat (McMichael and Burke 1996). However, little is known about the effect of high soil temperature on kernel characteristics or the quality of the grain for baked products. The kernel characteristics that are affected by root temperature, and the importance of those characteristics in milling quality, suggest that root temperature should be considered. The objective of this study was to assess the relative effects of shoot and root temperatures on the quality of wheat grain for milling and baking. Such information would be useful for understanding the role of high temperature on grain quality and developing strategies for improving wheat in heat-stressed environments.

## MATERIALS AND METHODS

### Plant Material

Hard spring wheat (*Triticum aestivum* L. cv. Len) seeds were germinated in moist vermiculate. Two-week-old seedlings were transplanted to 38-L opaque plastic containers with 15 seedlings in each container. The medium was a complete nutrient solution (Hoagland and Arnon 1950) that was aerated continuously, adjusted to pH 5.0 semiweekly, and changed biweekly throughout the growing period. Plants were grown in controlled environment chambers (model PGW-36, Conviron, Pembina, ND) at 15/10°C day/night temperature, 16-hr photoperiod, 1,000  $\mu\text{mol m}^{-2}\text{sec}^{-1}$  of radiation,

and 40–50% rh during the light period and 70–80% rh during the dark period.

Plants in containers were assigned randomly to four shoot/root temperature treatments, 15/15, 30/15, 15/30, and 30/30°C, 10 days after anthers were extruded from the florets. Shoot temperatures were imposed by setting the controlled environment chambers at 15/10°C and 30/25°C day/night. In the low temperature regime, one-half of the containers were held at the ambient air temperature (15/15°C shoot/root), and the solution in the other containers was warmed to 30°C with 150W aquatic aquarium heaters (Pulsar, Oakland, NJ) (15/30°C shoot/root). In the 30/25°C chambers, one-half of the containers were held at the ambient air temperature (30/30°C shoot/root), and the solution of the other containers was cooled to 15°C with an immersion cooler (Haake E12, Karlsruhe, Germany) (30/15°C shoot/root). Constant aeration of the medium ensured that the temperature of the roots remained uniform during the experiment. Air, shoot, and root temperatures were monitored continuously with temperature loggers (Hobo XT, Onset Computer, Pocasset, MA). Conditions other than the shoot/root temperatures were maintained as before. Each treatment had two sets of three containers.

### Kernel Physical Characteristics

Spikes were hand-harvested when the grain ripened. The grain was threshed with a single-spike thresher (Lincoln Manufacturing Co., Lincoln, NE). The harvest from plants in all three containers in each treatment was bulked, and kernel characteristics and milling quality were measured on the commingled grain.

Grain characteristics were determined with a single-kernel characterization system (SKCS) (model 4100, Perten Instruments, Reno, NV). Mean values of kernel weight, size dimensions, and hardness (crushing force) of 300 kernels were recorded. Test weight was measured by a microprocedure using a cup that contained the gram equivalent of pounds per bushel, and data were expressed as kg/hL.

Kernel size distribution of the bulked wheat samples was determined with a Ro-tap sifter (W.S. Tyler, Mentor, OH) and U.S. Standard Testing Sieves No. 7 (2.80 mm opening) and No. 10 (2.00 mm opening). The percentages of 100 g of kernels that remained on top of the No. 7 and No. 10 sieves and passed through the No. 10 sieve were recorded.

### Laboratory Milling

The grain from all four treatments was milled to flour. Moisture content of grain from each treatment was determined by Approved

TABLE I  
Kernel and Flour Milling Characteristics of Len Wheat Grown at Four Temperatures for Shoot and Root During Maturation

Treatment (°C)	Kernel Wt (mg)	Kernel Dia (mm)	Test Wt (kg/hL)	Kernel Size Distribution (%)			Hardness Index	Milling Fractions (%)		
				Over No. 7	Over No. 10	Through No. 10		Flour	Bran	Shorts
15/15	49.7	3.6	84.0	97.9	1.8	0.2	74.1	70.0	21.4	9.5
30/15	35.6	2.6	72.7	80.7	18.5	0.7	81.2	67.4	23.3	8.6
15/30	26.9	2.0	65.4	77.2	22.1	0.8	77.3	65.9	24.0	9.4
30/30	25.3	1.8	61.0	44.7	51.8	2.9	83.3	58.3	30.4	10.2
LSD <sup>a</sup>	5.3	0.5	4.2	5.4	3.8	0.9	2.8	5.2	2.5	ns <sup>b</sup>

<sup>a</sup> Least significant difference ( $P < 0.05$ ).

<sup>b</sup> Not significant.

TABLE II  
Correlation Coefficients ( $r$ ) Among Kernel and Milling Characteristics of Len Wheat Grown at Four Temperatures for Shoot and Root During Maturation

Parameter	Kernel Dia	Test Wt	Over No. 7	Over No. 10	Hardness Index	Flour Yield (%)
Kernel wt	0.95**** <sup>a</sup>	0.97***	0.81**	-0.81**	-0.66*	0.75**
Kernel dia		0.94***	0.83**	-0.84**	-0.81**	0.76**
Test wt			0.88**	-0.89**	-0.74*	0.85**
Over No. 7				-1.00***	-0.84**	0.98***
Over No.10					0.84**	-0.98***
Hardness Index						-0.81**

<sup>a</sup> \*, \*\*, \*\*\* = Significant at  $P < 0.05$ , 0.01, and 0.001, respectively.

Method 44-15A (AACC 2000). Wheat samples were tempered to 15% moisture for 24 hr before milling on a Brabender Quadrumat Sr. laboratory flour mill (C.W. Brabender Instruments, Hackensack, NJ) that was prestabilized at 30.6°C for 1 hr. Three products, flour, bran, and shorts, were obtained from each milling.

### Starch Composition of Flour

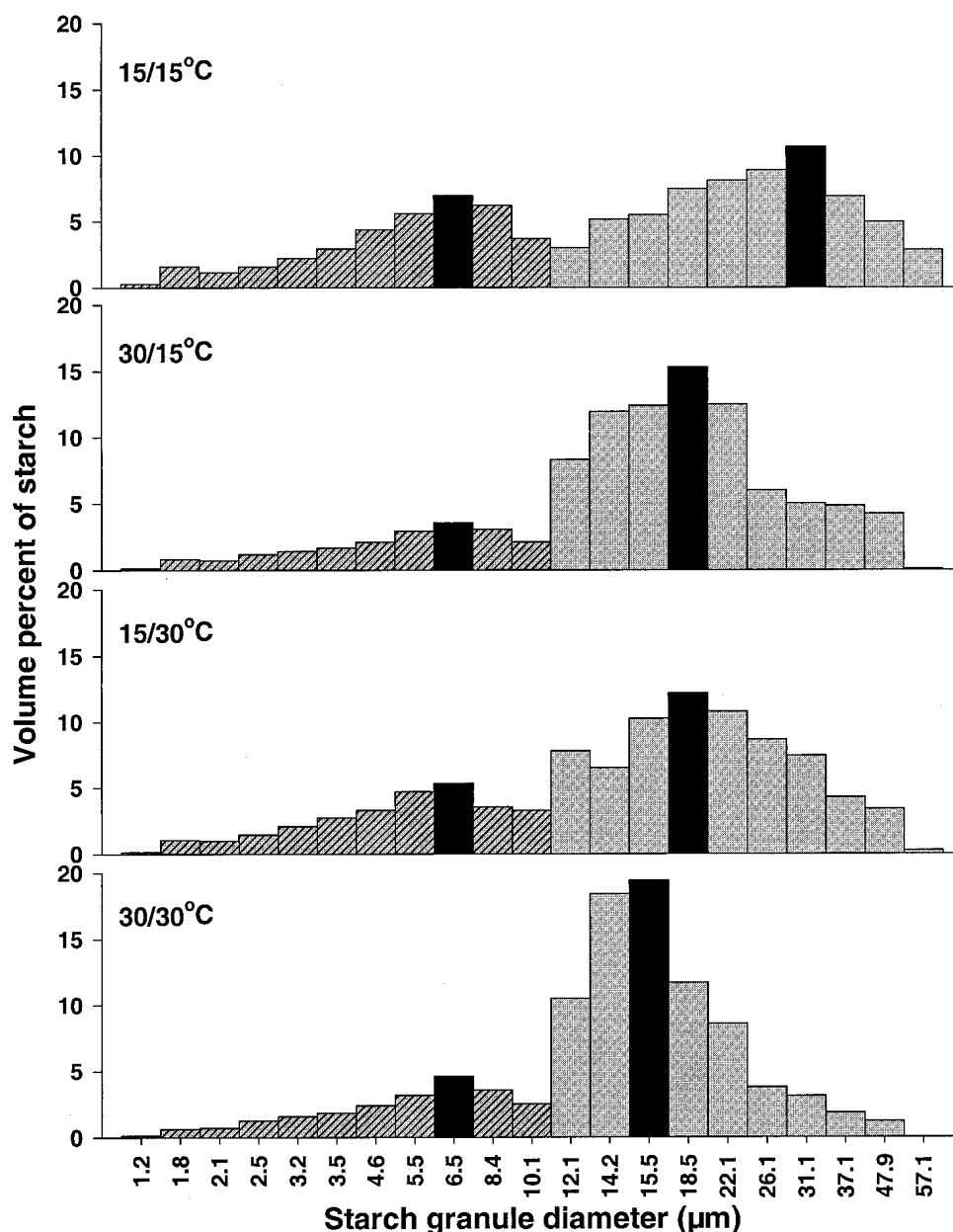
Particle size distribution of isolated starch from the flour was measured by the method of Stoddard (1999). Flour (1 g) was dispersed in 10 mL of 0.5M NaCl and soaked overnight at 4°C. The mixture was ground with a Teflon tip pestle (model S21, TRI-R Instruments, New York, NY) mounted on a mixer (Servall High Speed Omni-mixer, Norwalk, CN). The suspension formed a gluten ball, and starch slurry was decanted through Miracloth (Calbiochem, La Jolla, CA) into a tube. The starch was precipitated by centrifugation at 5,000 × g for 2 min; washed with a sequence of 50% (w/w) CsCl, 2% SDS, and twice in water followed by centrifugation after each step; washed with ethanol; and dried over silica gel. Starch granule size distribution was determined with a laser-dif-

fraction particle size analyzer (Lecotarc model LTS 150, Leco Corp., St. Joseph, MI) using the irregular mode setting. Scattered light from laser beams was projected through a stream of particles suspended in isopropanol to provide particle size distribution at 0.75–704 μm to Lecotarc analysis software. Particles ≤10.10 μm in diameter were B granules and those >10.10 μm were A granules. The low end of the range did not allow identification of C granules, which were included with B granules, if present.

Amylose concentration of the starch in the flour was determined by the method of Gibson et al (1997) using an amylose-amylopectin assay kit (Megazyme International, Wicklow, Ireland).

### Flour Pasting Characteristics

Pasting characteristics of the flour were measured with a Rapid Visco Analyser (RVA) (Newport Scientific Pty. Ltd., Sydney, Australia). Flour (3.5 g, 14% moisture) was placed in an aluminum can containing 25 mL of distilled water. The flour-water suspension was stirred constantly while it was heated at 50°C for 1.5 min, increased to 95°C at a constant rate for 3 min, held at 95°C for 3 min, and



**Fig. 1.** Mean starch particle size distribution of Len wheat grown at four temperatures for shoot and root. A-type granules (grey), B-type granules (striped), and mode values of diameter (solid).

cooled at a constant rate to 50°C for 5.5 min. The primary flour pasting characteristics derived from the RVA curve included peak time and viscosity (min and RVU), minimum viscosity, final viscosity (maximum viscosity during cooling to 50°C), breakdown (peak minus minimum viscosity), and setback (final minus minimum viscosity).

### Concentration and Composition of Flour Protein

Flour protein concentration ( $N \times 5.7$ ) was determined with a Leco model FP-2000 nitrogen analyzer. Flour protein composition (total, extractable, and unextractable protein) was measured by size-exclusion high-performance liquid chromatography (SE-HPLC) (Gupta et al 1993). Flour (10 mg) was suspended in 1 mL of 0.5% SDS-phosphate buffer (pH 6.9). For total protein, the suspension was vortexed for 5 min (output 7) and sonicated at 6W for 15 sec using a sonic dismembrator (model 60, Fisher Scientific, Pittsburgh, PA). The sonicated sample was centrifuged at  $14,800 \times g$  for 20 min, and the supernatant was recovered with a 3.0-mL disposable syringe and filtered through a 0.45- $\mu$ m filter into a HPLC glass vial. The extract was heated at 80°C for 2 min and then cooled in ice water. For extractable protein, the flour sample in SDS-phosphate buffer was vortexed for 5 min and centrifuged at  $14,800 \times g$  for 20 min. The supernatant containing the extractable protein was collected with a 3-mL syringe and treated by the procedure for total protein. The pellet containing the unextractable protein was resuspended in 1 mL of SDS-phosphate buffer by vortexing the sample at output 7 for 10 min and sonicated at 6W for 25 sec to solubilize the unextractable protein. The sample was then centrifuged at  $14,800 \times g$  for 20 min, and the supernatant was collected as described above.

**TABLE III**  
Flour Starch Composition of Grain from Len Wheat Grown at Four Temperatures for Shoot and Root During Maturation

Treatment (°C)	B Granules (% in Starch)	Amylose (%)
15/15	36.5	23.0
30/15	19.5	28.1
15/30	27.6	25.0
30/30	22.3	31.2
LSD <sup>a</sup>	4.2	2.1

<sup>a</sup> Least significant difference ( $P < 0.05$ ).

The SE-HPLC was conducted with a Hewlett-Packard 1100 HPLC using a variable wavelength UV detector set at 214 nm. A security guard (Phenomenex, Torrance, CA) connected to a  $300 \times 7.80$  mm Biosep-Sec-S4000 size-exclusion column, maintained at 25°C, was used for sample separation. Protein extract (20  $\mu$ L) was injected into the column. Sample was eluted with 50% (v/v) aqueous acetonitrile that contained 0.05% trifluoroacetic acid at a flow rate of 0.5 mL/min for 30 min with 10–15 min of posttime. All solvents were HPLC grade (Fisher Scientific). The elution profiles were integrated for 24 min by Hewlett-Packard HPLC Chemstation software.

Protein fractions were calculated as described by MacRitchie and Gupta (1993). The percentages in protein of total polymeric protein (TPP) (primarily glutenin), monomeric protein (gliadin), and low molecular weight albumins and globulins were determined from the total protein profile:

$$\%TPP = (\text{area of peak 1} / \text{total area profile}) \times 100 \quad (1)$$

The percentage of unextractable polymeric protein (UPP) in the TPP was calculated as:

$$\%UPP \text{ in TPP} = (\text{area of peak 1 [unextractable protein]} / (\text{area of peak 1 [extractable protein]} + \text{area of peak 1 [unextractable protein]}) \times 100 \quad (2)$$

and

$$\%UPP \text{ in protein} = ([1] \times [2]) / 100 \quad (3)$$

### Mixing Characteristics of Flour

The mixing characteristics of flour from the four treatments were determined by a 2-g mixograph using Approved Method 54-40 (AACC 2000) and analyzed with Mixsmart software (National Mfg. Div., TMCO, Lincoln, NE). Mixing was performed at variable absorption according to protein content. Indicators of dough quality were water absorption (%), time to peak height (sec), peak height (%), peak width (%), bandwidth after 2 min (%), and the descending slope of the mixograph curve from the peak until 2 min after the peak (percentage of full scale per min).

### Experimental Design and Statistical Analysis

Temperature treatments for culturing plants were arranged in a randomized complete block design and replicated twice. Data were analyzed by general linear model (GLM) procedures (SAS Institute,

**TABLE IV**  
Flour Pasting Characteristics of Grain from Len Wheat Grown at Four Temperatures for Shoot and Root During Maturation

Treatment (°C)	Peak Time (min)	Pasting Characteristics (RVU) <sup>a</sup>				
		Peak Viscosity	Minimum Viscosity	Final Viscosity	Breakdown	Setback
15/15	6.3	210.5	151.5	229.0	59.0	77.5
30/15	6.2	186.4	132.5	197.0	54.0	64.5
15/30	5.9	209.5	149.0	234.0	60.5	85.0
30/30	5.8	133.0	89.0	145.0	44.0	56.0
LSD <sup>b</sup>	ns <sup>c</sup>	5.8	6.6	4.5	3.8	4.3

<sup>a</sup> Rapid Visco Analyser (RVA) units.

<sup>b</sup> Least significant difference ( $P < 0.05$ ).

<sup>c</sup> Not significant.

**TABLE V**  
Flour Protein Concentration and Composition of Grain from Len Wheat Grown at Four Temperatures for Shoot and Root During Maturation

Treatment (°C)	Protein in Flour (%)	Total Polymer in Protein (%)	Monomer in Protein (%)	Mono/Poly <sup>a</sup> Ratio	Alb and Glo <sup>b</sup> in Protein (%)	UPP in TPP <sup>c</sup> (%)	UPP in Protein (%)
15/15	15.0	45.3	46.5	1.0	8.2	50.3	23.0
30/15	20.5	30.5	61.4	2.0	8.0	48.0	15.0
15/30	18.3	44.0	48.4	1.1	7.3	45.0	20.0
30/30	18.1	40.0	52.7	1.2	7.5	42.3	16.3
LSD <sup>d</sup>	0.6	1.3	0.8	0.4	0.3	1.8	1.2

<sup>a</sup> Monomer-to-polymer ratio.

<sup>b</sup> Unextractable polymeric protein in total polymer protein.

<sup>c</sup> Albumins and globulins.

<sup>d</sup> Least significant difference ( $P < 0.05$ ).

Cary, NC). Least significant differences were calculated at  $P < 0.05$ . Simple correlation coefficients among kernel characteristics were determined by SAS correlation (CORR) procedures.

## RESULTS

### Kernel Characteristics and Milling Properties

Kernels produced by plants at the low shoot and root temperature (15/15°C) had the highest weight, diameter, and test weight among the four treatments (Table I). High temperature applied to the shoots or roots, or both, significantly reduced kernel measurements. However, warming the shoots to 30°C while maintaining the roots at 15°C was less deleterious than holding the shoots at 15°C and the roots at 30°C. The latter treatment affected most kernel characteristics as severely as warming the whole plant to 30°C. All three kernel characteristics were highly significantly correlated (Table II).

Size distribution of kernels within the temperature treatments followed a pattern similar to that of kernel weight, kernel diameter, and test weight (Table I). The proportion of large kernels that remained over the No. 7 sieve was greatest for plants grown at the low shoot and root temperatures (15/15°C) and lowest for plants grown at 30/30°C. The proportion of small kernels that remained on or passed through the No. 10 sieve was greatest for the 30/30°C treatment. The amount of kernels that remained on the No. 7 sieve was highly positively correlated with kernel weight, kernel diameter, and test weight, whereas the proportion of kernels on the No. 10 sieve was negatively correlated with those other traits (Table II).

Kernel hardness index was low when either the whole plant or the shoots were at the low temperature (15/15 or 15/30°C) and was high when the shoot temperature was high, regardless of the root temperature (30/15 or 30/30°C) (Table I). Kernel hardness index was negatively associated with kernel weight, diameter, test weight, and the proportion that went over the No. 7 sieve (Table II).

Flour yield was equally high from kernels produced under treatments where at least one part of the plant was at 15°C and decreased significantly when the whole plant was at 30°C (Table I). The amount of bran was lowest when the shoots and roots were at 15°C. Increasing the shoots or roots to 30°C similarly increased the amount of bran. The highest amount of bran was obtained when both shoots and roots were at 30°C. The proportion of shorts in the milling fractions was similar for all treatments. Flour yield was correlated positively with most kernel characteristics (Table II). The exceptions were the proportion of kernels over the No. 10 sieve and hardness index, which were negatively associated with flour yield.

### Flour Starch Composition and Pasting Characteristics

Starch from the flour of kernels grown at the different temperatures exhibited a clear bimodal particle size distribution (Fig. 1). Starch from the grain at the low shoot and root temperatures (15/15°C) had mode diameter values of 6.5 and 37.1  $\mu\text{m}$  for B and A granules, respectively. None of the temperature treatments affected the size mode values of B granules. However, warming the shoots or the roots reduced the mode diameter of A granules to 18.5  $\mu\text{m}$ , and warming both parts further reduced it to 15.5  $\mu\text{m}$ .

Although modal diameter was not affected, the percentage of starch in B granules was reduced significantly by high temperature

(Table III). High shoot temperature caused the greatest reductions, regardless of the root temperature. Consequently, the percentage of starch in A granules was increased by most high temperature treatments, especially when applied to roots (data not shown).

The percentage of amylose was low in the starch of flour from grain grown at the low shoot and root temperatures (Table III). High shoot temperature significantly increased the proportion of amylose, and the highest concentration occurred when both shoots and roots were at 30°C.

The pasting characteristics of flour from grain at the four treatments are shown in Table IV. The peak time was not affected by the treatments, but the viscosity measurements responded markedly. Values were high when the shoot temperature was low and were reduced by high shoot temperature. High shoot and root temperatures together caused the lowest viscosity. Similar patterns were exhibited by the other RVA measurements. The breakdown and setback were high when the shoot temperature was low and were low when the shoot or shoot and root temperatures were high.

### Flour Protein Concentration and Composition

Flour protein concentration was 15.0–20.5% for all treatments (Table V). The values were high compared with typical values for flour because the plants were grown in hydroponic media that was rich in nutrients. The flour protein concentration was lowest when both shoot and root temperatures were at 15°C. Increasing the shoot temperature to 30°C increased the protein concentration to the highest level, whereas increasing the roots or the shoots and roots to 30°C increased flour protein concentration to similar, intermediate levels.

The proportion of total polymeric protein in the protein was 30–45.5%, and monomeric protein was 46.5–61.4% (Table V). The only treatment that had a marked effect on either fraction was the high shoot and low root temperature, which markedly decreased the total polymeric protein and increased the monomeric protein. The ratio of monomeric gliadin to polymeric glutenin protein in the flour increased only when the shoot temperature was 30°C and root temperature was 15°C.

Contents of albumin and globulin were high when the root temperature was low, and they were reduced significantly by high root temperature, regardless of the shoot temperature (Table V). The UPP in TPP followed a pattern similar to that of albumin and globulin, while the UPP in protein was reduced by high shoot temperature, regardless of the root temperature.

### Dough Properties

Water absorption was low when plants were grown at the low shoot and root temperature and increased under all three high temperature treatments (Table VI). The highest value was obtained at 30/15°C. Peak time was uniformly high when the shoot temperature was low. Peak height was high in most treatments and only decreased when both the shoots and roots were heated. Peak width was high when shoot temperature was low. Mixing tolerance, as indicated by the bandwidth after 2 min, was high when the grain was grown at low shoot and root temperatures, and was decreased by the other treatments, particularly by high shoot temperature. The decrease in the bandwidth after 2 min from high temperature was greater than the reductions in curve width at the peak in all treat-

TABLE VI  
Mixograph Characteristics of Flour from Grain of Len Wheat Grown at Four Temperatures for Shoot and Root During Maturation

Treatment (°C)	Water Absorption (%)	Peak Time (min)	Peak Ht (%)	Bandwidth (%)	Bandwidth + 2 min (%)	Slope (% min)
15/15	66.2	5.2	79.5	45.4	35.4	-2.7
30/15	74.2	4.0	78.0	31.0	18.6	-2.0
15/30	70.7	4.8	81.4	41.1	28.0	-2.4
30/30	71.0	3.7	74.0	30.0	17.1	-2.0
LSD <sup>a</sup>	0.1	0.6	2.6	4.0	2.4	0.2

<sup>a</sup> Least significant difference ( $P < 0.05$ ).

ments. The descending slope was lowest when plants were grown at low shoot and root temperatures, and it was increased by high temperature, particularly to the shoot.

## DISCUSSION

The extreme shoot/root treatments (15/15°C and 30/30°C) illustrated the marked effects of temperature during maturation on most kernel characteristics and quality attributes of wheat. The intermediate shoot/root regimes (30/15°C and 15/30°C) suggested that some effects of high temperature were associated with shoots, some with roots, and others with both structures.

Most of the changes in grain traits between the 15/15 and 30/30°C treatments would adversely affect all parts of the wheat industry. Producers' yields would decline similarly to the change in kernel weight a rate of 3.2%/1°C, which was within the range reported by Wardlaw and Wrigley (1994). The kernel weight of 25.3 mg at 30/30°C was only slightly lower than the mean value of grain from producers' fields on much of the Great Plains (Kansas Agricultural Statistics 1999). The loss of yield combined with the 27% decline in test weight, the other factor that is usually considered in payments for grain, would substantially decrease income of producers.

The flour yield of 70% from grain produced at 15/15°C was typical for wheat (Satumbaga et al 1996). The decline in flour yield to 58.3, or >16% between the extreme temperatures, was also noted in previous studies (Gibson et al 1998). The marked loss of flour recovery would be detrimental to the milling industry (Bequette 1989). Likewise, many of the changes from high temperature affect the quality of the grain for baked products. Loss of flour quality, as indicated by decreased pasting and mixing characteristics, would affect the end-use properties for the baking industry.

Hardness index of the kernels clearly was affected more by shoot temperature than root temperature. Apparently, the shoot temperature was important for the strength of starch-protein interactions that determine grain hardness (Barlow et al 1973). An increase in hardness index, such as that observed with high shoot temperature, would alter milling quality by requiring more power and break and reduction operations to fully mill the grain (Finney et al 1987). It would also slow movement of water into the kernel during tempering and increase starch damage during milling (Pomeranz and Williams 1990).

High shoot temperature was also associated with a decreased percentage of starch in B granules in flour, shifting the ratio in favor of A granules and increased amylose concentration. The A and B granules are initiated at 5 and 10 days after anthesis, respectively (Bechtel et al 1990). The timing of the application of the treatment and factors involved in the packing of starch granules may have contributed to the low percentage volumes of B granules observed in high shoot temperature treatments.

Changes in the composition of starch would have a large effect on flour quality. The B-type granules had higher surface-to-volume ratios and were associated with higher rate of water absorption than A granules, affecting the mixing and baking properties of the dough (Hoseney et al 1971; Bechtel et al 1990). Bread made with flour containing a high proportion of B granules was lower in volume than normal, whereas a high level of A granules led to reduced water absorption but no change in loaf volume (Hoseney et al 1971). Hence, high shoot temperature may improve flour quality if the proportion of generally undesirable starch granules is decreased, as suggested by Batey et al (1990).

A significant association between amylose concentration and the percentage volume of A granules ( $r = 0.84^{**}$ ) was expected because amylose content increased with the size of starch granules (Peng et al 1999). Amylose molecules exist as single helices within the starch granule and are interspersed with amylopectin (Smith et al 1997). Amylose is synthesized by insoluble (granule-bound) starch synthase, whereas amylopectin is formed by soluble starch

synthase and branching enzymes (Smith et al 1997). Low kernel starch content at high shoot temperature was associated with reduced activity of soluble starch synthase (Hawker and Jenner 1993; Guedira and Paulsen, *in press*).

Pasting characteristics of flour from grain grown at different temperature treatments generally reflected the amount of amylose in starch. Increased amylose concentration under high shoot temperature was associated with low peak viscosity and breakdown, a relationship similar to that reported by Moss and Miskelly (1984) and Zeng et al (1997). The decreased peak viscosity was related to increased quantity of free water and low swelling of starch (Crosbie 1991), making the flour unsuitable for noodles (Wang and Seib 1996).

Flour protein fractions (total monomer and polymer in protein) were affected more by shoot temperature than by root temperature. Increases in the monomer fraction under high temperature were reported in previous studies in which the whole plants were stressed (Stone and Nicolas 1994; Blumenthal et al 1995). However, it is not clear why the largest proportion of monomer was obtained with the high shoot and low root temperature treatment. Translocation of nitrogen to the kernel probably persisted longer under low root temperature as a result of a slow rise in proteolytic activity (Kuroyanagi and Paulsen 1988). Also, the high temperature of the sink may have affected the mechanisms by which disulfide-polymerized glutenins are formed (Wrigley et al 1998).

High shoot temperature decreased dough strength and mixing tolerance as measured by mixing time and peak width, and peak width after 2 min, respectively. The reduction in dough properties was independent of total flour protein concentration but was associated with the unextractable protein. Unextractable polymeric protein in protein was decreased more by high shoot temperature than by high root temperature, resulting in the strong association between mixing time and tolerance and unextractable polymeric fraction that was noted in previous studies (Gupta et al 1993; Blumenthal et al 1995).

Increased flour protein concentration under stress was associated with a reduction in kernel weight. The relationship was indicated by a strong negative correlation between kernel dry weight and grain nitrogen percent ( $r = 0.92$ ) (Guedira and Paulsen, *in press*). Starch accumulation was more sensitive than nitrogen to high temperature, with the result that the grain nitrogen percentage increased with high temperature applied either to shoots or roots, or both, as found by Bhullar and Jenner (1985) and Stone and Nicolas (1994) when whole plants were stressed.

The exceptionally high protein concentration in grain from the high shoot and low root temperature treatment indicated that the roots are directly involved in nitrogen mobilization. Dalling (1985) suggested that nitrogen mobilized from leaves was cycled to the roots before it was transferred to the grains. The high root activity under high shoot and low root temperature treatment might have contributed to the high protein concentration that was observed (Kuroyanagi and Paulsen 1988).

While shoot and root temperatures had several distinctive, independent effects on grain quality, the combined high shoot and high root temperatures were often most deleterious. The combined treatment particularly diminished kernel physical characteristics that caused low milling quality and altered flour starch composition, which resulted in decreased pasting properties. Diminished milling quality, as indicated by low flour yield and increased bran proportion, resulted from low grain test weight and kernel size. The inferior pasting characteristics, as indicated by low viscosity, likely resulted from increased flour amylose concentration. Amylose may have leached during pasting and increased the free water, leading to a less viscous network (Miller et al 1973).

Factors that control the grain quality of wheat are complex and not fully understood. This study showed that the interaction between shoots and roots temperatures plays an important role in grain quality. The interaction was most obvious on physical kernel characteristics but it was also evident in the chemical composition of grain.

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