Carbohydrate Starvation Stimulates Differential Expression of Rice α-Amylase Genes That Is Modulated through Complicated Transcriptional and Posttranscriptional Processes*

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Expression of α-amylase genes in cultured rice suspension cells is induced by sucrose starvation. To study the mechanism of sugar metabolite regulation on the expression of individual α-amylase genes, DNA fragments specific to each of eight rice α-amylase genes were synthesized and used as gene-specific probes. Comparison of the relative abundance of mRNA revealed that expression of the eight α-amylase genes in rice cells was differentially regulated by sucrose starvation. Accumulation of all the α-amylase mRNAs increased in response to sucrose starvation; however, levels of the αAmy3 and αAmy8 mRNAs were distinctly higher and constituted 90% of total α-amylase mRNAs. RNA gel blot and nuclear run-on transcription analyses demonstrated a positive correlation between the increased transcription rates and the elevated steady-state levels of α-amylase mRNAs induced by sucrose starvation. The half-lives of αAmy3, αAmy7, and αAmy8 were prolonged by sucrose-starvation; however, the stability of the three mRNAs seems controlled by different mechanisms. The translation inhibitors cycloheximide and anisomycin preferentially blocked the sucrose-suppressed expression of αAmy3 but not that of αAmy7 and αAmy8. These inhibitors also enhanced the sucrose starvation-induced accumulation of αAmy3 mRNA but not that of αAmy7 or αAmy8 mRNAs. Cycloheximide did not significantly alter the transcription rates of α-amylase genes, suggesting that labile proteins may selectively stabilize the αAmy7 and αAmy6 mRNAs but destabilize the αAmy3 mRNA.

Carbon catabolite repression is a fundamental and ubiquitous regulatory system in both prokaryotic and eukaryotic cells (1–4). In bacteria and yeast, catabolite-regulated gene expression is an essential mechanism for adjusting to changes in nutrient availability (5–7). Studies using Saccharomyces cerevisiae mutants have revealed many of the components involved in the response to carbon catabolite repression, but it is still unclear how all of these components interact to regulate transcription (2, 8). In higher plants, carbon metabolite regulation of gene expression provides a mechanism for maintaining an economical balance between supply (source) and demand (sink) for carbohydrate allocation and utilization within and among various organs and tissues (9). Expression of enzymes involved in carbohydrate metabolism often is feedback-regulated by the sugar metabolites (9). For example, expression of seven maize photosynthetic genes in mesophyll protoplasts is repressed by sucrose and the mechanism involves transcriptional control (10). Phosphorylation of hexose sugars by hexokinase has been proposed to act as a key signal transmitter in initiating sugar repression responses of photosynthetic genes (11), and of malate synthase and isocitrate lyase genes involved in the glyoxylate cycle (12).

α-Amylases are major amylolytic enzymes for hydrolysis of stored starch in the endosperm during germination of cereal grains. In germinating cereal grains, gibberellic acid stimulates and abscisic acid represses α-amylase gene expression (reviewed in Ref. 13). We have previously reported that expression of α-amylase genes in rice is under two different modes of tissue-specific regulation; the genes are activated by hormones in the aleurone of germinating seed and suppressed by sugars in cultured suspension cells (14, 15). Later, expression of one α-amylase gene in the embryo of germinating rice seed was also reported to be suppressed by sugars (16). Recently, we observed that sugars that accumulate in the embryo and endosperm during germination act as signals and osmotica to regulate the expression of α-amylase genes and the metabolic activities in germinating rice seeds (17). To study the mechanism of metabolite regulation of α-amylase gene expression in plants, we have used the cultured rice suspension cells as a model system. Previous work shows that, in cultured rice suspension cells, α-amylase expression, carbohydrate metabolism, and vacuolar autophagy are coordinately regulated by sucrose levels in the medium (18). Both the transcription rate and mRNA stability of α-amylase genes in cells increase in response to sucrose deprivation in the culture medium (19). Use of transgenic rice carrying an α-amylase gene promoter/β-glucoronidase gene proved that the regulation of α-amylase gene expression by sugars involves a transcriptional control mechanism (20–22).

Our previous study on metabolite regulation involved measurement at the total α-amylase mRNA level rather than dealing with the individual mRNA encoding different α-amylase isozymes. To further study the mechanism(s) of metabolite regulation in detail, it is necessary to identify the individual α-amylase genes whose expression is regulated by sugars. This report demonstrates that the expression of various α-amylase genes in rice suspension cells is regulated in a coordinated way by sucrose present in the medium, but in a distinctly different manner according to the specific α-amylase genes. Both transcription rate and mRNA stability contribute to the regulation of the transcript level of the individual α-amylase gene.

EXPERIMENTAL PROCEDURES

Plant Material—Suspension cell cultures of rice (Oryza sativa cv. Tainan 5) were propagated as described previously (14). Cells for puri-

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Metabolic Regulation of α-Amylase Genes

Plasmids—Plasmid αAmy8-C carries a 1.4-kb α-amylase cDNA insert in pBluescript KS I (Stratagene) (15). Plasmid pRcRac1.3 contains a 1.4-kb rice actin (Act1) cDNA insert in pBluescriptII-KS (23). Plasmid pRY18 carries a 3.8-kb DNA fragment, which contains a rice genomic DNA region including the 3′ half portion of 17 S rRNA, the 5.8 S rRNA, and the 5′ half portion of 25 S rRNA genes in pUC13 (24).

Polymerase Chain Reaction (PCR)—The paired 5′ and 3′ gene-specific primers derived from the regions surrounding the stop codons and the 3′-untranslated regions of various α-amylase genes (Fig. 1) were used for PCR. PCR was carried out in a 50-μl solution containing 15 μM Tris-HCl, pH 8.0, 60 μM KCl, 2.75 mM MgCl2, 10% Me2SO, 0.4 μM of each deoxynucleoside triphosphate (dATP, dCTP, dGTP, dTTP), 150 μM of each primer, 0.5 μg of rice genomic DNA, and 2.5 units of Taq DNA polymerase (Promega). Cycling was performed by a programmable thermal cycler (MJ Research) programmed with conditions described by Sambrook et al. (25). The annealing temperatures were 40°C for RAmy3A, 42°C for RAmy3, RAmy6, RAmy7, RAmy8, and RAmy10, and 45°C for RAmy1B and RAmy2A. The amplified DNA fragments were excised from agarose gels and purified using a gel extraction kit (QIAquick; Qiagen). The DNA fragments were cloned into pBluescript IIKS and sequenced.

Genomic DNA Isolation and DNA Gel Blot Analysis—One gram of rice suspension cells was ground in liquid N2 with a mortar and pestle in a 2-ml Eppendorf tube. The ground tissue was suspended in 1 ml of phenol:chloroform:isoamyl alcohol (25:24:1) at room temperature. The mixture was centrifuged at 8000 rpm and 4°C for 10 min. The aqueous phase was mixed with 200 μl of 3 M sodium acetate (pH 5.2) and 1 ml of isopropanol. DNA was spooled out, placed in 70% ethanol, and centrifuged at 8000 rpm for 10 s. The DNA pellet was washed with 70% and 100% ethanol and air-dried. The genomic DNA was resuspended in TE buffer and stored at 4°C.

Differential Expression of α-Amylase Genes under Sucrose Starvation—The steady-state levels of α-amylase mRNA in rice suspension cells before and after sucrose starvation were examined by RNA gel blot analysis. Amount of rRNA was used as RNA amount loading control in the RNA gel blot analysis, although previously we have shown that the total transcription rate in cells provided with sucrose was twice that in cells starved for sucrose (19). Accumulation of α-amylase mRNAs was very low or undetectable in cells provided with sucrose (Fig. 3, lane 2). In contrast, in sucrose-starved cells, accumulation of the α-amylase mRNAs increased (Fig. 3, lane 1). The magnitude of increase in mRNA concentrations varied with α-amylase genes and was particularly dramatic for αAmy3 and αAmy8.

To compare the relative abundance of mRNA of the eight α-amylase genes, an excess of rice rRNA gene, actin cDNA, and α-amylase gene-specific DNAs was spotted onto a membrane and hybridized with the 32P-labeled, single-stranded cDNA probe transcribed from the total mRNA of sucrose-starved cells. The relative mRNA levels, corresponding to different genes in a given population of RNA, were then compared. The cDNA of the rRNA was also synthesized, probably due to the presence of the repeated short stretch of the poly(A) sequence in the rRNA (31, 32). In sucrose-starved cells, the amounts of mRNAs hybridized to the α-amylase gene-specific DNAs were 2 to 100 times those in cells provided with sucrose.
aAmy3 and aAmy8 mRNAs were distinctly higher than those of other a-amylase genes (Fig. 4). The aAmy3 mRNA was the most abundant (Fig. 4, slot 9), with aAmy8 mRNA the next most abundant (Fig. 4, slot 10). Together the results shown in Figs. 3 and 4 suggest that the a-amylase genes are subject to differential metabolic regulation at the transcriptional and/or post-transcriptional level.

**Differential Activation of a-Amylase Gene Transcription upon Sucrose Starvation**—To define the mechanism that differentially regulates the expression of a-amylase genes, we compared the transcription rates of individual a-amylase genes. The nuclear run-on transcription analyses were performed with nuclei isolated from cells grown in the absence or presence of sucrose. In cells provided with sucrose, the transcription rates of all the a-amylase genes were undetectable (Fig. 5, upper panel). In contrast, in cells starved for sucrose for 12 h, the transcription rates of all the a-amylase genes increased, with aAmy3 the highest (Fig. 5, upper panel, slot 7) and aAmy8 the next highest (Fig. 5, upper panel, slot 8). In cells starved for 24 h (Fig. 5, lower panel), the transcription rates of all the tested genes decreased significantly; however, the transcription rates of aAmy3 and aAmy8 were still distinctly higher than that of the other a-amylase genes. Comparison of Figs. 4 and 5 reveals that there is a positive correlation between the transcription rates and the steady-state levels of a-amylase mRNAs in cells starved for sucrose.

**Increase in Stability of a-Amylase mRNA upon Sucrose Starvation**—To examine the effect of sucrose starvation on the half-life of individual a-amylase mRNA, degradation of the aAmy3, aAmy7, and aAmy8 mRNAs in vivo was monitored by RNA gel blot analysis following the inhibition of transcription with actinomycin D. Addition of 10 μg ml⁻¹ actinomycin D to the medium has been shown previously to inhibit total RNA transcription by more than 95% over a 12-h time course (19). The levels of individual a-amylase mRNAs were low in cells grown in the sucrose-containing medium (Fig. 6A, lane 1) and increased significantly after cells had been shifted to sucrose-free medium for 24, 36, and 45 h (Fig. 6A, lanes 2–4). The levels of individual a-amylase mRNAs that accumulated after cells have been starved for 24 h and then pretreated with actinomycin D in the absence of sucrose for 12 h (Fig. 6A, lane 5 or lane 15) decreased slowly during the subsequent 9-h incubation in
the medium still lacking sucrose but containing actinomycin D (Fig. 6A, lanes 14–19). In contrast, the levels of α-amylase mRNA decreased with time during the 9-h incubation in the medium containing both sucrose and actinomycin D (Fig. 6A, lanes 6–12). The level of actin mRNA was high in cells grown in the presence of sucrose (Fig. 6A, lane 1), but was low in the absence of sucrose (Fig. 6A, lanes 2–4). In the medium containing actinomycin D, the levels of actin mRNA remained low regardless of the presence (Fig. 6A, lanes 5–12) or absence (Fig. 6A, lanes 13–19) of sucrose. The result of actin gene expression suggests that transcription of total mRNA was almost completely inhibited by actinomycin D; otherwise, accumulation of actin mRNA would increase in medium containing both sucrose and actinomycin D.

The amounts of mRNA shown in Fig. 6A were quantified, and Fig. 6B shows the log plots of the α-amylase mRNA levels as a function of time. The half-life of mRNA was calculated from the slope of the line in the log plot of the data. The relative half-lives of αAmy3 and αAmy8, which were 82 and 98 min, respectively, in cells provided with sucrose, increased to 6 h in cells starved for sucrose (Fig. 6B). Both the half-lives of αAmy3 and αAmy8 mRNAs were substantially shorter than that of αAmy7 mRNA, regardless of the presence or absence of sucrose in the medium. The relative half-life of αAmy7 was almost 5 h in cells provided with sucrose and increased to 23 h in cells starved for sucrose. These results suggest that the α-amylase mRNAs are more stable in cells starved for sucrose.
heximide did not inhibit but instead effectively enhanced the accumulation of actin mRNA either in the presence (Fig. 7A) or absence (Fig. 7A) of sucrose (Fig. 7B). Anisomycin under our experimental condition.

ably due to the less efficient inhibition of protein synthesis by cycloheximide (Fig. 7B) or without (−S) sucrose for 12 h. Lower panel, nuclei isolated from cells cultured without sucrose for 24 h.

Diverse Effect of Translation Inhibitors on the Accumulation of α-Amylase mRNA—To examine whether the increase in mRNA levels of various α-amylase genes requires a prior synthesis of other gene products, cells were treated with translation inhibitors and accumulation of mRNA was monitored with RNA gel blot analysis. Levels of α-amylase mRNAs were very low or almost undetectable in cells provided with sucrose (Fig. 7A, lanes 1 and 2), but increased greatly in cells starved for sucrose for 2 days (Fig. 7A, lanes 8 and 9). Cycloheximide, an inhibitor of translocase (33), with concentrations ranging from 20 to 300 µM inhibited total protein synthesis by 90–98%. Cycloheximide inhibited the accumulation of αAmy7 and αAmy8 mRNAs regardless of the presence (Fig. 7A, lanes 3–7) or absence (Fig. 7A, lanes 10–14) of sucrose. In contrast, cycloheximide did not inhibit but instead effectively enhanced the accumulation of αAmy3 mRNA. In the absence of sucrose, cycloheximide significantly increased the level of αAmy3 mRNA independent of its dosage (Fig. 7A, lanes 10–14). In the presence of sucrose, cycloheximide increased the level of αAmy3 mRNA in a dose-dependent manner (Fig. 7A, lanes 3–7). Accumulation of actin mRNA was high in the presence of sucrose (Fig. 7A, lanes 1 and 2) and became low in the absence of sucrose (Fig. 7A, lanes 8 and 9). Cycloheximide also inhibited the accumulation of actin mRNA either in the presence (Fig. 7A, lanes 3–7) or absence (Fig. 7A, lanes 10–14) of sucrose but to a lesser extent as compared with the αAmy7 and αAmy8 mRNAs.

Anisomycin, an inhibitor of transpeptidase (33), with concentration of 300 µM only 50% effective in inhibiting total protein synthesis, but the trends are exactly in the same direction as what was found when cycloheximide was used. Anisomycin promoted αAmy3 mRNA accumulation but suppressed αAmy7 and αAmy8 mRNA accumulation under both plus and minus sucrose conditions (Fig. 7B). Anisomycin also suppressed the actin mRNA accumulation under both plus and minus sucrose conditions. The suppression of αAmy8 mRNA accumulation in sucrose-starved cells by anisomycin (Fig. 7B, lane 4) was not as complete as that by cycloheximide (Fig. 7A, lanes 10–14), probably due to the less efficient inhibition of protein synthesis by anisomycin under our experimental condition.

FIG. 5. Activation of α-amylase gene transcription by sucrose starvation. Rice suspension cells were cultured in sucrose-containing or sucrose-free medium for 12 or 24 h, and nuclei were isolated. In vitro run-on transcription reactions were carried out, and the 32P-labeled RNAs were hybridized to 5 µg each of rice rRNA gene, actin cDNA, and α-amylase gene-specific DNAs immobilized on a membrane. pBS, pBluescript vector containing no α-amylase cDNA. Upper panel, nuclei isolated from cells cultured without sucrose for 12 days (RNA in lane 2) and transferred to sucrose-free (−S) medium for 24 h (RNA in lane 2). Actinomycin D was added to the medium to a final concentration of 10 µg/ml. Cells were incubated in the sucrose-free medium containing actinomycin D for another 12 h and then divided into two halves. Half the cells were transferred to a medium containing both sucrose and actinomycin D (RNAs in lanes 5–12). The other half were transferred to a medium lacking sucrose but containing actinomycin D (RNAs in lanes 13–19). Cells were collected after 0.5–9 h, and RNAs were purified. Five micrograms of total RNA were loaded in each lane. Lanes 3 and 4, cells incubated in sucrose-free medium lacking actinomycin D for 36 and 45 h, respectively. B, levels of mRNA shown in lanes 5–19 of A were quantified densitometrically. The relative α-amylase mRNA levels were then determined by dividing the mRNA levels in lanes 5–19 by levels of lane 1 or lane 13. The data collected were subjected to linear regression analysis, and the graph was plotted using a linear regression algorithm in the Crickgraph Program of a Macintosh computer. The open and filled dots indicate mRNA from cells grown in sucrose-containing or sucrose-free medium, respectively. The dashed line indicates the time at which 50% of mRNA remained. The half-life of α-amylase mRNA is shown on the right side of the graph.

α-amylase genes has enabled us to examine the abundance of mRNA encoding specific α-amylase isozymes. Although expression of the eight α-amylase genes increased in response to sucrose starvation (Fig. 3), levels of αAmy3 and αAmy8 mRNAs were significantly higher than those of other α-amylase genes and constituted approximately 90% of total α-amylase mRNA in cells starved for sucrose (Fig. 4). Therefore, expression of the α-amylase genes is coordinately up-regulated but in a distinct manner by sucrose starvation. A positive correlation between

DISCUSSION

Increase in Transcription Rates Is Essential for Increase in Level of α-Amylase mRNA upon Sucrose Starvation—The availability of gene-specific probes corresponding to each of the eight
the transcription rates and the steady-state mRNA levels suggest that the transcriptional regulation plays an important role in the differential expression of α-amylase genes.

Alteration in transcriptional activity suggests a model in which sugar-regulated transcription factors interact with cis-acting elements in the α-amylase gene promoters. Regions upstream from the TATA box of αAmy3 (RAMy3D) (22) and αAmy8 (21) share conserved sequences (34) and possess the elements necessary for sugar repression. However, none of these sequence elements has been demonstrated to play a role in the regulation of rice α-amylase gene expression. Metabolic regulation of α-amylase gene expression by glucose has also been reported in other eukaryotes such as Drosophila melanogaster and Aspergillus oryzae. No significant sequence similarity is found between the Aspergillus (35) and the Drosophila (36) α-amylase gene promoters. However, some conserved sequences are found between the promoter region of either the Drosophila or the Aspergillus α-amylase gene with that of αAmy3.

Increase in mRNA Stability Enhances the Level of α-Amylase mRNA upon Sucrose Starvation—Under conditions in which transcription was inhibited, the half-lives of α-amylase mRNAs were longer in cells starved for sucrose than in cells provided with sucrose (Fig. 6), suggesting that increased mRNA stability contributed to an increase in α-amylase mRNA level in sucrose-starved cells. The αAmy7 mRNA seems inherently more stable because its half-life was 3–4 times longer than those of the αAmy3 and αAmy8 mRNAs, regardless of whether or not the cells were sucrose-starved. Compared with the αAmy7 mRNA, the αAmy3 and αAmy8 mRNAs were transcribed more rapidly in cells in response to sucrose starvation (Fig. 5) and were degraded more rapidly (Fig. 6) if cells were provided with sucrose. These results suggest that expression of αAmy3 and αAmy8 is under a stricter regulation and may encode isozymes essential for responses to changes of carbohydrate availability.

It is unclear what mechanism directs the α-amylase mRNA to be degraded faster in cells provided with sucrose than in cells starved for sucrose. Regulated mRNA turnover has been described in detail in several vertebrate system (37), but the common regulatory mechanisms for mRNA turnover have not been found. Little is known about the processes responsible for the alteration of mRNA stability in plants, although mRNA stability can be affected by environmental conditions such as temperature (38, 39) and illumination levels (40, 41). The sucrose-induced acceleration of α-amylase mRNA degradation indicates that the transcription factor(s) of the mRNA decay system is likely to be regulated. This may be an α-amylase transcript-specific, since transcripts of the three α-amylase genes are affected similarly but the actin transcripts are not affected (Fig. 6). The differential stabilities among α-amylase transcripts, on the other hand, may be provided with sucrose or anomycin. CHX, cycloheximide; AN, anisomycin.

Stabilities of Different α-Amylase mRNAs Are Selectively Regulated by a Labile Protein—Interestingly, although the α-amylase mRNA seems to be generally stabilized by starvation of cells (Fig. 6), the mechanism controlling the stability of different α-amylase mRNAs varied. Both the translation inhibitors cycloheximide and anisomycin enhanced the accumulation of αAmy3 mRNA regardless of whether or not the cells were provided with sucrose (Fig. 7). Such an effect of translation inhibitors was specific to αAmy3 mRNA, as the accumulation of αAmy7 and αAmy8 mRNA was suppressed by the inhibitors, even in cells starved for sucrose. Nuclear run-on transcription analyses demonstrated that cycloheximide did not significantly alter the transcription rates of αAmy3, αAmy7, and αAmy8 regardless of whether or not the cells were provided with sucrose (data not shown). Together, the results suggest that labile proteins are involved in the destabilization of αAmy3 mRNA and the stabilization of αAmy7 and αAmy8 mRNAs.

In conclusion, the differential response of α-amylase genes to sugars provides a potential mechanism for altering the pattern of enzyme accumulation in response to changing carbohydrate status and sugar import. Although transcription of the α-amylase genes is induced by sucrose starvation, the dramatic increase in their steady-state mRNA levels requires stabilization of the mRNA as well. The combined processes may lead to more rapid and more marked shifts in the expression of α-amylase genes.
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Yeast genes. Both processes may share similar upstream signaling pathways and contribute differently and in gene-specific manners to the regulation of the pool size of transcripts of individual α-amylase genes.

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