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Molecular cloning and expression of glyceraldehyde-3-phosphate dehydrogenase gene under environmental stresses in sweetpotato

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ABSTRACT Glyceraldehyde-3-phosphate dehydrogenase (GAPDH), a main enzyme in the glycolytic pathway, is involved in cellular energy production and regarded as a housekeeping gene. Previously, cytosolic GAPDH was selected as the most significantly abundant gene in EST library of sweetpotato suspension cells. In this study, a full-length of cDNA clone (*IbGAPDH*) encoding GAPDH was isolated from suspension-cultured cells of sweetpotato (*Ipomoea babatas*), and its expression was investigated with a view to understanding the physiological function of GAPDH in relation to environmental stresses. *IbGAPDH* encoded a 36.9 kDa polypeptide consisting of 337 amino acids. When the deduced amino acid of *IbGAPDH* was compared with other higher plants, *IbGAPDH* showed high homology with cytosolic GAPDH. The mRNA level of *IbGAPDH* significantly increased under environmental stresses, such as H_2O_2, MV and cold treatments. Among them, the transcript level of *IbGAPDH* gene was the highest under cold stress. Further investigation of the transcription level under 10℃ or 15℃ was performed with different tissues of sweetpotato. The transcription of *IbGAPDH* was increased by cold stress with tissue-specificity, moreover, showed different patterns according to temperature.

Introduction

Glyceraldehyde-3-phosphate dehydrogenase (GAPDH, EC 1.2.1.12) is a catalytic enzyme commonly known to be involved in glycolysis and regarded as a housekeeping gene. GAPDH catalyzes the reversible reduction of 1,3-bisphosphoglycerate to glyceraldehyde-3-phosphate in the presence of NADPH, one of the most important metabolic reactions in the glycolytic pathway. However, recent studies demonstrated that GAPDH displays a number of diverse activities that are unrelated to its glycolytic function (Sirover 1999). In mammalian cells, many studies showed that GAPDH is not simply classical metabolic protein involved in energy production, it is a multifunctional protein with defined functions in numerous subcellular processes, such as membrane fusion, microtubule bundling, phosphotransferase activity, nuclear RNA export, DNA replication and DNA repair (Sirover 2005).

As like mammalian cells, increased levels of GAPDH transcript have already been observed for environmental stress conditions in plants. In anaerobic environment, glycolysis is important for energy production and the genes involved in this process, e.g. GAPDH, enolase, alcohol dehydrogenase and pyruvate decarboxylase, are dramatically induced (Umeda et al. 1994; Sachs et al. 1996). The induction of these genes is essential for anaerobic tolerance. The maize cytosolic GAPDH gene (*GapC4*) was upregulated under anaerobic conditions (Kö hler et al. 1995). The *GapC4* promoter was strongly and specifically induced under anaerobic conditions in tobacco and potato (Büllow et al. 1999). Jeong et al. (2000) isolated and characterized of the GAPDH gene from mushroom, *Pleurotus sajor-caju*. They showed the gene expression was highly

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induced according to abiotic stress, such as salt, cold, heat and drought. And they confirmed the function of the gene by overexpression in potato plants. The transgenic potato showed improved tolerance against salt loading (Jeong et al. 2001). Cytosolic GAPDH from *Craterostigma plantagineum* was induced by dehydration and ABA treatment (Velasco et al. 1994). Moreover, it was reported that the novel function of GAPDH in *Arabidopsis* was involved in cellular redox regulation, especially. GAPDH can suppress ROS by controlling generation of H_2O_2 in plant cells (Hancock et al. 2005; Baek et al. 2008). The activation of the GAPDH gene may be an adaptive response to stress-induced cell damage.

In a previous study, we reported that cytosolic GAPDH was one of the most significantly abundant genes in EST library of sweetpotato suspension cells. Northern blot analysis revealed that its expression was strongly induced in suspension cells but not in roots and leaves of the whole plants of sweetpotato (Kim et al. 2006). In this work, we isolated cDNA clone encoding cytosolic GAPDH (*IbGAPDH*) with a view to understanding the physiological functions of cytosolic GAPDH that are highly expressed in suspension-cultured cells of sweetpotato. We describe the molecular cloning and expression patterns of *IbGAPDH* in response to environmental stresses since plant cells in culture are considered to be under conditions of high oxidative stress.

Materials and methods

Plant material

Sweetpotato plants (*Ipomoea batatas* cv. Yulmi) were maintained in a pot in a greenhouse at 25℃ under 16-h photoperiod. Sweetpotato was propagated by cutting at the top and grown for 2 or 3 weeks for stress treatment.

Stress treatments

For cold stress, sweetpotato plants in a pot were exposed at 10℃ and 15℃ for 12, 24 and 48 h, respectively. 50 μM methyl viologen (MV) solution containing 0.125% Triton X-100 was sprayed onto whole plants for MV treatment. After treatment for 6, 12 and 24 h, the second and third leaves from the top were removed from plants. For H_2O_2 treatments, leaves were incubated in Falcon tubes containing 440 mM H_2O_2 solution at 25℃ for 12 and 24 h. Sterile water was used as a control for H_2O_2 treatment. All treated plant materials were immediately frozen in liquid nitrogen and stored at -70℃ until further use.

RNA purification

One gram of plant tissues were ground in liquid nitrogen and homogenized in the extraction buffer (0.25 M Tris-Cl, 0.25 M NaCl, 0.05 M EDTA, 27 mM naphthalene disulfonic acid, 0.25 M *p*-aminosalicylic acid) containing 0.7 M β-mercaptoethanol and phenol. The solution was extracted with chloroform, and phenol: chloroform:isoamyl alcohol (25:24:1) again. Nucleic acids in aqueous phase were isopropanol-precipitated. The pellet was washed, dried at room temperature and resuspended 1 mL TE buffer. RNA was precipitated with 2 M LiCl for overnight at 4℃. After centrifugation, the pellet was washed with 70% ethanol and dried at room temperature, resuspended in TE buffer. RNA was stored at -70℃ until use.

RT-PCR analysis

Reverse transcription was performed with the RETROscript™ (Ambion). Two micrograms of total RNA was reverse-transcribed in a volume of 20 μL containing 0.5 mM each dNTPs, 50 pmol random primer, 100 U of M-MLV reverse transcriptase. The mixture was denatured at 70℃ for 3 min and incubated 42℃ for 1 h. An aliquot of the reaction was subjected to PCR amplification using gene specific primers together with a competimer/primer mixture specific for 18S ribosomal RNA (QuantumRNA 18S Internal Standards, Ambion). PCR was carried out in a 20 μL reaction mixture containing 0.2 mM of each dNTP, 10 pmol of each forward and reverse primers and 0.125 U of Taq polymerase (NEB). The 18S PCR primer and competimer mixture was added to the tube. After an initial denaturation at 94℃ for 5 min, amplification was carried out at 25 cycles of 94℃ for 30 sec, 60℃ for 1 min, 72℃ for 1 min, followed by incubation for 7 min at 72℃.

Sequences of the *IbGAPDH* gene specific primers were 5'-TCT AGA AGC TTC AAG CCT CC-3' and 5'-GCT GCC AAT ATG TTG GAG GC-3'. Semi-quantitative RT-PCR was also performed using tubulin primers for quantitative control as described in Kim et al. (2006). The amplified PCR products were separated on a 1% agarose gel.

Results

Isolation of *IbGAPDH* gene and sequence analysis

Previously we constructed EST library from sweetpotato suspension-cultured cells to identify highly abundant and cell culture-specific genes. GAPDH was selected as one of the significantly abundant and unique gene in the EST library of suspension-cultured cells (Kim et al. 2006). From the EST library, full-length cDNA of *IbGAPDH* gene was isolated and sequenced. The *IbGAPDH* gene consists of 1,363 nucleotides, predicted to encode a 36.9 kDa and an isoelectric point of 7.44. The largest open reading frame within 1,363 bp cDNA encodes a polypeptide of 337 amino acids (Figure 1).

In plants, there are two distinct isoforms of the GAPDH, NAD-dependent cytosolic enzyme and NADP-specific chloroplastic form (Cerff et al. 1982). The deduced amino acid sequence of *IbGAPDH* showed the highest identity (84~87%) with that of the cytosolic GAPDH from other higher plants, while the deduced amino acid sequence of chloroplastic GAPDH showed 48~49% identity with that of *IbGAPDH*. The identity of protein sequences was determined with the known sequences available in NCBI with the BLAST search program.

As shown in Figure 2, *IbGAPDH* showed a highly conserved region around Pro-193 which confers NAD^+ specificity to the GAPDH tetramer, Cys-154 that is the binding site of glyceraldehyde-3-phosphate, and Lys-196 which has been implicated as a possible phosphate binding site. Catalytically essential amino acid His-181 is also present, suggesting that it might code for functional enzyme.

Expression of *IbGAPDH* gene under environmental stresses

A previous study indicated that *IbGAPDH* gene was highly expressed in suspension-culture cells but not in roots and leaves (Kim et al. 2006). Since plant cells in culture are considered to be under conditions of high oxidative stress, sweetpotato plants were treated with H_2O_2, MV, and cold (15℃) to investigate the expression level of *IbGAPDH* gene. Total RNA was collected from leaves after various times of stress treatments. The expression of *IbGAPDH* was investigated on the mRNA level by relative quantitative RT-PCR analysis. The time-course transcript of the *IbGAPDH* gene was found out under stresses. For cold stress, the transcription was highly induced after 12 h treatment and increased until 48 h treatment. The expression of *IbGAPDH* gene was also induced by MV treatment, a superoxide-generating herbicide, and showed time-dependent increase. For H_2O_2 stress as an oxidant, the

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1     ATTCTTCAACTTACTCTCTCGCTCTAAACTTTTCAACTTTCATCTCTCTAGAAGCT
57    TCAAGCCTCCGCCATGGGGAAGATCAAGATTGGAATCAACGGATTTGGAAGGATCGGACG
            M  G  K  I  K  I  G  I  N  G  F  G  R  I  G  R  16
117   ATTGGTTGCTAGGGTTGCTCTGCACAGTGAGGATGTCGAGCTCGTTGCAGTCAACGACCC
      L  V  A  R  V  A  L  H  S  E  D  V  E  L  V  A  V  N  D  P  36
177   GTTCATCAGTACTGAATACATGACATACATGTTCAAGTATGATACTGTGCACGGGCAATG
      F  I  S  T  E  Y  M  T  Y  M  F  K  Y  D  T  V  H  G  Q  W  56
237   GAAGCACCATGACGTGAAGGTCCAAGATGAGAAGACTCTTCTGTTTGGCGAGAAGTCAGT
      K  H  H  D  V  K  V  Q  D  E  K  T  L  L  F  G  E  K  S  V  76
297   TAAGGTCTTTGGATGCAGGAATCCGGAAGAGATTCCATGGGCTGAAGCTGGTGCTGAGTA
      K  V  F  G  C  R  N  P  E  E  I  P  W  A  E  A  G  A  E  Y  96
357   TGTTGTGGAGTCTACTGGAGTCTTCACTGACAAGGACAAGGCTGCCGCTCACTTGAAGGC
      V  V  E  S  T  G  V  F  T  D  K  D  K  A  A  A  H  L  K  A  116
417   TGGTGCCAAGAAGGTTGTGATCTCTGCTCCTAGCAAAGATGCTCCCATGTTTGTTGTGGG
      G  A  K  K  V  V  I  S  A  P  S  K  D  A  P  M  F  V  V  G  136
477   AGTTAACGAGAAGGAATACAAGCCAGAGCTTAACATTGTTTCCAATGCAAGCTGCACTAC
      V  N  E  K  E  Y  K  P  E  L  N  I  V  S  N  A  S  C  T  T  156
537   CAACTGCCTTGCTCCTTTGGCTAAGGTCATCCATGATAGGTTTGGCATTGTGGAGGGTCT
      N  C  L  A  P  L  A  K  V  I  H  D  R  F  G  I  V  E  G  L  176
597   CATGACCACTGTCCACTCCATCACTGCCACTCAGAAGACTGTTGATGGTCCATCCATGAA
      M  T  T  V  H  S  I  T  A  T  Q  K  T  V  D  G  P  S  M  K  196
657   GGACTGGAGAGGTGGAAGAGCTGCTTCATTCAACATCATTCCTAGCAGCACTGGTGCAGC
      D  W  R  G  G  R  A  A  S  F  N  I  I  P  S  S  T  G  A  A  216
717   CAAGGCTGTTGGAAAAGTTCTCCCAGCCCTTAATGGGAAACTGACTGGAATGTCCTTCAG
      K  A  V  G  K  V  L  P  A  L  N  G  K  L  T  G  M  S  F  R  236
777   AGTTCCCACTGTGGATGTTTCAGTTGTTGACCTCACTGTCCGAACTGAGAAAAAGGCTAC
      V  P  T  V  D  V  S  V  V  D  L  T  V  R  T  E  K  K  A  T  256
837   CTATGAGGATGTCAAGAAGGCCATCAAGGAGGAGTCTGAGGGTAAGCTCAAGGGCATCTT
      Y  E  D  V  K  K  A  I  K  E  E  S  E  G  K  L  K  G  I  L  276
897   GGGTTACATCGATGAAGACTTGGTATCATCCGACTTTGTTGGTGATTGCAGGTCAAGCAT
      G  Y  I  D  E  D  L  V  S  S  D  F  V  G  D  C  R  S  S  I  296
957   CTTTGATGCCAAGGCTGGAATCTCGTTGAACGAGAACTTCTTCAAGGTTGTTGCTTGGTA
      F  D  A  K  A  G  I  S  L  N  E  N  F  F  K  V  V  A  W  Y  316
1017  TGACAACGAATGGGGTTACAGTTCCCGTGTCGTCGATCTGATCCGCCATATGCATTCTGC
      D  N  E  W  G  Y  S  S  R  V  V  D  L  I  R  H  M  H  S  A  336
1077  TGCTTAAGGGCTTAATGCCTCCAAATATTGGCAGCTTTTGGAGCACCCGGGGGGTTTTTG
      A  *                                                        337
1137  AGTATTTATTTTGATTCCTGCAATTCTGAAAAAAGTTTGTTTTAGTTTCTGATTTTCTTG
1197  TCAAGTGAATAAACCAGAAGAGTCTTGTCTTGACTCTTGAACAGGTTTTACCCCGTTCTT
1257  TTTGAGCTTGTATAATTTTACAACTTACCTTGGGTTGCTAATGAGTAAAATTAACTTTTG
1317  TCCAAAAAAAAAAAAAAAAAAAAAAAAAAAAAAAAAAAAAAAAAAAAAAAAAAAAAAA
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Figure 1. Nucleotide sequence and deduced amino acid sequence of cDNA clone for *IbGAPDH*. The *IbGAPDH* sequence is 1,363 bp long with one major ORF of 337 amino acids, and has a 5' untranslated region of 69 bp and 3' untranslated region 243 bp including 48 A residues of poly (A+) tail.

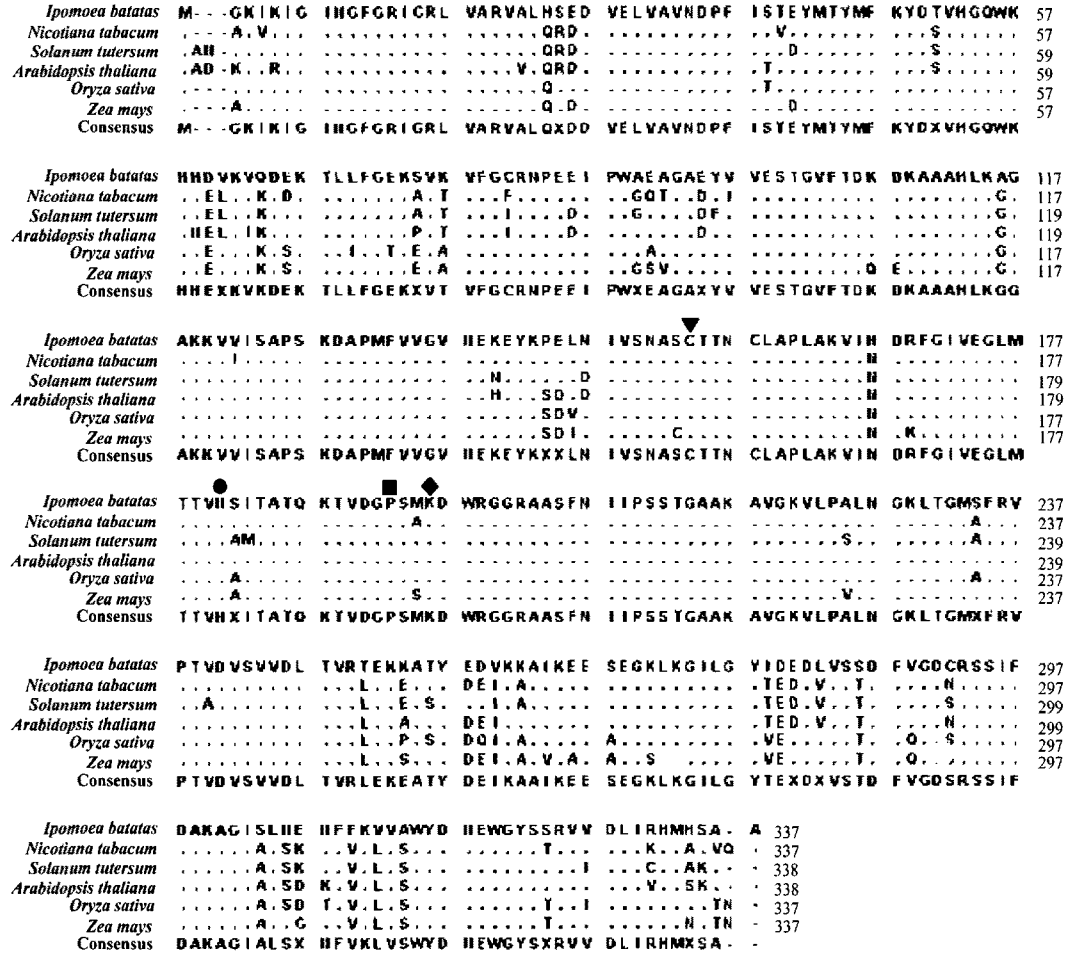

Figure 2. Comparison of the deduced amino acid sequence of *IbGAPDH* with the cytosolic *GAPDH* gene from other higher plants, *Nicotiana tabacum* (CAB39974), *Solanum tubersum* (AAM922008), *Arabidopsis thaliana* (BAE98901), *Oryza sativa* (ABL75274), and *Zea mays* (AAA87580). Sequence alignment was performed using the program CLC Workbench 4. Identical amino acids are given as dots. Cys-154, ▼; His-181, ●; Pro-193, ■; Lys-196, ◆.

transcription level was increased at 12 h treatment and did not changed until 24 h treatment (Figure 3).

Cold stress induced *IbGAPDH* expression

Since the transcript of *IbGAPDH* gene was increased dramatically in leaf by cold stress (15℃), the expression level of *IbGAPDH* was further investigated in different tissues under different temperatures, 15℃ and 10℃. Total RNA was isolated from leaves, petioles and roots at different time point (0, 12, 24, and 48 h). Semi-quantitative RT-PCR with *IbGAPDH* specific primers revealed that transcript levels were different according to tissues and temperatures.

At 15℃, the mRNA level of *IbGAPDH* gene was steadily

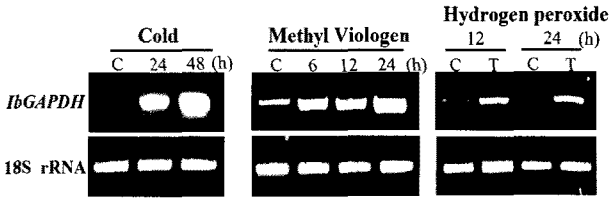

Figure 3. RT-PCR analysis of *IbGAPDH* expression in response to abiotic stresses. Sweetpotato plants were exposed to 15℃ for cold stress. 50 μM methyl viologen (MV) solution was sprayed onto whole plants and 440 mM H_2O_2 was treated with the second or third leaves from the top of plants. After stress treatments, total RNA was isolated and RT-PCR analysis was performed according to the manufacture's instruction. 18S rRNA was used as a relative internal control. C, control; T, treatment.

increased after 12 h cold treatment and reached to maximum level at 48 h in leaves. At 10℃, the transcript of *IbGAPDH*

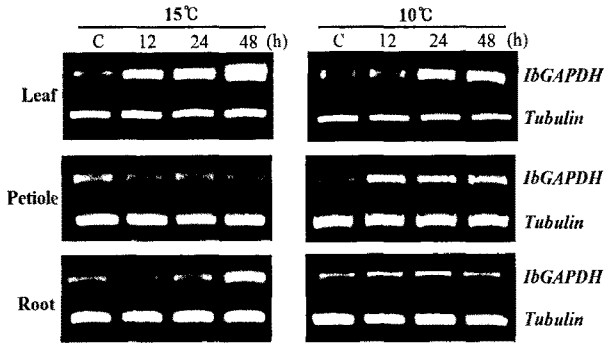

Figure 4. RT-PCR analysis of *IbGAPDH* expression in response to cold stress. Sweetpotato was exposed at 10℃ and 15℃ for 0, 12, 24, 48 h. Total RNA was isolated from leaves, petioles and roots, and then RT-PCR analysis was performed using gene -specific primers. Tubulin was used as an internal control.

gene was increased after 24 h cold treatment in leaves and did not change until 48 h. In petioles, the expression pattern was quite different between 15℃ and 10℃ treatments. At 15℃, the mRNA level of *IbGAPDH* gene was decreased after 12 h treatment and did not change until 48 h. However, the expression of *IbGAPDH* gene was rapidly induced from12 h treatment at 10℃-treated petioles. In roots, the mRNA level of *IbGAPDH* gene was not changed until 24 h and then increased highly at 48 h under 15℃ treatment. In while, the expression level of *IbGAPDH* gene was not changed during 10℃ treatment in roots (Figure 4). Taken together, the transcript of *IbGAPDH* gene was highly induced and rapidly increased at 1 5℃ temperature rather than 10℃ in leaves and roots. These results indicate that transcription of *IbGAPDH* gene is differently regulated with tissue-specificity according to temperatures.

Discussion

Previously it has been reported that *IbGAPDH* was one of the most significantly abundant genes in EST library of sweetpotato suspension cells and its expression was strongly induced in suspension cells but not in roots and leaves of the whole plants of sweetpotato (Kim et al. 2006). Here we cloned a full-length cDNA of *GAPDH* gene from sweetpotato suspension-cultured cells to investigate the gene structure for protein coding region and the transcript level under environmental stresses. All plants have two isoforms of GAPDH, one for glycolytic activity in the cytosol and the other for Calvin cycle reaction in the chloroplast. By comparing the deduced amino acid of GAPDH in other higher plants, *IbGAPDH* showed high homology with cytosolic GAPDH.

Recent studies are suggesting that GAPDH has diverse biological properties including a cellular redox regulation and adaptive response to stress-induced cell damage, not just a simple protein involved in glycolysis (Hancock et al. 2005; Baek et al. 2008). Overexpression of *GAPDH* from *Arabidopsis* (*GAPDHa*) in yeast cells resulted in an increase in cellular antioxidative capacity with higher levels of GSH. *GAPDHa* showed a novel function involved in cellular redox regulation (Baek et al. 2008). Moreover, several studies indicate that GAPDH is linked to ROS signaling in yeast and plant. GAPDH expression during apoptosis was increased in *S. cerevisiae*, and they suggested that GAPDH could be an intracellular sensor of oxidative stress during apoptosis induced by H_2O_2 (Magherini et al. 2007). Cytosolic GAPDH in *Arabidopsis* has a role in mediate ROS signaling, suggesting GAPDH is a direct target of H_2O_2 (Hancock et al. 2005).

We previously have reported that it was hard to detect the transcripts of *IbGAPDH* gene in whole plants of sweetpotao, but the transcript of *IbGAPDH* gene was abundant in suspension-cultured cells. When the whole plants of sweetpotato were subjected into environmental stresses such as cold, MV and H_2O_2, the expression of *IbGAPDH* gene was rapidly induced, indicating that the biological function of *IbGAPDH* gene is related to defense mechanism against oxidative stress in suspension-cultured cells. Our results indirectly support the recent reports that cytosolic GAPDH involves in ROS signaling or in cellular redox regulation.

Under cold stress, the transcription level of *IbGAPDH* gene was the highest. Sweetpotato is a chilling sensitive plant because they grown in tropical region. The growth rate is retarded under low temperature condition. Chilling stress leads to elevated levels of ROS, resulting damage to cellular components and severely disrupted metabolic functions (Prasad et al. 1994). Here we further investigated the transcriptional regulation of *IbGAPDH* gene in different tissues of sweetpotato under different temperatures, 10℃ and 15℃. The transcription

of *IbGAPDH* gene under both 10℃ and 15℃ was induced with the highest expression level in leaf compared than other tissues of sweetpotato. However, the expression patterns of leaves, petioles or roots were quite different. When we compared the mRNA level between 15℃ and 10℃ treatment, the transcript of *IbGAPDH* gene was highly induced and rapidly increased at 15℃ temperature rather than 10℃ in leaves and roots. These results indicate that transcription of *IbGAPDH* gene is differently regulated with tissue-specificity and the regulation of defense will be different according to chilling temperature. Further physiological understanding of the gene might be lead to development of transgenic sweetpotato plants with resistance to environmental stresses.

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