

Effect of Growth Location in the United States on Amylose Content, Amylopectin Fine Structure, and Thermal Properties of Starches of Long Grain Rice Cultivars

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ABSTRACT

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Starch was isolated from kernels of 27 rice samples consisting of nine U.S. long grain rice cultivars grown in three different locations (Missouri, Arkansas, Texas). Amylose (AM) content of the starches and the fine structure of the respective amylopectin (AP) were determined and used to explain differences observed in gelatinization properties. The AM content of rice cultivars grown at the lower temperature Missouri location increased 0.4–3% and 0.5–4% when compared with the same rices grown in Arkansas and Texas, respectively. AP values of the rice samples were isolated, debranched, and separated by low-pressure size-exclusion chromatography. The eluted AP linear chains were divided into three fractions to represent extra long (FrI), long (FrII), and short chains (FrIII). The corresponding average degree of polymerization (DP_n) at the peaks of fractions FrI, FrII, and FrIII were 100, 39, and 16, respectively. Total carbohydrate analysis of the fractions indicated that cultivars grown in

Missouri had a consistently higher proportion of FrIII and lower proportion of FrII as the same cultivars grown in Arkansas and Texas. Furthermore, the Missouri samples showed a shift toward shorter DP_n in FrII and FrIII and had more of the shortest chain components ($DP_n < 16$) of AP. The proportion of FrI did not follow a trend and varied depending on the cultivar and across location. Thermal analysis indicated that the higher temperature growth environments (Arkansas and Texas) resulted in higher onset, peak, and heat of gelatinization for the starches, suggesting longer cooking time and higher heat requirement. Overall, the data support the nonfield findings of other researchers that higher growing temperature results in AP with more DP_n short chains that are within a range of $DP > 10$ to form consistent crystallites, and thus results in higher gelatinization temperatures and enthalpies.

It is now well known that temperature during the grain filling period of the developmental stage of plant growth has significant effects on composition, structure, and physical properties of starch from many crop species. In rice, Asaoka et al (1985) and Inouchi et al (2000) found that starch from cultivars grown at low temperature (25°C) had significantly higher amylose content than cultivars grown at high temperature (30°C). They also reported that rice plants grown at the low temperature had a higher proportion of amylopectin (AP) short chains and a decreased proportion of long chains compared with the same rice cultivars grown at higher temperatures. Similar results were reported for maize starch (Lu et al 1996) where elevated temperature (35°C) decreased amylose (AM) content and the proportion of short branch chain fractions of AP compared with a lower temperature (25°C) growing environment. Working on sweet potato, Noda et al (2001) also came to the conclusion that increasing soil temperature from 15 to 33°C resulted in a reduction of AP short chains. Starch gelatinization properties have also been reported to be affected by growth temperature. In this connection, Asaoka et al (1985) found that the onset and conclusion temperatures and heat of gelatinization of endosperm starch of rice plants grown at 30°C were higher than those grown at 25°C. These findings were recently confirmed by Suzuki et al (2003), who reported significant increases in gelatinization temperatures and enthalpies of nonwaxy, low-amylose, and waxy rice starches as growth temperature was increased from 21 to 28°C. Other studies have reported similar results in starches of barley (Tester et al 1991), wheat (Shi et al 1994), maize (Lu et al 1996), sweet potato (Noda et al 2001), and potato (Protserov et al 2002).

All of the above studies were conducted under controlled conditions focusing on growth temperature as the main factor affecting starch properties. The important new knowledge generated by these fundamental studies has not been applied to explain the cause of variability in eating quality and functionality observed in same rice cultivars when grown in different locations in the United States. Rice is cultivated in several states and environmental conditions, especially day/night temperatures, and significantly vary in quality from one rice growing region to another.

This is a report of the first significant study, conducted under field conditions, on the effect of growth location on starch properties of U.S. long grain rice cultivars.

MATERIALS AND METHODS

Rice Samples

Twenty-seven rice samples consisting of nine U.S. long grain rice cultivars grown at three locations were used for the study. The rice cultivars (Cocodrie, Cypress, Della, Drew, Jefferson, LaGrue, Maybelle, Ahrent, Wells) were grown in 2000 at the Rice Research and Extension Center in Stuttgart, AR, at the Rice Research and Demonstration farm in Glennonville, MO, and at the Agricultural Research and Extension Center in Beaumont, TX. These locations were selected based on differences in day/night temperature variation. The mean day/night temperatures during the grain filling period, when starch is actively synthesized in the plant, were 30°C/19°C, 31°C/22°C, and 35°C/24°C, respectively, for Missouri, Arkansas, and Texas (Table I). The temperature data were obtained from the respective Agricultural Research stations. Harvested rice samples were dried and stored in a conditioning chamber to achieve $\approx 13\%$ kernel moisture. Rough rice was milled and debranched according to standard procedures at the Rice Research and Extension Center in Arkansas. Milled rice was kept in sealed bags under refrigeration (4°C) until time of analysis.

Starch Extraction and AM Determination

Starch was isolated from whole milled rice kernels using the alkaline steeping method described by Yang et al (1984). The isolated starch was defatted in 80% methanol and dried overnight

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at 40°C. AM content of starch was determined using a modification of the method of Juliano (1971): starch (50 mg) was weighed into a 50-mL volumetric flask and 2.5 mL purified water was added to disperse the starch powder. A solution (2.5 mL) of 2N NaOH was added to the suspension and the flask was placed in a shaking water bath set at 70°C to gelatinize the starch. Starch gelatinization was assumed complete when the solution appeared clear (5–7 min). The solution was brought to volume (50 mL) with purified water and mixed. An aliquot (2.5 mL) was transferred to a 50-mL volumetric flask, mixed with 25 mL of purified water, and 2 drops of phenolphthalein were added. The solution was neutralized by the addition of 0.1N HCl until the color was clear. One milliliter of 0.2% iodine solution (0.2 g of I₂ + 2 g of KI in 100 mL of purified water) was added to the clear solution and diluted to volume. The final solution was allowed to set for ≈30 min at room temperature. Absorbance was read against a blank (1 mL of iodine solution in 50 mL of purified water) at a wavelength of 600 nm. AM content was calculated from a standard curve prepared using potato AM.

AP Isolation

Starch was solubilized as described by Jane et al (1992). Starch (50 mg) was mixed with 5 mL of 90% (v/v) dimethylsulfoxide

(DMSO), stirred in a water bath at 96°C for 1 hr, and then stirred for another 24 hr at 25°C. Starch was precipitated from solution by addition of absolute ethanol (20 mL) and recovered by centrifugation (300 × g, 10 min). The precipitated starch was re-dissolved in 10 mL of purified water and stirred in a boiling water bath for 20 min. After cooling to room temperature, the solution was injected into a column (1.6 × 70 cm) of Sepharose CL-2B (exclusion range M_r $1 \times 10^5 - 2 \times 10^7$, Pharmacia, Sweden) and fractionated by ascending chromatography at a 24 mL/hr flow rate using water containing 0.02% sodium azide as eluent (Chinnaswamy and Bhattacharya 1986). Fractions (3 mL) were collected in test tubes. An aliquot (200 μL) from each tube was reacted with 100 μL of 2% iodine solution (2 g of I₂ + 20 g of KI in 1,000 mL of purified water) and the absorbance was read at 630 nm in a spectrophotometer. The minimum absorbance value from iodine staining of the material eluting at the void volume was used as the end of the AP peak. The tubes containing AP were then pooled and freeze-dried.

Debranching and Fractionation of AP

Samples (8 mg) of freeze-dried AP were dissolved in 1 mL of purified water and placed in a boiling water bath for 20 min. After cooling to room temperature, 1.5 mL acetate buffer (0.1M, pH

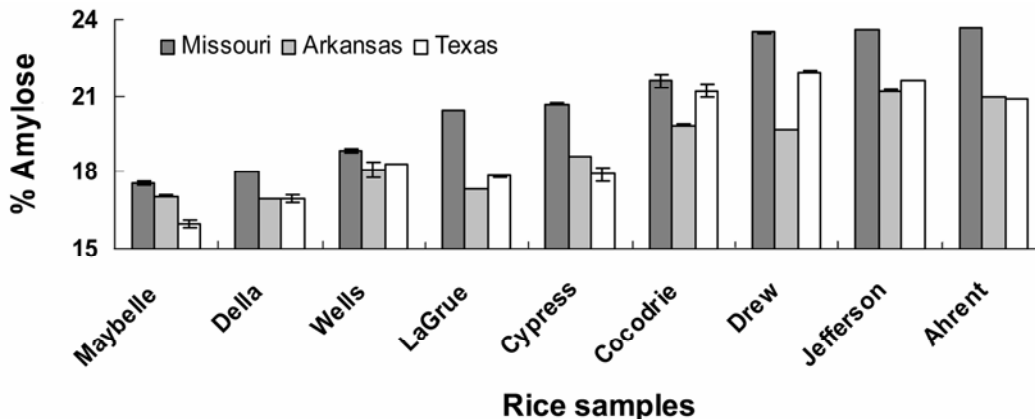


Fig. 1. Amylose content of rice samples grown at three locations.

TABLE I
Minimum and Maximum Growth Location Temperatures (°C) During the Grain Filling Period
(5–15 days after heading)^a

Missouri			Arkansas			Texas		
Date	Min	Max	Date	Min	Max	Date	Min	Max
7/16	21	32	7/30	21	36	6/27	24	35
7/17	23	29	7/31	22	34	6/28	22	35
7/18	23	33	8/01	22	28	6/29	23	34
7/19	23	31	8/02	21	31	6/30	22	34
7/20	18	24	8/03	22	30	7/01	24	35
7/21	18	26	8/04	23	33	7/02	24	34
7/22	17	26	8/05	23	33	7/03	26	34
7/23	17	28	8/06	23	31	7/04	24	34
7/24	14	28	8/07	23	29	7/05	22	33
7/25	14	30	8/08	23	25	7/06	23	33
7/26	16	32	8/09	23	26	7/07	23	34
7/27	18	33	8/10	24	28	7/08	24	36
7/28	19	33	8/11	22	31	7/09	25	37
7/29	21	24	8/12	19	32	7/10	24	34
7/30	21	29	8/13	18	32	7/11	22	34
7/31	19	30	8/14	20	28	7/12	23	35
8/01	20	31	8/15	21	31	7/13	23	37
8/02	20	32	8/16	21	33	7/14	22	37
8/03	22	34	8/17	24	34	7/15	24	38
Range	14–23	24–34		18–24	25–36		22–26	33–38
Average	19	30		22	31		23	35

^a Rice cultivars differed in beginning and length of heading period.

4.0) and 10 μ L of isoamylase (Megazyme, Australia) were added to the solution. The suspension was incubated in a 40°C water bath for 24 hr. The enzyme-substrate reaction was stopped by heating the solution in a boiling water bath for 10 min. The solution was diluted to 5 mL with purified water and fractionated by descending chromatography on a Bio-Gel P-10 (exclusion range M_r 1,500–20,000) column (1.6 \times 53 cm) operating at a flow rate of 16 mL/hr using water containing 0.02% sodium azide as eluent. Fractions (3 mL) were collected for total carbohydrates and iodine staining tests. Total carbohydrate in 0.5-mL aliquots were determined by the phenol-sulfuric acid method (Dubois et al 1956) as measured at 490 nm against a glucose standard. Aliquots (1 mL) were also stained with the iodine solution and scanned to determine the wavelength of maximum absorption (λ_{max}) of the material in each tube. The λ_{max} values were used to determine the average degree of polymerization (DP_n) according to the equation of Fales (1980)

$$DP_n = 3.290/635 - \lambda_{max}$$

Thermal Properties of Starches

A differential scanning calorimetry (DSC) instrument equipped with an evaluation and control center (DSC-30, TC11 TA, Mettler, Hightstown, NJ) was used to determine the thermal properties of the starches. Starch-to-water mixtures (1:2, w/w) were hermetically sealed in a 40- μ L aluminum pan and heated from 25 to 100°C at a rate of 10°C/min. An empty pan was used as reference. The onset, peak, and conclusion gelatinization temperatures (GT), and enthalpy were obtained from the heating curve.

Statistical Analysis

The study was a factorial design examining the effect of environment (location), genotype (cultivar), and environment-by-genotype interactions. All experiments were conducted in duplicate. The data collected were analyzed by the general linear model procedure using statistical software (SPSS Inc., Chicago, IL).

RESULTS

AM Content of Starches

The AM content of the rice cultivars ranged from 17.6 to 23.7%, from 17.1 to 21.2%, and from 16.0 to 22.0%, respectively, for Missouri, Arkansas, and Texas. As shown in Fig. 1, rice cultivars grown in Missouri have consistently higher AM content than the same cultivars grown in Arkansas and Texas. Figure 1 also indicates that the extent of the increase in AM content is cultivar-dependent, indicating that some cultivars (e.g., Wells) are more stable than others (e.g., Drew) over growth location. As indicated in Table II, there was a strong cultivar effect ($F = 1,898, P < 0.0001$) followed by location effect ($F = 1606, P < 0.0001$) for AM content of the starches. There was also a significant effect ($F = 79.8, P < 0.0001$) due to location-by-cultivar interaction. This is because AM content of the cultivars grown in the hot environments of Arkansas and Texas did not vary consistently across the two locations.

Wavelength of Maximum Absorption (λ_{max}) and Average Degree of Polymerization (DP_n)

Figure 2 shows Bio-gel P-10 size-exclusion profiles of AP from one rice cultivar (LaGrue) grown at three locations. Similar trimodal distributions were obtained from chromatograms of all nine rice cultivars. The profiles were divided into three fractions (FrI, FrII, and FrIII) at the minimum of the elution curves to correspond to extra long B (FrI), long B (FrII), and short B + A (FrIII) chains (Hizukuri 1986). The λ_{max} values at the peak of these fractions were 602 nm for extra long B, 550 nm for long B, and 428 nm for short B + A chains. These λ_{max} values corresponded to DP_n of 100 (FrI), 39 (FrII), and 16 (FrIII) as calculated from the equation of Fales (1980). All the Missouri samples showed a shift toward shorter DP_n of FrII and FrIII. The extent of the shift was more pronounced in some cultivars (LaGrue, Wells, Cypress) than in others (Della, Drew, Maybelle).

Carbohydrate Distributions

Table III lists the carbohydrate proportions of the fractions for the nine rice cultivars grown at the three locations. Rice cultivars grown in Missouri had a consistently higher proportion of FrIII (short B and A chains) and a lower proportion of FrII (long B chains) as the same cultivars grown in Arkansas and Texas. Table II also indicates the extent of these differences that were cultivar-dependent. For example, the differences were more pronounced in cultivars LaGrue, Ahrent, and Wells compared with cultivars Jefferson, Maybelle, and Della. The trend in the proportions of FrIII and FrII was not consistent between rice grown in Arkansas and Texas and varied depending on the cultivar. No consistent location trend was observed in the proportion of FrI among the cultivars. These conclusions can also be drawn from the statistical results in Table II, where the effects of location, cultivar, and location-by-cultivar interactions on proportions of FrII and FrIII are more pronounced than the effects on FrI.

Thermal Properties

DSC thermograms of starches from a representative rice cultivar (LaGrue) are presented in Fig. 3. The GT of the nine rice

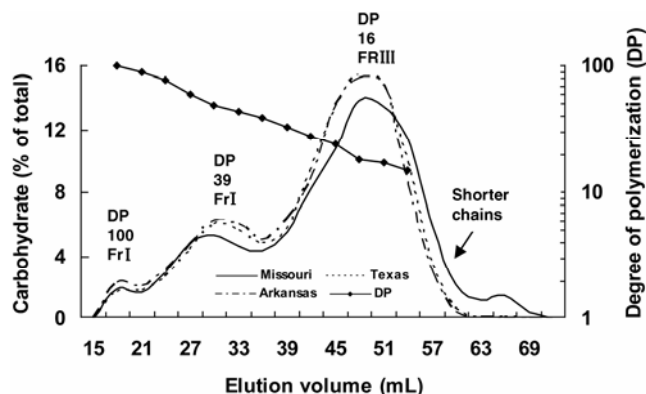


Fig. 2. Carbohydrate distributions and DP of isoamylase-debranched amylopectin from a representative rice cultivar (LaGrue).

TABLE II
Levels of Significance of F -Values for Effects of Location, Cultivar, and Location-by-Cultivar Interactions^a

Source of Variation	Amylose Content	GT ^b			ΔHg^c	Proportions of AP fractions		
		T_o	T_p	T_c		FrI	FrII	FrIII
Location (L)	1,604***	34.5***	245***	14.4***	60***	15.5**	33.2***	39.1***
Cultivar (C)	1,898***	6.4***	52***	4.4*	3.8*	6.0**	19.8***	15.7***
L \times C	79.8***	1.1ns	6.2***	2.3*	3.8**	7.2**	7.6***	7.5***

^a *, **, *** = Significant at $P < 0.01, P < 0.001, P < 0.0001$, respectively.

^b Gelatinization temperature; T_o, T_p, T_c = onset, peak, conclusion temperatures, respectively; ns = not significant.

^c Gelatinization enthalpy.

TABLE III
Carbohydrate Proportions (%) of Linear Chain Fractions of Isoamylase-Debranched Amylopectin from Nine Rice Cultivars

Rice Samples	Location	FrI	FrII	FrIII	FrIII/FrII
Cocodrie	Missouri	3.9	24.7	71.5	2.90
	Arkansas	5.6	25.6	68.8	2.69
	Texas	3.4	25.9	70.7	2.73
Cypress	Missouri	4.0	23.5	72.5	3.10
	Arkansas	3.9	25.2	70.9	2.81
	Texas	3.7	25.7	70.6	2.75
Della	Missouri	3.7	25.8	70.6	2.74
	Arkansas	3.3	27.8	68.8	2.47
	Texas	3.4	27.1	69.5	2.57
Drew	Missouri	4.2	25.2	70.6	2.80
	Arkansas	4.0	26.3	69.6	2.65
	Texas	4.3	27.4	68.3	2.49
Jefferson	Missouri	4.2	24.4	71.8	2.94
	Arkansas	3.5	25.1	71.4	2.85
	Texas	4.2	25.3	70.5	2.79
LaGrue	Missouri	3.9	22.1	74.0	3.35
	Arkansas	4.3	25.2	70.5	2.80
	Texas	3.4	23.6	73.0	3.09
Maybelle	Missouri	3.4	24.3	72.0	2.96
	Arkansas	4.0	24.9	71.1	2.86
	Texas	3.9	24.6	71.9	2.92
Ahrent	Missouri	3.6	24.6	71.8	2.92
	Arkansas	4.2	28.0	67.9	2.42
	Texas	3.6	25.2	71.2	2.83
Wells	Missouri	3.7	24.1	72.2	3.00
	Arkansas	4.2	25.5	70.3	2.76
	Texas	3.9	28.0	68.2	2.44

cultivars are presented in Table IV. Starches from rice grown in Missouri had consistently lower onset GT than those from the rice grown in Arkansas and Texas. The onset (T_o), peak (T_p), and conclusion (T_c) GT of the nine rice cultivars had ranges of 66–68°C, 73–75°C, and 82–85°C, respectively, for Missouri. Corresponding values were 69–71°C, 75–78°C, and 85–87°C, respectively, for Arkansas, and 68–71°C, 76–78°C, and 84–87°C, respectively, for Texas. As indicated by the F -values (Table III), differences due to location are more pronounced than differences due to cultivar for all the GT values.

Figure 4 compares the heat of gelatinization (ΔH_g) of the rice samples. Except for one sample (Drew), all the cultivars exhibited significantly lower ΔH_g values when grown in Missouri compared with Arkansas or Texas. Average ΔH_g values were 10.8, 12.9, and 12.5 J/g, respectively, for Missouri, Arkansas, and Texas. ANOVA (Table III) indicated a stronger location effect ($P < 0.0001$) than effects due to cultivar ($P < 0.01$) or location-by-cultivar interaction ($P < 0.001$) for this particular property.

DISCUSSION

Effect of Growth Temperature on AM Content

AM synthesis in plants is under genetic control and is affected by the amount of the wx protein or granule-bound starch synthase I (GBSSI) (MacDonald and Preiss 1985; Denyer et al 2001). Sano et al (1985) found significant increases in both the amount of wx protein and AM in endosperm of rice plants grown at cool temperatures (21°C) as compared with the levels observed in the same plants grown at normal temperatures (27°C). More recently, Hirano and Sano (1998) showed that expression of the wx gene encoding GBSSI was enhanced in response to a cool temperature (18°C) and that the level of the wx gene transcripts was higher at 18°C than at a normal temperature (28°C). The effect of temperature on AM content mainly occurs 5–15 days after heading during the period when endosperm starch is most actively synthesized (Asoaka et al 1984; Inouchi et al 2000). In the present study, the rice plants grown in Missouri were exposed to relatively cooler

TABLE IV
Onset (T_o), Peak (T_p), and Conclusion (T_c) Gelatinization Temperatures of Nine Rice Cultivars

Rice Samples	Location	T_o	T_p	T_c
Cocodrie	Missouri	68.2	75.1	85.4
	Arkansas	70.0	76.8	85.4
	Texas	69.5	76.5	86.1
Cypress	Missouri	67.1	75.1	83.9
	Arkansas	69.4	76.9	86.7
	Texas	69.8	77.1	85.6
Della	Missouri	67.8	75.3	84.9
	Arkansas	71.4	77.9	87.1
	Texas	70.5	77.4	86.8
Drew	Missouri	66.2	73.0	84.4
	Arkansas	68.7	75.1	85.9
	Texas	68.2	75.5	84.5
Jefferson	Missouri	67.0	74.9	85.0
	Arkansas	69.3	74.9	85.0
	Texas	69.5	76.3	86.4
LaGrue	Missouri	66.9	73.0	82.4
	Arkansas	68.6	76.1	85.5
	Texas	69.6	75.8	86.0
Maybelle	Missouri	66.6	74.1	83.0
	Arkansas	68.0	75.3	84.9
	Texas	68.9	76.5	84.3
Ahrent	Missouri	65.3	75.1	84.4
	Arkansas	69.5	75.9	84.5
	Texas	69.3	77.1	86.2
Wells	Missouri	67.5	75.0	83.7
	Arkansas	70.2	76.8	87.0
	Texas	70.3	76.6	84.3

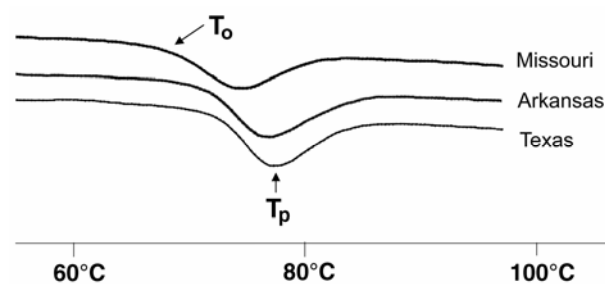


Fig. 3. DSC thermograms of starches from a representative rice cultivar (LaGrue) grown at three locations.

postheading day/night temperatures than the same plants grown in Arkansas and Texas. These temperatures averaged 30°C/19°C, 31°C/22°C, and 35°C/24°C for Missouri, Arkansas, and Texas, respectively (Table I). Moreover, a detailed look at Table I reveals that the Missouri plants were exposed to cooler night temperatures of $\leq 20^\circ\text{C}$ for 12 out of 19 days compared with only 3 out of 19 days in Arkansas. Night temperatures at the Texas location were all $> 20^\circ\text{C}$. We found that rice cultivars grown in the cool temperature location of Missouri had 0.4–3% and 0.5–4% more AM than the same cultivars grown in Arkansas and Texas, respectively.

Effect of Growth Temperature on AP Fine Structure

AP is a highly branched molecule and its synthesis is controlled by both starch synthase and many isoforms of branching enzymes (BE). Lu et al (1996) showed that the branching enzymes BEI and BEII in maize are sensitive to growth temperature. Both enzymes have also been reported in rice (Yamanouchi and Nakamura 1992). BEII transfers shorter chains during AP synthesis and has a lower optimum temperature of activity than BEI (Takeda et al 1993). Umemoto et al (1999) found significant increases in the proportions of shorter AP chains ($\text{DP} < 15$) and decreased proportions of longer chains ($\text{DP} = 21\text{--}30$ and $\text{DP} > 43$) in both japonica and

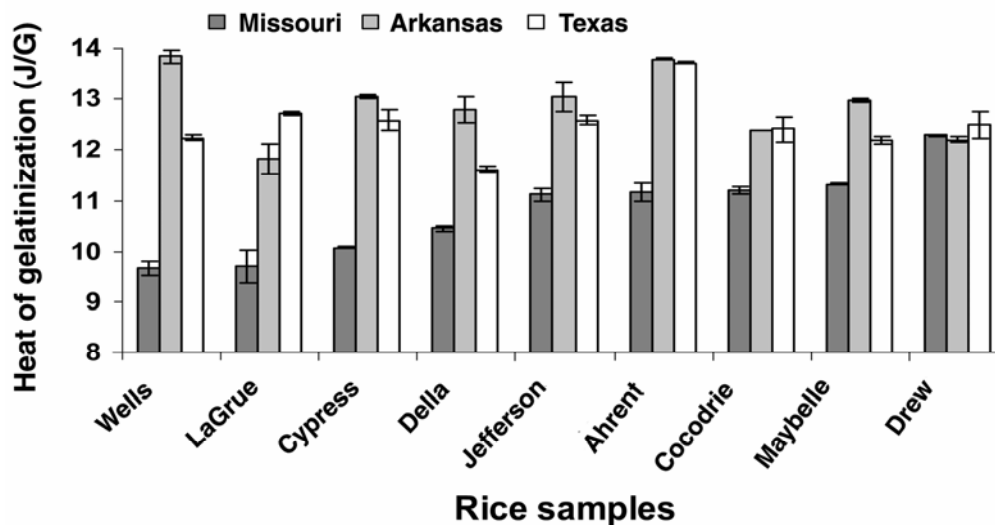


Fig. 4. Enthalpies of gelatinization of starch from rice samples grown at the three locations.

indica subspecies of rice, as well as in waxy mutants when day/night growth temperatures were decreased from 32/27°C to 25/20°C and to 18/13°C. The authors suggested that lowering the temperature resulted in an increase in the relative activity of BEII to BEI, which led to an increase in the proportions of shorter chains. In our study, day/night temperatures during the grain-filling period at the Missouri location were an average of 1/3°C and 5/6°C lower than those of Arkansas and Texas, respectively. Moreover, as noted above, the Missouri samples were exposed to cooler temperatures of $\leq 20^{\circ}\text{C}$ for many more days than the Arkansas and Texas samples. We found that rice cultivars grown in the Missouri location have higher proportions of FrIII (peak DP 16) and lower proportions of FrII (peak DP 39) than cultivars grown in Arkansas and Texas (Table II, Fig. 2). Accordingly, the ratio FrIII/FrII is higher in rice grown in Missouri compared with Arkansas and Texas. This ratio has been used as a measure of the extent of AP branching (Biliaderis et al 1981), with higher values indicating more chain branching and it has also been shown to negatively correlate with average chain length of AP (Hizukuri 1985).

Relationship Between AP Fine Structure and Starch Thermal Properties

Heating starch in the presence of water causes irreversible changes that include swelling and disruption of starch granules or the gelatinization phenomenon. Starch gelatinization properties are strongly affected by AP fine structure (distribution, length, and arrangement of linear chains). Cooke and Gidley (1992) reported that higher gelatinization temperatures and enthalpies in starch granules may be due to a higher degree of crystallinity and molecular order. As reported above, we found that rice cultivars grown in Missouri have consistently lower GT and ΔH_g values. It is also evident from Table III and Fig. 2 that the rice grown in Missouri have greater proportions of short AP chains and, more importantly, higher amounts of the shortest chains with DP < 10. Gidley and Bulpin (1987) studied the relationships between chain length and crystallite formation and reported that linear glucan chains of at least DP 10 are required for the formation of double helical structure that lead to crystallization. The registration of such double helices within starch crystallites of potato improved as a result of higher growth temperature (Tester et al 1999; Protserov et al 2002). On the other hand, high proportions of shorter DP outer chains in AP were reported to reduce the efficiency of packing of starch crystallites and result in lower temperatures and enthalpies of gelatinization (Noda et al 1998). This likely explains the lower GT and ΔH_g values observed in the Missouri samples.

CONCLUSIONS

This study demonstrates that AM content and the distribution of AP linear chains of U.S. long grain rice cultivars are sensitive to growth location. The variability in these starch properties has considerable effects on rice starch gelatinization, which is known to affect rice eating quality and functionality. This confirms controlled environment experiments and helps explain variability in the same rice cultivars grown in different locations in the United States. The impact of this study is that the food processor's use of rice should be made with the realization that growth location has a significant effect on rice quality and ingredient functionality. We have also observed that the extent of these effects are cultivar-dependent, indicating that some rice cultivars may be more stable than others over growth location. This should give impetus to breeders to select for or manipulate rice cultivars with the purpose of obtaining types that are stable over a wide range of growing environments.

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