Sucrose Synthase Activity as a Potential Indicator of High Rice Grain Yield

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ABSTRACT

The Chinese rice cultivar Guichao2 is a potentially valuable resource for breeding rice (*Oryza sativa* L.) with many valuable characteristics including upright leaves, prolific tillering ability, and high yields. The objectives of this study were to compare grain yields and yield components between Guichao2 and U.S. rice lines and to determine if the enzyme sucrose synthase was associated with the observed differences in grain yield and yield components. Grain yield, grain dry matter accumulation, yield components, and endosperm sucrose synthase activity were measured in field and greenhouse experiments with Guichao2 and 'Lemont' rice, as a U.S. standard, and various other lines. In three of four field tests, Guichao2 had higher grain yields than Lemont and other U.S. rice cultivars. Guichao2 also usually had higher sucrose synthase activity per grain and per unit of protein, in three of four field tests. The cultivar Qiguizao, derived from a cross of Guichao2 and Qiyouzhan, also had higher sucrose synthase activity on a protein basis. Since the grains of Qiguizao weigh less by approximately one half of the other cultivars, the sucrose synthase activity per grain was somewhat lower. Greenhouse tests supported these findings. In one test, the F_1 hybrids of Guichao and Lemont had higher sucrose synthase activity than either Guichao2 or IR36. From this research, we conclude that sucrose synthase activity, and perhaps the genes coding for sucrose synthase, will be a valuable resource in transferring the yield characteristics of Guichao2 and Qiguizao into U.S. rice cultivars.

SUCROSE is the primary transport carbohydrate in rice and most other higher plants (Avigad and Dey, 1996; Taiz and Zeiger, 1998). Sucrose is actively loaded into the rice grain and subsequently converted into starch by a series of enzymatic steps (Avigad and Dey, 1996). In most actively filling sinks, sucrose is broken down by sucrose synthase to form uridine diphosphoglucose (UDPG) and fructose, the first step in starch synthesis. Greater than 80% of the rice grain consists of starch. The conversion of sucrose into starch molecules can potentially limit grain filling.

There are three sucrolytic enzymes in higher plants: sucrose synthase, acid invertase, and neutral invertase. In most rapidly filling sinks such as seeds, sucrose synthase has the highest activity (Sung et al., 1989). Sucrose synthase is first in the line of conversion of sucrose to starch and thus, the activity of sucrose synthase is an excellent predictor of sink strength (Sung et al., 1989). Sink strength is the ability of a sink to attract or import carbohydrate and, in the case of rice, fill grain. Accordingly, sucrose synthase may be valuable to assess relative sink strength among rice breeding lines.

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Published in Crop Sci. 46:1501–1507 (2006).
Crop Physiology & Metabolism
doi:10.2135/cropsci2005.0240

Guichao2 and Other Chinese Rice Cultivars

Guichao2 is a potentially valuable resource for U.S. rice breeding programs. Huang Yue Xiang in Guangdong Province, People's Republic of China (PRC), developed Guichao2. The grain yields of Guichao2 are high throughout the world including in Arkansas (Table 1). Qiguizao is a cultivar also developed in the Guangdong Province, PRC from the cross Guichao2 × Qiyouzhan (♀ × ♂). The valuable attributes of Guichao2 and Qiguizao include high grain yield and some resistance to stress (other than photooxidative stress). Another positive attribute of Guichao2 is its greater competitiveness with weeds compared with U.S. rice cultivars (Gealy et al., 2003), possibly a result of allelopathy in Guichao2 (Mattice et al., 2001).

In a number of situations, the photosynthetically active radiation that powers photosynthesis also generates active oxygen species such as superoxide and oxygen singlets. Guichao2 and Qiguizao are prone to photooxidative damage (Tu et al., 1988). Part of the photooxidative damage sustained by Guichao and Qiguizao appears to be a smaller pool of reduced xanthophyll cycle carotenoids (Black et al., 1995b). Consequently, Guichao2 and Qiguizao are less resistant than U.S. rice cultivars to high light and low temperature stresses. Other negative characteristics of Guichao2 and Qiguizao, for U.S. rice cultivar improvement, include pubescence, relatively long growing season, proclivity for lodging, and poor milling yields, which results from low percentages of whole kernels after milling removes the hull and bran layers. Counce et al. (1998) found Qiguizao, Guichao2, and Teqing all had increased photooxidative damage relative to American rice lines Lemont, Bengal, and Adair and relative to the F_1 hybrid of Lemont and Qiguizao.

The objectives of this study were to compare grain yields and yield components between Guichao2 and U.S. rice lines and to determine if the enzyme sucrose synthase was associated with the observed differences in grain yield and yield components.

MATERIALS AND METHODS

Greenhouse Experiments

The experiments were conducted in a greenhouse in Keiser, Arkansas (35°40′ N, 90°5′ W) from January to June of 1992, 1993, 1995, and 1996. Plants were grown in pots filled with Sharkey silty clay loam soil (very-fine, smectitic, thermic

Abbreviations: NAD, nicotinimide adenine dinucleotide; NADH, nicotinimide adenine dinucleotide reduced form; PRC, People's Republic of China; UDP, uridine diphosphate; UDPG, uridine diphosphoglucose.

Table 1. Rice yields obtained from the Uniform Rice Regional Nursery conducted at Stuttgart, AR, during 1990 through 1992.

Variety	1990	1991	1992
		Mg ha^{-1}	
Lemont	8.76† b‡	8.25 b	8.12 b
Guichao2	10.87 a	10.44 a	11.53 a
$LSD_{0.05}$	1.12	0.97	1.29

† Values are means of four replications for Lemont and two replications for Guichao.
‡ Values followed by the different letters within the column are different at the 5% probability level.

Chromic Epiaquert). Plots (individual pots) were arranged in randomized complete blocks with at least five replications. Pot size was 4.5 L. In 1992 and 1993, rice was grown in circles around the inside (approximately 25 mm) of the perimeters of the pots (12 equally spaced seeds). In 1995 and 1996, seeds were planted near the center of the pot and thinned to one plant per pot. Pots were rotated in both directions across the greenhouse tables at least weekly. Replications were rotated in whole while individual plants within replications were rotated in the opposite direction. The plants were grown under metal halide lamps plus incident sunlight. The lamps extended the daylength to 14 h per day. The plants were fertilized weekly with a complete mixed soluble fertilizer. In 1992, the rice cultivars were Lemont, Qiguizao, and an F_1 hybrid of Lemont and Qiguizao. In 1993, the lines were Guichao2, M15–117, and M15–123. M15–117 and M15–123 were promising lines of rice developed from a cross made by Karen Moldenhauer (University of Arkansas, Rice Research and Extension Center, Stuttgart, AR). The cross was Bond × Lemont. In 1995, the rice lines were Guichao2, Lemont, Qiguizao, the Lemont × Qiguizao F_1 hybrid and reciprocals of Lemont × Guichao2. In 1996, the lines were Guichao2, the reciprocal hybrids of Lemont × Guichao2 and IR36.

Field Experiments

Field experiments were conducted at the Northeast Research and Extension Center at Keiser, AR, in 1993, 1994, 1995, and 1996. Plots were planted in rows spaced 0.18 m apart at 450 seeds m^{-2}. Plot dimensions were 1.8 by 21.4 m in 1993 and 1994 and 1.8 by 7.65 m in 1995 and 1996. The soil at the Keiser location was Sharkey silty clay loam. The experiments were arranged in randomized complete blocks. The treatments in the experiments were rice cultivars. In all years, Guichao2 and Lemont were in all tests. In 1994, 1995, and 1996, Bengal was added. In 1995 and 1996, Adair and Qiguizao were added as treatments. There were five replications in all years, with the exceptions of 1994 and 1996 when there were six replications. Yield components were determined from 1 m (2 m in 1994) bordered row length samples. The samples were taken at grain maturity at ground level to harvest whole shoots for determining total aboveground dry matter.

Rice was fertilized with 134 kg N ha^{-1} and flooded at the V5 to V7 stage of development (Counce et al., 2000). At R1 and 7 d after R1, 34 kg N ha^{-1} was applied to the crop. A flood was maintained until 7 d after 50% heading (approximately R3) for the later heading cultivar Guichao2. Grain yields were determined by harvesting a 0.71 by 6.1 m area in the center rows of the plots. Consequently, the ends of the rows were trimmed so that all harvested areas were bordered. The stover (leaves and culms without the grain) samples were dried at 70°C until weights stabilized. Rough rice samples were weighed and weights were adjusted to a 120 g kg^{-1} moisture basis. Yield components were determined from the center row with a 1 m (2 m in 1994) length taken at grain maturity at ground level.

Panicle Tagging

Panicles that were used for the enzyme analysis and the individual grain weight estimates were tagged on the date of beginning anthesis (R4) in both field and greenhouse experiments. In the greenhouse experiments, the panicles were harvested at five-day intervals beginning 5 d after the start of anthesis for individual panicles. Sampling continued at five-day intervals until grain filling was complete. In the field, tagged panicles were harvested at seven-day intervals to determine enzyme activity and weight increases. In both field and greenhouse experiments, samples were immediately placed on ice after removal from the plant. In the field in 1993, panicles were divided into upper and lower halves by counting branches. If there was an odd number of branches, the extra branch was assigned to the upper half of the panicle. Grain dry matter accumulation was determined for a panicle collection made concurrently with the enzyme assay samples.

By 1995, we had consistently seen that maximum grain-filling rates under our greenhouse conditions occurred at or near 10 d after anthesis. In the field experiments, maximum grain-filling rates occurred at or near 14 d after anthesis. Consequently, we took panicle samples at 10 d after anthesis for the greenhouse experiment and at 14 d after anthesis for the field experiment in 1995.

Enzyme Extraction and Assay

For the enzyme extraction, the endosperm was removed from the grain within 3 h of collection. Subsequently, the endosperm was ground in liquid N and extracted with a 200 m*M* Hepes extraction buffer followed by desalting and assayed as described by Xu et al. (1989). Grain endosperm was collected and weighed for each separate assay. For the assay, the number of grains and the number of panicles were recorded so that enzyme activity could be expressed on the basis of fresh weight, protein, per grain, per panicle, or per plant. A 0.5- to 1.0-g sample of each tissue was powdered in liquid N with a mortar and pestle. Extraction media was a 200 m*M* Hepes, 3 m*M* magnesium acetate, 5 m*M* dithiothreitol, 1% (w/w) PVP-40 (polyvinylpyrolidone), and 2% (v/v) glycerol corrected to pH 7.5 with NaOH. The extraction media/tissue ratio was 5 mL g^{-1}. During grinding, 1% (w/w) Dowex-1 Chloride (Sigma, St. Louis, MO) form and 1% (w/v) insoluble PVP were added. The ground material was centrifuged at 4°C at 17 000 *g* for 5 min. The supernatant was collected and desalted using PD-10 columns (Pharmacia, Wikströms, Sweden). Enzymes assayed were sucrose synthase (EC 2.4.1.13), UDP glucose pyrophosphorylase (EC 2.7.7.9), and acid and neutral invertases (EC 3.2.1.26). In this study, we mainly report sucrose synthase activity as this is the main enzyme of interest to us. UDP glucose pyrophosphorylase activity must be ascertained as the assay for sucrose synthase is coupled through UDP glucose pyrophosphorylase. Briefly, the sucrose synthase assay utilizes the conversion of NAD to NADH by the addition of two coupling enzymes (phosphoglucomutase from rabbit muscle and glucose-6-phosphate dehydrogenase from *Leuconostoc mesenteroides*) to the extraction media. The change in absorption is measured at 340 nm and the molar extinction coefficient for NADH is used to determine the breakdown of sucrose. By the addition of the coupling enzymes to the assay mixture, the breakdown in sucrose to UDP glucose became the limiting factor in the production of NADH. The continuous absorbance change of NAD reduction was used to calculate sucrose synthase activity from the molar extinction coefficient for NADH. Both acid and neutral invertases were assayed but the values were considerably lower than sucrose synthase activity so these

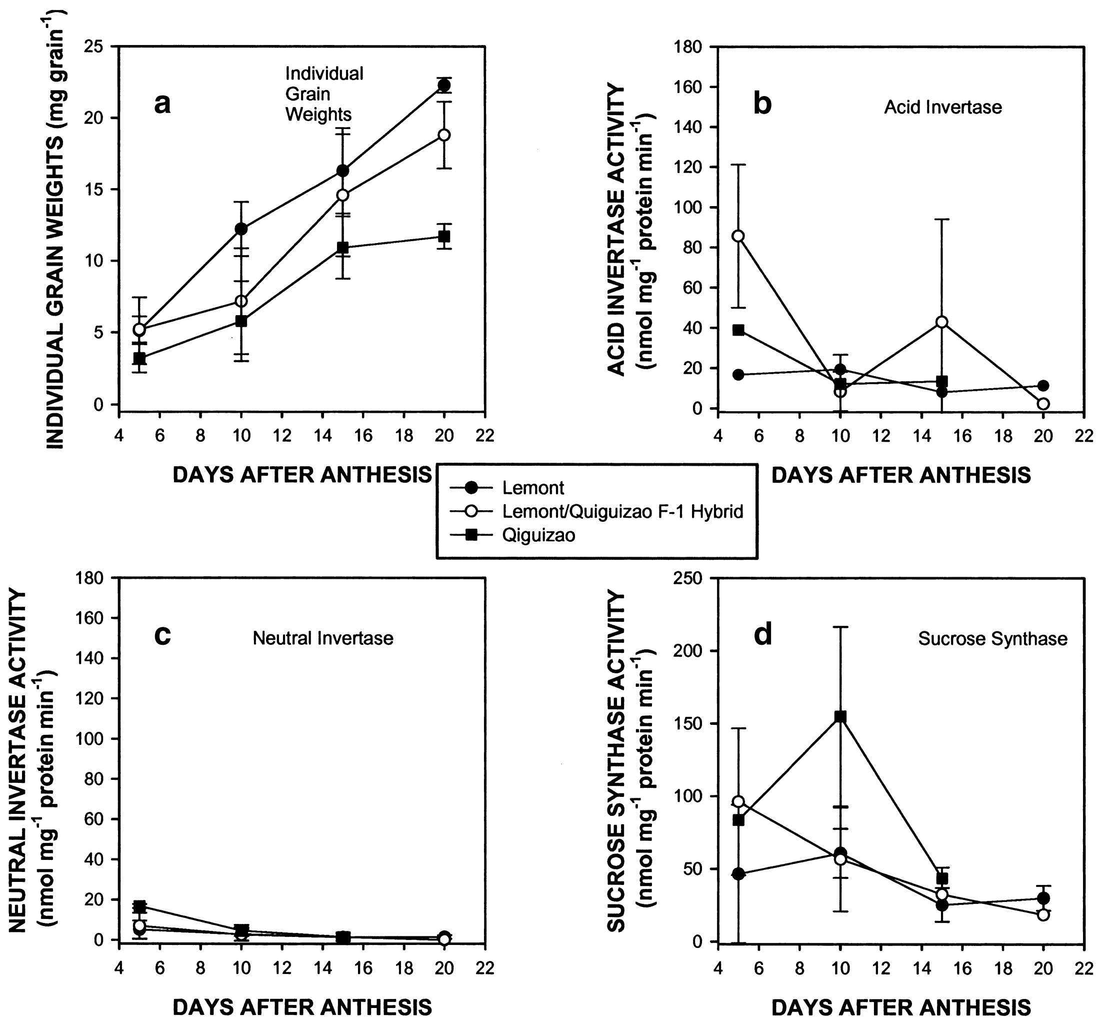

Fig. 1. Grain weights and sucrolytic enzyme activities for three cultivars of rice: Lemont, Qiguizao, and an F_1 hybrid of Lemont and Qiguizao. Data collected are means of up to four samples per sampling date per cultivar from an experiment conducted in a greenhouse in the winter of 1992. Bars are standard errors of the mean.

values are only reported for the 1992 experiment. Enzyme analyses, with three repeats of each analysis, were done within 7 h of collection except for the invertases. In some cases, acid and neutral invertase assays were done within 30 h of collection due to the finding that invertase activities of desalted extract did not decline below initial activities for 3 d with desalted protein extract being stored at 4°C.

Data Analysis

Field yield and yield component data were submitted to analysis of variance with LSDs calculated for means comparison if the cultivar effect was found to be significant at a probability level of ≤0.05 (SAS Institute, 2000). Some of the enzyme data was submitted to analysis of variance with LSDs calculated if the cultivar effect was found to be significant at a probability level of ≤0.05. In some cases, LSDs were calculated from the standard errors of the means as described in Steel and Torrie (1960). For the Stuttgart yield data presented in the Introduction, the PROC MIXED procedure (SAS Institute, 2000) was used to analyze the data. Least square means were estimated, and mean separation was accomplished using the PDIFF option where a probability level of ≤0.05 was considered significant. In addition, LSDs were calculated for the Stuttgart data.

Table 2. Panicle, grain characteristics, and endosperm sucrose synthase activities for Guichao2 and two F_2 derived lines from a Bond × Lemont cross grown in a greenhouse at Keiser, AR, in 1993.

Line	Grains per panicle	Individual grain weight	Percentage filled grain†	Activity per grain	Specific activity
	No.	mg	%	nmol grain^{-1} min^{-1}	nmol mg^{-1} protein min^{-1}
Guichao2	82.9‡ a§	24.7 a	96.0 a	18.6 a	95.5 a
M15–117	52.3 b	23.6 ab	69.8 b	16.6 a	80.4 ab
M15–123	56.2 b	23.4 b	78.3 c	10.4 a	72.7 b
$LSD_{0.05}$	13.9	1.2	6.0	NS	22.4

† 100[filled grains/(filled + unfilled grains)].
‡ Values are means of five replications.
§ Values followed by the different letters within the column are different at the 5% probability level.

Table 3. Grain yield and yield components from a field experiment with Guichao2 and Lemont rice cultivars conducted at Keiser, AR, in 1993. Grain yields, yield components (at grain maturity R8 to R9), and endosperm sucrose synthase activities (at 14 d after anthesis) were taken at grain maturity.

							Sucrose synthase activity			
							Activity per grain		Specific activity	
Cultivar	Grain yield	Culm density	Panicle density	Grains per panicle	Individual grain weight	Harvest index†	Top of panicle	Bottom of panicle	Top of panicle	Bottom of panicle
	Mg ha^{-1}	culms m^{-2}	panicles m^{-2}		mg		nmol grain^{-1} min^{-1}		nmol mg^{-1} protein min^{-1}	
Guichao2	8.52‡ a§	663 a	610 a	69 a	21.4 b	0.441 b	20.6 a	101.8 a	21.8 a	75.9 a
Lemont	8.62 a	417 b	386 b	79 b	24.7 a	0.482 a	20.3 a	102.7 a	12.1 b	103.4a
$LSD_{0.05}$	NS	113	78	7	1.9	0.025	NS	NS	7.3	NS

† Harvest index = grain weight/(grain + stover weight).
‡ Values are means from five replications.
§ Values followed by the different letters within the column are different at the 5% probability level.

RESULTS

In an initial greenhouse experiment, Qiguizao completed grain filling in 15 to 20 d after the beginning of anthesis (R4), whereas both Lemont and the F_1 Lemont × Qiguizao hybrid continued to fill grain until at least 20 d after the beginning of anthesis (Fig. 1a). Acid invertase activity was highest at 5 d after anthesis followed by a decline in activity for Qiguizao, Lemont, and the F_1 hybrid (Fig. 1b). Neutral invertase was low throughout the sampling period for the two parents and the hybrid (Fig. 1c). Qiguizao had higher maximal sucrose synthase activity than either Lemont or the hybrid (Fig. 1d). In addition, sucrolytic activity was greatest for sucrose synthase during the rapid grain-filling stage (10 d after anthesis) when compared to either acid or neutral invertases.

In the greenhouse experiment in 1993, Guichao2 had more grains per panicle than either M15–117 or M15–123 (Table 2). Guichao2 had greater grain weights than M15–123, and M15–117 was intermediate. Filled grain percentages were higher for Guichao2 than either M15–117 or M15–123, and M15–123 had a greater filled grain percentage than M15–117 (Table 2). Guichao2 grains filled at a greater rate per day than M15–117 or M15–123 grains (data not shown). At 10 d after anthesis (during the period of maximum grain filling), sucrose synthase activity per grain did not differ significantly among the three lines. Sucrose synthase specific activity was higher for Guichao2 than M15–123, and M15–117 was intermediate between Guichao2 and M15–123.

In the field experiment in 1993, grain yields did not differ between Lemont and Guichao2 (Table 3). Culm and panicle densities were higher for Guichao2 than for Lemont. Grains per panicle were higher for Lemont. Individual grain weights and harvest index were also greater for Lemont. In that year the heading dates were somewhat late and the grain-filling period for Guichao2 may have had lower than optimum grain-filling conditions. Sucrose synthase activities at mid–grain filling, however, were not different for Guichao2 and Lemont except for the specific activity for the top half of the panicle which was higher for Guichao2. Lemont at-

Table 4. Grain yield and yield components from a field experiment for Chinese and U.S. rice cultivars cultivars conducted at Keiser, AR, in 1994, 1995, and 1996. Grain yields and yield components were taken at grain maturity (R8 to R9 stages of development) and endosperm sucrose synthase activities were taken at 14 d after anthesis (approximately the R6 stage of development).

							Sucrose synthase activity	
Cultivar	Grain yield	Culm density	Panicle density	Grains per panicle	Individual grain weight	Harvest index†	Activity per grain	Specific activity
	Mg ha^{-1}	culms m^{-2}	panicles m^{-2}		mg		nmol grain^{-1} min^{-1}	nmol mg^{-1} protein min^{-1}
					1994			
Bengal	8.47‡ a§	428 b	342 b	87 b	28.8 a	0.582 a	15.5 b	66.5 b
Guichao2	9.32 a	610 a	513 a	99 a	26.0 b	0.552 b	24.0 a	138.5 a
Lemont	6.65 b	492 b	385 b	76 c	28.5 a	0.497 c	16.5 b	56.8 b
$LSD_{0.05}$	0.86	115	87	11	1.2	0.021	3.6	37.0
					1995			
Adair	8.21 bc	506 b	486 b	84 a	25.7 a	0.515 a	9.4 ab	62.1 b
Bengal	7.83 c	452 b	447 b	86 a	25.2 a	0.517 a	8.7 ab	46.0 b
Guichao2	9.90 a	504 b	462 b	92 a	24.6 a	0.513 a	14.1 a	83.9 a
Lemont	6.89 d	477 b	434 b	90 a	26.2 a	0.508 a	10.5 ab	62.9 ab
Qiguizao	8.74 b	613 a	575 a	94 a	17.7 b	0.515 a	7.3 b	74.2 ab
$LSD_{0.05}$	0.75	59	57	NS	1.7	NS	6.7	21.4
					1996			
Adair	7.96 bc	629 bc	546 bc	61 c	26.4 ab	0.449 b	18.2 a	73.1 a
Bengal	8.37 b	574 c	497 c	89 a	24.9 b	0.497 a	10.9 a	64.5 a
Guichao2	9.68 a	712 b	582 b	74 b	27.0 a	0.466 b	15.9 a	99.6 a
Lemont	7.51 c	585 c	542 bc	72 bc	24.5 b	0.505 ab	11.0 a	80.7 a
Qiguizao	9.53 a	839 a	682 a	82 ab	20.6 c	0.494 a	13.5 a	172.8 a
$LSD_{0.05}$	0.64	111	82	13	2.0	0.031	NS	NS

† Harvest index = grain weight/(grain + stover weight).
‡ Values are means from five replications in 1995 and six replications in 1994 and 1996.
§ Values followed by the different letters within the column for each year are different at the 5% probability level.

tained 50% heading in late August, and the Guichao2 plots attained 50% heading approximately 1 wk later. Sucrose synthase activities tended to remain greater after mid–grain filling for Guichao2 in this experiment (data not shown).

In 1994, Guichao2 and 'Bengal' yielded more grain than Lemont (Table 4). (It should be noted that the difference between Guichao2 and Bengal is within rounding error of the $LSD_{0.05}$.) The increased grain yield was the result of more culms per square meter, more panicles per square meter, and more grains per panicle for Guichao2. Guichao2 had lower individual grain weights than Bengal or Lemont. The harvest index was similar for Bengal and Guichao2, with both having higher harvest indices than Lemont. In 1994, the grains developed at similar rates for all three cultivars, although Bengal grains grew to be much heavier than Guichao2 or Lemont grains (Fig. 2a). From rapid grain-filling on, Guichao2 in most cases tended toward having higher sucrose synthase activity (per grain or per milligram of protein) than either Lemont or Bengal (Fig. 2b,c and Table 4).

In the 1995 field test, Guichao2 had higher grain yields than all of the U.S. lines in the test and Qiguizao (Table 4). The yield rankings were, from highest to

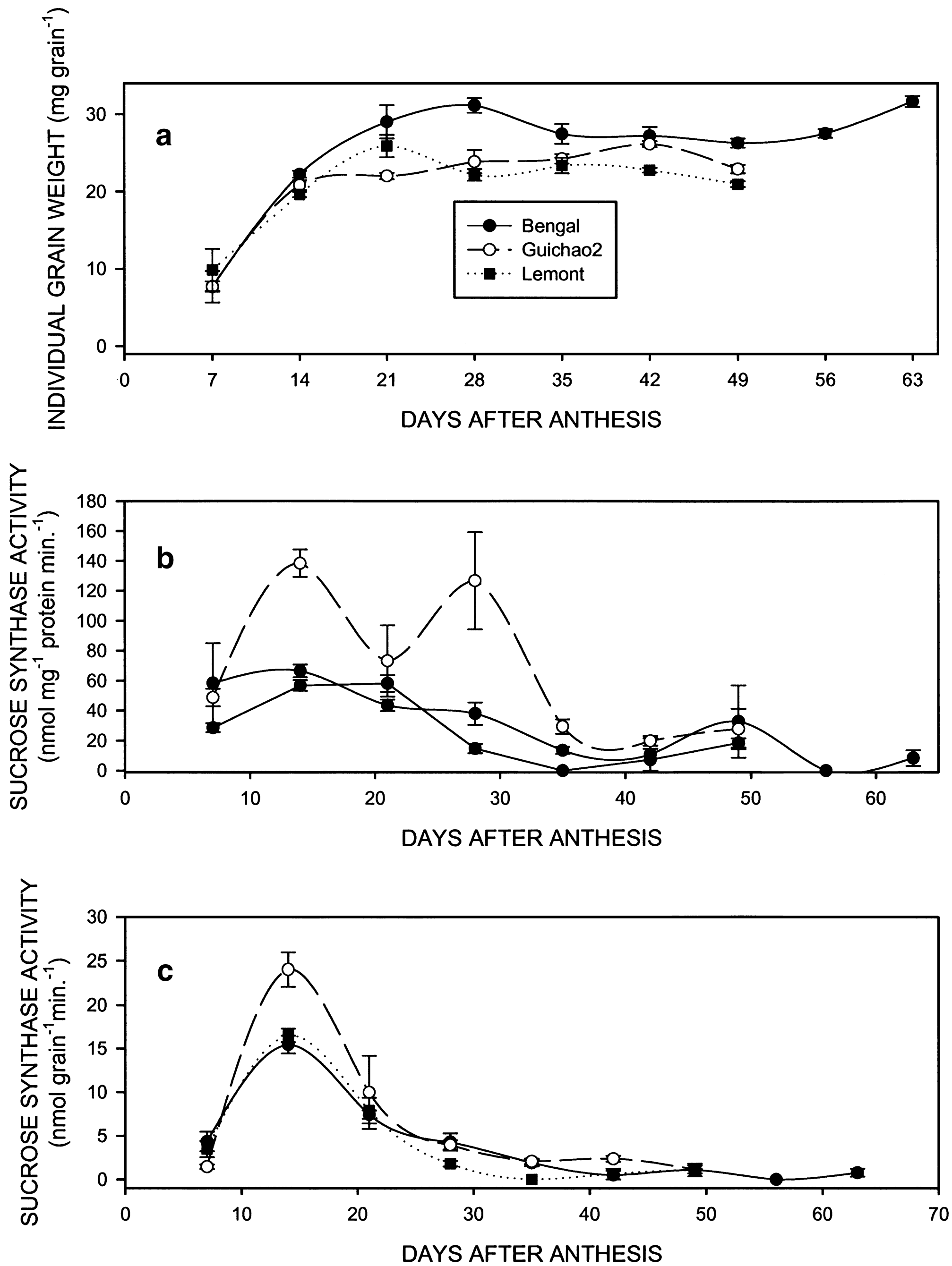

Fig. 2. Individual grain weights and sucrose synthase activities for Bengal, Lemont, and Guichao2 rice grown in the field at Keiser, AR, in 1994. Point values are means of four replications per sampling date per cultivar. Bars are standard errors of the mean.

Table 5. Endosperm sucrose synthase activity during rapid grain filling (which is 10 d after anthesis for these greenhouse plants) for Chinese and U.S. rice cultivars grown in a greenhouse at Keiser, AR, in 1995 and 1996.

Cultivars and hybrids	Sucrose synthase activity	
	nmol grain^{-1} min^{-1}	nmol mg^{-1} protein min^{-1}
	1995	
Lemont	29.8† a‡	136.6a
F_1 Guichao2 × Lemont	30.5 a	135.5 a
F_1 Lemont × Guichao2	30.8 a	140.5 a
F_1 Lemont × Qiguizao	26.8 a	126.0 a
Qiguizao	22.1a	149.6 a
Guichao2	28.5 a	138.5 a
$LSD_{0.05}$	NS	NS
	1996	
Guichao2	26.6 b	219 b
F_1 Guichao2 × Lemont	38.3 a	304 a
F_1 Lemont × Guichao2	38.7 a	339 a
IR36	15.2 c	199 b
$LSD_{0.05}$	10.6	82

† Values are means of five replications.
‡ Values followed by the different letters within the column for each year are different at the 5% probability level.

lowest: Guichao2, Qiguizao ≈ Adair, Bengal, and Lemont. Unlike the field tests conducted in 1993 and 1994, culm and panicle densities were not greater for Guichao2 but were greater for Qiguizao. Grains per panicle did not differ among the cultivars. Individual grain weights were lower for Qiguizao than for the other cultivars. Harvest indices did not differ among the cultivars. In spite of culm and panicle numbers which did not differ for Guichao2, the grain yield difference between U.S. cultivars and Guichao2 was greater than in previous field tests. Sucrose synthase activity per grain was greater for Guichao2 than for Qiguizao and did not differ significantly among Guichao2 and the other cultivars in the test. Sucrose synthase specific activity was higher for Guichao2 than for Adair and Bengal but not Lemont and Qiguizao. Sucrose synthase specific activity also tended toward being higher for Qiguizao compared to the U.S. cultivars.

In 1996, both Guichao2 and Qiguizao had higher grain yields than all of the U.S. cultivars (Table 4). Qiguizao had a higher culm density than any other cultivar, and Guichao2 had a higher culm density than any of the remaining cultivars except Adair. The same was also true of panicle density, except that the value for Guichao2 did not differ significantly from that of Lemont. Grains per panicle rankings from highest to lowest were Bengal ≈ Qiguizao, Qiguizao ≈ Guichao2 ≈ Lemont, and Lemont ≈ Adair. Individual grain weights were greater for Guichao2 than for the other rice cultivars except Adair. Individual grain weights were lowest for Qiguizao. Sucrose synthase activity per grain was similar for all lines in 1996, with Adair, Guichao2, and Qiguizao tending toward having higher activity. Sucrose synthase specific activity also tended toward being higher for Qiguizao than for the other cultivars including Guichao2.

In the greenhouse experiment in 1995, sucrose synthase activities among Lemont, Guichao2, Qiguizao, and F_1 hybrids of Lemont and Guichao2 and Lemont and Qiguizao did not differ, although the Qiguizao specific activity tended to be higher than for the other cultivars (Table 5). In the greenhouse experiment in 1996, the F_1 hybrids between Guichao2 × Lemont and Lemont × Guichao2 had higher sucrose synthase activities than either Guichao2 or IR36. Guichao2 had a higher sucrose synthase activity per grain than IR36 but not specific activity. Lemont was not planted in the 1996 experiment but IR36 was added for a comparison to a cultivar in the indica race of *O. sativa*. The 1996 greenhouse sucrose synthase activities were considerably higher than in the other experiments.

If we take the yield from field experiments conducted in this study and plot them against sucrose synthase

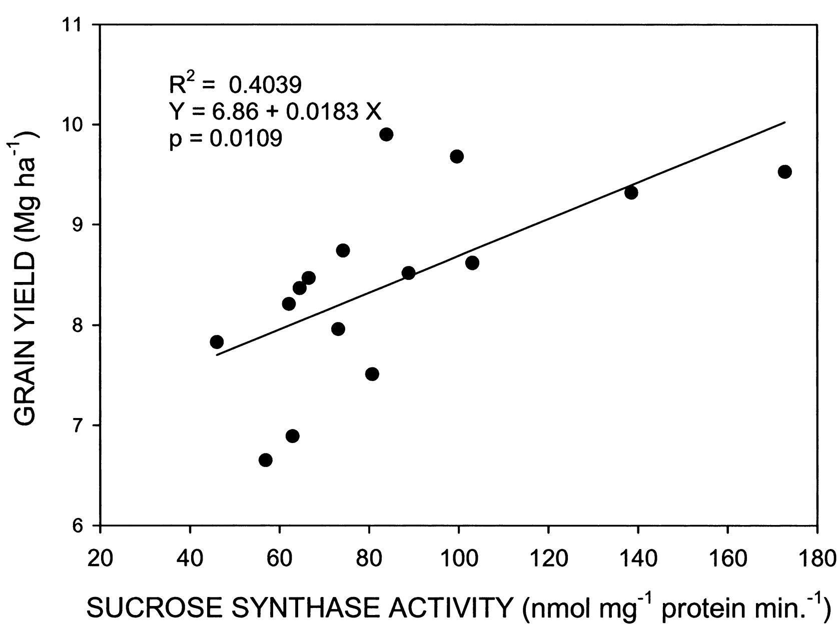

Fig. 3. Rice field grain yields versus sucrose synthase specific activity in Keiser, AR, from 1993 to 1996. Points are means of five or six replications for both rice grain yield at maturity (R9) and sucrose synthase specific activity at 14 d after anthesis.

activity per milligram of protein, we see a positive, statistically significant relationship (Fig. 3).

DISCUSSION

The positive relationship between crop grain yield and sucrose synthase specific activity (Fig. 3) is reasonable based on the crucial role of sucrose synthase in the grain-filling process. Sucrose synthase activity is a linchpin in filling grain. Understanding the complex interactions of the biochemistry, genetics, and morphology of the process promises to be helpful in accomplishing future yield improvements.

This research presents several factors that may be useful to rice breeders seeking to improve rice grain yields. First, in the field, sucrose synthase activities for Guichao2 and Qiguizao were generally higher than for U.S. rice cultivars. For Qiguizao, sucrose synthase activity per grain is somewhat misleading because Qiguizao has grain weights that are approximately half of those of the other cultivars in the field tests. Since grain fresh weight is part of the calculation of sucrose synthase activity per grain, this may not be a useful basis on which to compare Qiguizao to the other cultivars in the experiments. Furthermore, increased sucrose synthase activity appeared to be extended after maximum grain filling in the cases where individual grain weights and sucrose synthase were monitored over the course of grain filling. The greater duration of sucrose synthase activity for Guichao2 may allow grain filling for an extended time.

The increased sucrose synthase activity for the F_1 hybrids of Guichao2 and Lemont in the greenhouse in 1996 (although not in 1995) is intriguing. We surmise that perhaps heterosis for sucrose synthase activity was the cause of the difference and may be a basis for hybrid vigor in some wide crosses. We did not have a hybrid among U.S. cultivars. This would be a useful hypothesis to pursue.

These results indicate that sucrose synthase activity may indeed be a key to transferring the grain yield potential of Guichao2 to U.S. rice cultivars. The increased sucrose synthase activity may result in the greater grain-filling percentage, individual grain weight, and/or grains per panicle that we have seen in the Chinese cultivars. Obviously, all rice plants require sucrose synthase activity to carry out the grain-filling process. Consequently, like grain yield, sucrose synthase is a plastic trait, which is subject to environmental conditions as well as genetic control. A better understanding of environmental conditions associated with grain filling and sucrose synthase activity is warranted. Also, other factors such as increased sucrose content in the grain can lead to increased sucrose synthase activity (Black et al., 1995a).

Future research will utilize a population of rice lines derived from the F_1 hybrids examined in Table 5. We have developed pure lines from the materials collected at the F_2 generation of the reciprocal crosses of Guichao2 and Lemont. We have developed 150 lines that are homozygous and or near homozygosity. Grain yield testing has begun with these lines. This collection of lines and crosses made to these lines with 'Wells' and 'LaGrue' will be used to determine the value of the physiological characteristics to yield. We envision this project as an effective means to employ knowledge of the physiology of the rice plant to improve rice breeding.

ACKNOWLEDGMENTS

We greatly appreciate the work done on this effort by several members of the staff of the University of Arkansas Northeast Research and Extension Center. In particular, we thank Mr. Mark Poag and Mrs. Mary Lawson for their excellent contributions to this overall research effort.

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