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Analysis of Genotypic and Environmental Effects on Rice Starch. 2. Thermal and Retrogradation Properties

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Eight rice varieties with wide diversity in apparent amylose content (AC) were selected and planted in the early (HZE) and late season (HZL) in Hangzhou and in the winter season in Hainan (HN) for two consecutive years to study the genotypic and environmental effects on starch thermal and retrogradation properties of grain. Genotypic variation (all at $P < 0.01$) accounted for >56% of the total variation for onset (T_o), peak (T_p), and completion (T_c) temperature, width at half-peak height ($\Delta T_{1/2}$) of gelatinization, enthalpy (ΔH_r) of retrograded starch, percentage of retrogradation (R%), and 45.8% for enthalpy (ΔH_g) of gelatinization. Seasonal variation accounted for about one-fifth for T_o, T_p, and T_c and one-third for ΔH_g, but less for $T_{1/2}$, ΔH_r, and R% of the total variation, indicating that T_o, T_p, T_c, and ΔH_g were highly affected by seasonal environment in addition to the genotypic variation. The T_o, T_p, T_c, and ΔH_g in HZL were much smaller than those in HZE and HN. Correlation analysis for the eight genotypes showed that AC was significantly correlated with ΔH_g ($r = -0.83$, $P < 0.01$) and R% ($r = 0.734$, $P < 0.05$). ΔH_g was also positively correlated with T_c ($r = 0.878$, $P < 0.05$), but it did not have any correlation with ΔH_r, whereas the latter was positively correlated with R% ($r = 0.994$, $P < 0.001$). The intercorrelation of T_o, T_p, T_c, and $\Delta T_{1/2}$ themselves was significant at $P < 0.001$. The correlation analysis results suggest that there are different molecular mechanisms to regulate thermal properties (T_o, T_p, T_c, and ΔH_g) and retrogradation properties (ΔH_r and R%) as affected by environmental conditions. The implications of the results for rice breeders and starch-based food processors are discussed.

KEYWORDS: Rice; starch; gelatinization temperature; thermal property; retrogradation; environment

INTRODUCTION

Thermal and retrogradation properties are among the most important physicochemical properties of starch. The gelatinization temperature (GT) tested either by alkali spreading value or by differential scanning calorimetry (DSC) reflects the ease or difficulty of cooking the rice and the energy required. Starch retrogradation is a process that occurs when gelatinized starch begins to reassociate in an ordered structure under low energy input, as in freezing and chilling (*1*, *2*). Starch properties are affected by heredity as well as environment (*3*, *4*). GT and thermal properties are reported to be mainly controlled by the *alk* gene closely linked with *Wx* (*4*−*6*). Umemoto et al. reported that the starch synthase IIa (*SSIIa*) gene is located at the *alk* locus on chromosome 6 in the rice genome (*7*). The genetic basis of retrogradation properties has received little attention. Quantitative trait loci (QTL) analysis showed that QTL controlling retrogradation properties, such as enthalpy of retrograded starch and percentage of retrogradation, are located at the *Wx* locus (*8*).

Besides the genetic effects, environmental conditions will modify the starch gelatinization properties in various aspects (*3*, *9*). Elevation of growth temperature increases the gelatinization temperature and enthalpy of rice starch due primarily to the enhanced registration of amylopectin double helices and probably enhanced rigidity of amorphous regions (*9*−*11*). Choi et al. (*12*, *13*) reported the effect of varietal and locational variation on grain quality components of rice produced in a hilly and high altitude area and in the middle and southern plain areas in Korea and showed significant varietal and locational variation for gelatinization temperature. It is also reported that postharvest treatments, such as storage temperature, moisture content, and duration, affect the enthalpies and temperatures of gelatinization and retrogradation properties of rice flour (*14*, *15*). These studies suggest that the environment together with other postharvest

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Table 1. Analysis of Variance for Thermal and Retrogradation Property Parameters[a]

source	df	T_o	T_p	T_c	ΔH_g	$T_{1/2}$	ΔH^r	R%
year	1	45.3***	24.4***	20.6***	2.5***	0.5**	1.7**	396.5***
season	2	134.4***	75.3***	75.6***	13.1***	2.6***	1.7**	11.0
genotype	7	477.9***	268.9***	183.4***	17.6***	39.3**	44.5***	5759.7***
year × season	2	27.3***	42.2***	42.8***	3.9***	1.2***	0.7*	49.1
year × genotype	7	0.3	1.3***	1.5***	0.2	0.4***	0.1	15.9
season × genotype	14	2.6***	1.9***	2.3***	0.6***	0.8***	0.9***	57.4
year × season × genotype	14	1.9***	0.7***	0.9**	0.5**	0.3***	0.3	49.8

[a] Abbreviations: df, degree of freedom; T_o, onset temperature; T_p, peak temperature, T_c, completion temperature; ΔH_g, enthalpy of gelatinization; $T_{1/2}$, width at half-peak; ΔH_r, enthalpy of retrograded starch; R%, percentage of retrogradation. *, **, and *** indicate significance at 0.05, 0.01, and 0.001 levels, respectively.

treatments will modify the gelatinization and retrogradation properties, further to the genotypic difference. However, no studies combining different years, seasons, or locations and genotype on rice starch properties have been published.

In China, more emphasis is being directed toward the improvement of the eating and cooking quality of rice. Understanding the magnitude of the effects of environmental conditions on starch properties will add impetus to rice breeding by aiding determination of when and how to select for starch properties during breeding. In the Zhejiang province of eastern China, *indica* rice is generally planted as an early crop, whereas *japonica* rice is generally planted as a late or intermediate crop. However, to accelerate one generation in rice breeding, *indica* rice is also planted as a late crop right after the harvest of the early crop. After the late crop, rice materials are sent to Hainan province, the southernmost province in China, to advance another generation. Because the environmental conditions differ dramatically between the early and late seasons of Zhejiang province and the winter season of Hainan province, how the environment affects rice starch quality is of great important to rice breeders. In addition, such information is also important to food processors if stable starch properties are required for their production.

In this study, eight rice varieties (or breeding lines) with wide variations in apparent amylose content and gelatinization temperature were planted during the early season of Zhejiang province, the late season of Zhejiang province, and the winter season of Hainan province for two consecutive years, and the genotypic, year, and season or location effects on starch thermal and retrogradation properties were studied.

MATERIALS AND METHODS

Plant Materials. Eight rice (*Oryza sativa* L.) genotypes were selected for this study: Zhefu 802 (P1), Jiayu 293 (P2), Zhefu 504 (P3), Jiayu 280 (P4), Zaojing T3 (P5), Zaoxiannuo (P6), Zaojingnuo (P7), and Zaojing T1 (P8). Among them, P5 and P8 are *japonica*, whereas the others are *indica*. All of the genotypes were grown in 1998−1999 in three seasons: the early season of Hangzhou (30° N, HZE) and the late season of Hangzhou (HZL) in Zhejiang province and the winter season in Hainan province (18° N, HN), China. For the early season in Hangzhou, the rice was sown in early April, transplanted on May 1, and harvested in mid-July. For the late-season crop, rice was sown around July 15, transplanted on August 5, and harvested in late October. For the winter-season crop in Hainan, rice was sown in late November, transplanted in late December, and harvested in late March or early April of the next year. The year 1998 denotes the three crops harvested in July and October 1998 and late March 1999, respectively. The year 1999 denotes the three crops harvested in July and October 1999 and early April 2000, respectively.

After being air-dried and stored at room temperature for 3 months, the rice samples were stored in cooling rooms at 3 °C until all six season rice samples were obtained. The samples were milled to white rice using a Satake rice machine (Satake Corp.) and then ground to flour in a Cyclone sample mill (UDY Corp., Fort Collins, CO).

Thermal Properties. These were analyzed using a DSC 2920 thermal analyzer (TA Instruments, Newcastle, DE) equipped with DSC standard and dual sample cells. Rice flour (1.8 mg, db) was weighed into an aluminum pan, and 12 μL of distilled water was added. The pan was hermetically sealed and then heated at a rate of 10 °C/min from 30 to 110 °C. A sealed pan with 12 μL of distilled water was used as a reference. Onset (T_o), peak (T_p), and conclusion (T_c) temperatures, width at half-peak height ($\Delta T_{1/2}$), and enthalpy (ΔH_g) of gelatinization were calculated by a Universal Analysis Program, version 1.9D (TA Instruments).

Retrogradation. The gelatinized samples from DSC were then kept at 4 °C for 1 week (in the sample pans) and subsequently rescanned from 25 to 85 °C at 10 °C/min to determine the enthalpy (ΔH_r) of the retrograded starch. The percentage of retrogradation (R%) was calculated as $(\Delta H_r)/(\Delta H_g) \times 100$.

Statistical Analysis. All of the starch property parameters were measured in duplicate. All of the data analyses were performed with the SAS program version 8 (SAS Institute Inc., Cary, NC). Means and ranges were determined using Proc means for the eight genotypes, two years, and three seasons. Analysis of variance (ANOVA) was carried out to determine genotypic and environmental variation among starch properties using the general linear model procedure (Proc glm). Mean squares were used to calculate F statistics for tests of significance. The total variation was the sum of all mean squares of the main and interaction effects. The percentage of the total variation for a specific effect was calculated by dividing its mean square by the total variation. Proc corr was used to examine correlations between these traits.

RESULTS

Thermal Properties. ANOVA indicated that most variation components such as year, season, genotype, year × season, year × genotype, season × genotype, and year × season × genotype were significant at $P < 0.01$ for T_o, T_p, T_c, ΔH_g, and $\Delta T_{1/2}$ of the gelatinization, but no significant effects of year × genotype interaction were found for T_o and ΔH_g (**Table 1**). The gelatinization properties were mainly influenced by the genotypic variation because this accounted for 69.3, 64.8, 56.1, 45.8, and 87.1% of the total variation for T_o, T_p, T_c, ΔH_g, and $\Delta T_{1/2}$, respectively (**Table 1**). Variation of season accounted for about one-fifth of the total for T_o, T_p, and T_c and one-third for ΔH_g, whereas for $T_{1/2}$ it was rather smaller than the genotypic variation.

The rice materials selected for this study represented wide variation in GT. P5 and P8 had the lowest T_o, T_p, and T_c, whereas the other six had intermediate or high GT (**Table 2**). The average T_o and T_p were different significantly in the two years, whereas T_c did not differ (**Table 2**). As shown by ANOVA (**Table 1**), season had great influence on the GT, with T_o, T_p, and T_c lowest in HZL, highest in HZE, and intermediate in HN (**Table 2**; **Figure 1**). The ranges for 1998 were much larger than those for 1999 for these three parameters (**Figure 1**). For the low-GT varieties (P5 and P8), the ranges were near 10 °C in different seasons, whereas for the others they were ∼3−7 °C for T_o, T_p, and T_c, respectively (**Figure 1**).

Table 2. Mean and Range (in Parentheses) of the Thermal and Retrogradation Parameters of Different Genotypes at Different Years and Seasons[a,b]

genotype[c]	T_o (°C)	T_p (°C)	T_c (°C)	ΔH_g (J/g)	$\Delta T_{1/2}$ (°C)	ΔH_r (J/g)	R%
P1	69.5 c	74.9 b	81.5 b	8.6 cd	6.6 b	5.4 a	63.5 a
	(68.1–71.8)	(73.9–76.7)	(80.1–83.1)	(7.1–9.7)	(5.9–7.9)	(4.4–6.2)	(56.1–73.1)
P2	71.3 b	76.0 b	82.5 b	9.3 b	6.1 bc	5.9 a	63.7 a
	(69.4–74.3)	(74.4–79.1)	(81.0–85.7)	(8.5–9.8)	(5.6–7.2)	(4.7–7.0)	(53.0–70.4)
P3	73.6 a	78.7 a	84.6 a	9.34 b	5.9 c	2.9 b	31.6 b
	(71.1–76.5)	(76.8–81.6)	(82.4–87.5)	(8.0–10.6)	(5.4–7.2)	(2.2–3.5)	(22.9–37.9)
P4	73.2 a	78.5 a	84.6 a	9.1 bc	6.1 bc	2.9 b	31.6 b
	(70.4–77.1)	(76.3–82.2)	(82.7–88.2)	(7.8–10.3)	(5.2–6.9)	(2.4–3.5)	(23.4–40.0)
P5	58.7 d	68.1 c	76.5 c	8.0 d	10.3 a	1.0 c	12.2 c
	(55.8–64.8)	(65.1–74.2)	(72.9–82.7)	(6.7–8.6)	(9.6–10.6)	(0.7–1.3)	(8.3–19.8)
P6	73.8 a	79.0 a	86.0 a	11.1 a	6.0 bc	1.5 c	14.0 c
	(71.9–76.3)	(77.3–81.1)	(84.7–88.5)	(10.0–11.8)	(5.5–6.8)	(1.4–1.9)	(11.8–19.2)
P7	72.5 ab	77.9 a	85.2 a	11.3 a	6.4 bc	1.4 c	12.8 c
	(70.9–75.5)	(76.8–80.7)	(84.4–88.1)	(10.0–12.0)	(6.2–7.2)	(1.0–2.5)	(8.1–19.7)
P8	59.4 b	67.3 c	76.0 c	8.4 d	9.8 a	1.3 c	15.2 c
	(55.7–65.6)	(64.9–72.1)	(64.9–72.1)	(7.1–9.5)	(9.2–10.5)	(1.0–1.8)	(11.1–24.3)
year							
1998	69.7 a	75.6 a	82.6 a	9.5 a	7.1 a	2.9 a	32.6 a
1999	68.3 b	74.5 b	81.7 a	9.2 a	7.2 a	2.7 a	28.6 b
season[d]							
HZE	71.0 a	76.6 a	83.8 a	9.6 a	7.0 a	2.9 a	31.3 a
HZL	66.9 c	73.6 c	80.7 c	8.7 b	7.5 a	2.5 b	30.2 a
HN	69.0 b	74.9 b	81.8 b	9.9 a	7.0 a	3.0 a	30.2 a

[a] Different letters in the same column indicate significant difference at the 0.05 level. [b] See **Table 1** for definitions of parameters. [c] P1, Zhefu 802; P2, Jiayu 293; P3, Zhefu 504; P4, Jiayu 280; P5, Zaojing T3; P6, Zaoxiannuo; P7, Zaojingnuo; P8, Zaojing T1. [d] HZE, early season in Hangzhou; HZL, late season in Hangzhou; HN, winter season in Hainan.

Width at half-peak ($\Delta T_{1/2}$), a measure of gelatinization range, ranged from 5.9 °C for P3 (a high-GT rice) to 10.3 °C for P5 (a low-GT rice), showing a reverse relationship with GT (**Table 2**). Although significant year and season variations were detected, the average $\Delta T_{1/2}$ remained similar in the two years and in the three seasons (**Table 2**).

ΔH_g had a wide variation, ranging from 8.0 J/g in P5 to 11.3 J/g in P7, indicating the different amounts of energy required for gelatinization of various genotypes. ΔH_g remained the same in the two years, but that in HZL was lower than those in HZE and HN (**Table 2**; **Figure 1**).

Retrogradation. ANOVA showed that 90% of the total variation was from genotypic variation for both ΔH_r and R%, indicating that they were mainly affected by the genotypes. In addition to the genotypic variation, year, season, year × season, and season × genotype variations were also significant for ΔH_r. However, only year variation was significant for R%.

The ΔH_r of the retrograded starches varied from 1.0 J/g in P5 to 5.9 J/g in P2. There was no significant difference in ΔH_r between the two years, but significant differences were found among the three seasons, in which the ΔH_r in HZL was lower than those in the other two seasons (**Table 2**).

Significant differences in R% were found among different genotypes, ranging from 12.2% of P5 to 63.7% of P2. The R% in 1998 was higher than that in 1999, but it was similar among the three seasons (**Table 2**; **Figure 1**).

Correlation Analysis. The starch thermal and retrogradation parameters of eight genotypes either in the full data set from six seasons among two years ($n = 48$) or in the genotype mean data set averaged from six seasons ($n = 8$) were used for correlation analysis (**Table 3**). Because apparent amylose content (AC) is the most important determinant of the eating and cooking quality of rice quality, it was also included in the correlation analysis. Most correlations were significant in the set of full data, but only some of them were significant for the genotype mean data set (**Table 3**). The results indicated that AC did not correlate with $\Delta T_{1/2}$ in the all-data group ($n = 48$), but significantly correlated with nearly all other parameters (**Table 3**). However, in the genotype mean set, AC correlated only negatively with ΔH_g ($P < 0.01$) and positively with R% ($P < 0.5$). In addition to significant correlation with AC, ΔH_g was also positively correlated with T_c ($r = 0.878$, $P < 0.05$), but it did not have any correlation with ΔH_r. ΔH_r was positively correlated with R% ($r = 0.994$, $P < 0.001$). The intercorrelation of T_o, T_p, T_c, and $\Delta T_{1/2}$ was significant at $P < 0.001$ (**Table 3**).

DISCUSSION

The starch gelatinization temperatures, such as T_o, T_p, and T_c, of rice grain are mainly affected by genotypic variation (**Table 1**), which agrees with the control of GT by the *alk* locus (*4*, *6*) that encodes soluble starch synthase IIa (*7*). The direction of change of GT as affected by environment was opposite that of AC (*16*), also proving that GT and AC were under different genetic controls. As a result, the relationships between AC and thermal properties vary in different studies (*17*, *18*).

However, T_o, T_p, and T_c were also significantly affected by environment and interaction effects. The same rice had different GT when planted in different seasons (**Table 2**); the highest GT was found in the early season of Hangzhou (HZE), whereas the lowest GT was in the late season of Hangzhou (HZL). The difference between these two seasons was as much as 10 °C for low-GT rice, but only 3−7 °C for intermediate- or high-GT rice. The variation of GT in the three seasons of year 1999 fluctuated slightly. The results could be partially explained by the environmental differences between the different seasons in the two years (*16*). In June and July of 1998, there was much higher temperature, more sunshine, and less rainfall than in the same season of 1999. The temperature in October in both years was much lower than in June and July in the same location and in March in Hainan (see **Table 1** in ref *16*). These distinct differences in environmental conditions would undoubtedly modify the GT. $\Delta T_{1/2}$ was distinctly different between low-GT and high-GT rices; it was negatively correlated with GT (**Table 3**), indicating less cooperative melting between the amorphous

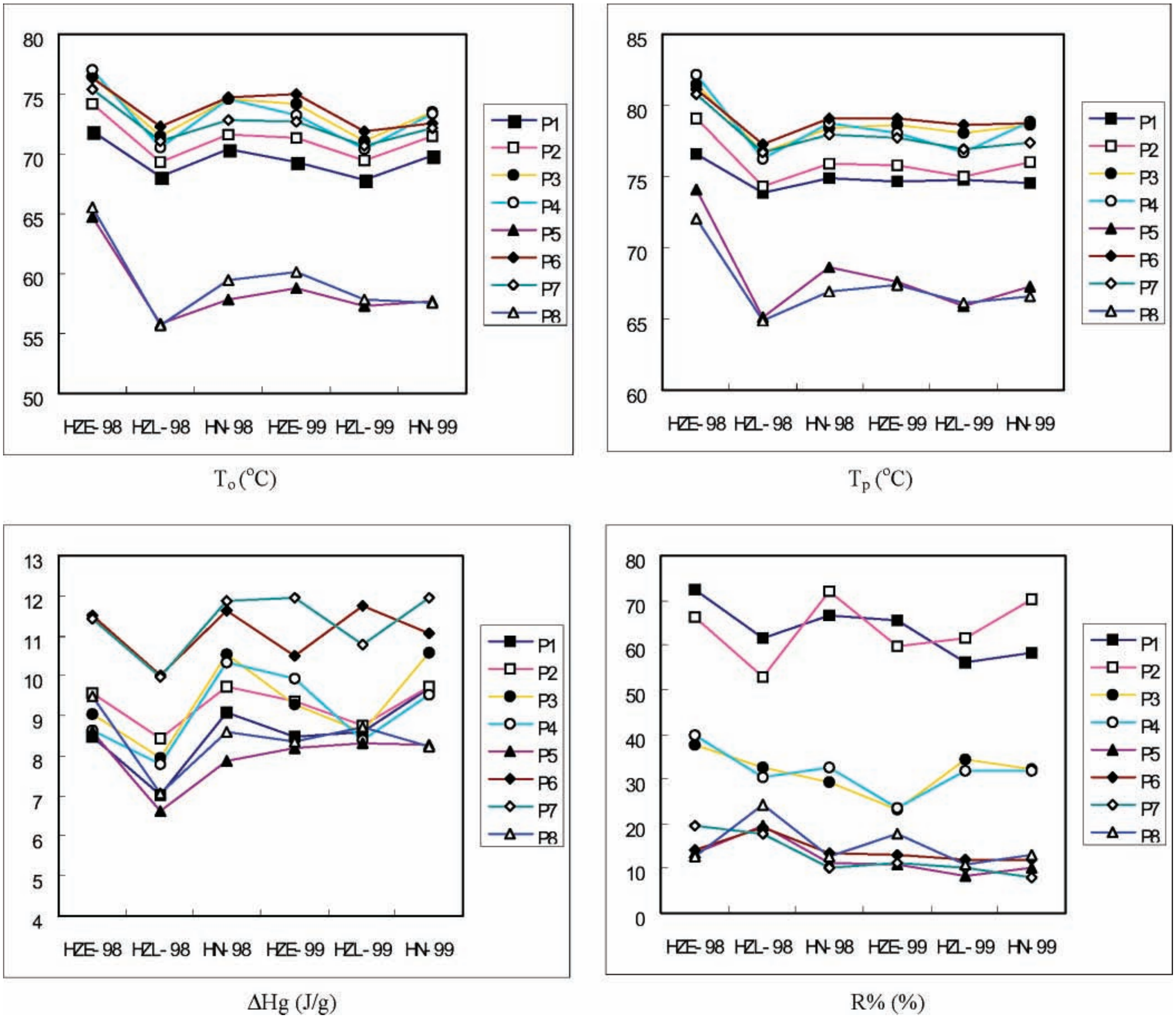

Figure 1. Genetic and environmental variation in some properties of starches from rice genotypes: P1, Zhefu 802; P2, Jiayu 293; P3, Zhefu 504; P4, Jiayu 280; P5, Zaojing T3; P6, Zaoxiannuo; P7, Zaojingnuo; P8, Zaojing T1; HZE, early season in Hangzhou; HZL, late season in Hangzhou; HN, Hainan; T_o, onset temperature; T_p, peak temperature; ΔH_g, enthalpy of gelatinization; R%, percentage of retrogradation.

Table 3. Correlation Analysis of Starch Properties of Rice Genotypes with the Full Data from All Seasons (above Diagonal, $n = 48$) and with the Genotype Mean Data (below Diagonal, $n = 8$)[a,b]

	AC[c]	T_o	T_p	T_c	ΔH_g	$\Delta T_{1/2}$	ΔH_r	R%
AC		−0.377**	−0.441**	−0.524***	−0.695***	0.229	0.645***	0.707***
T_o	−0.373		0.986***	0.964***	0.635***	−0.471***	0.380**	0.295*
T_p	−0.445	0.993***		0.988***	0.635***	−0.920***	0.302*	0.220
T_c	−0.547	0.979***	0.991***		0.684***	−0.800***	−0.216	0.129
ΔH_g	−0.830**	0.683	0.703	0.787*		−0.544***	−0.126	−0.266
$\Delta T_{1/2}$	0.242	−0.988**	−0.965***	−0.938***	−0.610		−0.496***	−0.420**
ΔH_r	0.675	0.385	0.301	0.206	−0.199	−0.514		0.985***
R%	0.734*	0.311	0.226	0.127	−0.287	−0.445	0.994***	

[a] *,**, and *** indicate significance at 0.05, 0.01 and 0.001 levels, respectively. [b] See **Table 1** for definitions of parameters. [c] AC, apparent amylose content.

and crystalline domains in low-GT starches than in high-GT starches during gelatinization. Because $\Delta T_{1/2}$ was significantly correlated with GT, the mechanism of the effect of environment on it should be similar to the mechanism acting on GT.

Although convincing evidence has shown that GT was controlled by the soluble starch synthase IIa (*7*), there are yet no reports on how the expression of the gene and the enzyme fluctuate in relation to the change of environmental conditions, such as growth temperature. Soluble starch synthase IIa is also found to control the amylopectin side-chain length (*7*). The amount of short chains in the amylopectin of rice starch of plants grown at lower temperature was significantly increased, whereas the amount of longer chains decreased as compared with that grown at higher temperature (*19*, *20*).

ΔH_g was significantly influenced by genotypic variation (**Table 1**). It was significantly correlated with both AC ($r = -0.83$, $P < 0.01$), which is controlled by the *Wx* locus, and T_c ($r = 0.787$, $P < 0.05$), which is controlled by the *alk* locus (**Table 3**). The complex relationship of ΔH_g with AC and GT was also found in other studies (*4*, *8*, *17*). In a study on Thai rice starch, Varavinit et al. did not observe a correlation between AC and ΔH_g (*18*). Sodhi and Singh found that rice with the lowest AC had the highest ΔH_g among five rice cultivars studied (*21*). Vandeputte et al. observed that both absolute and free AC decreased ΔH_g (*17*). On the other hand, different QTL were identified in the studies of Bao et al. (*8*) using a recombinant inbred line population and Bao et al. (*4*) using the doubled-haploid population derived from the same parents. Together with the complex relationships stated above, it is evident that ΔH_g was under a complex genetic control. The environmental conditions have great effects on the ΔH_g (**Tables 1** and **2**; **Figure 1**). That in the HZL season was lower in ΔH_g than those in the other seasons (**Table 2**; **Figure 1**). Previous studies also showed that elevation of growth temperature increased the enthalpy of rice and other starches (*9*, *10*). However, the temperature concomitantly regulates AC and GT, so the question as to which one, AC or GT, was more important to ΔH_g is also difficult to answer.

The retrogradation properties, ΔH_r and R%, were greatly influenced by the genotypic variation (**Table 1**). Vandeputte et al. (*22*) indicated that the amylopectin retrogradation enthalpies of the investigated starches increased with T_o, T_p, and T_c for all storage conditions. However, the present study indicated that ΔH_r of rice flour positively correlated only with T_o and T_p of the full data set but not in the genotype mean data set (**Table 3**). The difference might result from different sample preparations (starch versus flour) and different storage durations between the two studies. ΔH_r and R% were positively correlated with AC, and themselves were significantly and positively correlated (**Table 3**), which is in agreement with the previous study, in which the *Wx* locus was identified genetically to control them (*8*). Therefore, the environment effects on them should be the same as AC to some degree. However, it could be also found that the ΔH_r and R% of rices P5 and P8 (intermediate-AC rice) were the same as those of P6 and P7 (two waxy rices) (**Table 2**; **Figure 1**). This could be explained by the difference in gelatinization temperature, more accurately, by the amylopectin structure (*23*). Bao et al. (*24*) also found that the ΔH_r and R% of low-GT waxy rice and intermediate-AC rice were much lower than those of the high-GT waxy rice when the gelatinized starch was stored at 4 °C for 1 month, suggesting that the role of amylopectin in long-term retrogradation was more important than that of amylose.

The present study has implications for rice breeders and processors. Rice planted in different seasons will vary greatly in starch gelatinization and retrogradation properties. Hence, rice breeders carefully select for starch properties of the breeding lines in the earlier generations in target environment. Screening the desired thermal properties could be easily conducted with DSC with half seeds for testing and the remainder for planting to advance another generation. Quick selection with the alkali spreading value test would also give satisfactory results. The retrogradation properties of rice could be indirectly predicted by AC in combination with GT. They should be screened separately only when their usefulness can be demonstrated for a particular purpose, such as in starch-based food systems. For food processors, the best way to keep the desired quality of the starch-based food is to produce rice under similar environments so as to achieve minimum variation in starch thermal and retrogradation properties of a given genotype. It is apparent that even the same rice variety harvested during different seasons or from different locations cannot guarantee the same starch qualities.

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