Postprint: Comparative Analysis of Expression Abundance of Rubber Biosynthesis Regulatory Genes in Rubber Tree

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Abstract

Proteins constitute one of the basic building blocks of life systems and are the executors of most biological functions. Protein abundance is intimately linked to their biological functions, and their abundance is strictly and precisely regulated at various stages of the gene expression process. Among these, protein abundance exhibits a strong correlation with its corresponding mRNA abundance, with 40% of the variation in protein abundance being explainable by mRNA abundance. The jasmonic acid signaling pathway regulates natural rubber biosynthesis in Hevea brasiliensis, yet the differences in expression abundance among related genes remain to be elucidated. This study compared the expression abundance differences of 15 genes related to the regulation of rubber biosynthesis—HbCOI1, HbJAZ1, HbJAZ2, HbJAZ3, HbMYC1, HbMYC2, HbMYC3, HbMYC4, HbMYC5, HbGAPDH, HbHMGR1, HbSRPP, HbREF, HbHRT1, HbHRT2—and two commonly used reference genes, Hb18S and HbACTIN1, in the latex of 10 Hevea brasiliensis germplasms under the S/2D d/3 tapping system; the expression abundance of HbACTIN1 was set to 1, serving as the standard for calculating the expression abundance of other genes in the samples. The results showed that the transcriptional abundance of different genes in the same individual varied significantly, and the ranking of abundance levels of the same gene set differed among different individuals; the transcriptional abundance of the same gene also varied significantly among different individuals, with the maximum abundance of these 16 genes being 9.43, 6.04, 10.02, 12.29, 18.82, 9.22, 38.46, 112.83, 121.36, 15.34, 19.09, 13.54, 10.05, 19.80, 24.83, and 11.82 times their minimum abundance, respectively, and their coefficients of variation were 73.05%, 55.19%, 69.09%, 67.37%, 66.59%, 53.87%, 83.25%, 122.02%, 166.34%, 59.89%, 70.59%, 75.67%, 74.20%, 68.34%, 84.23%, and 78.59%, respectively; overall, at the population level, the transcriptional abundance of the 16 genes from high to low was:

18S>SRPP>HMGR1>REF>MYC2/HRT1>COI1>MYC1/MYC4>GAPDH/JAZ1/MYC5>JAZ2>HRT2/M and their population average abundances were 28382.26, 43.64, 11.39, 7.16, 5.47, 5.10, 1.07, 0.75, 0.74, 0.45, 0.42, 0.33, 0.12, 0.06, 0.06, and 0.04 times that of HbACTIN1, respectively. Notably, at both individual and population levels, the abundance of Hb18S was undoubtedly the highest; among mRNAs, HbSRPP had the highest abundance, HbJAZ1 was greater than HbJAZ2 and HbJAZ3, HbMYC2 was greater than HbMYC1, HbMYC3, HbMYC4, and HbMYC5, and HbHRT1 was greater than HbHRT2. The results indicated that the abundance of structural and functional genes was higher than that of regulatory genes. In gene relative expression analysis, target genes and reference genes are often normalized, thereby masking the true abundance differences among different genes; therefore, in gene expression analysis, attention should be paid to both the relative expression level of genes and the abundance differences among genes, which facilitates a more comprehensive understanding of gene function.

Full Text

Comparison of the Expression Abundance of Genes Related to Rubber Biosynthesis Regulation in Hevea brasiliensis

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Abstract

Proteins are fundamental components of life systems and executors of most biological functions. Protein abundance is closely related to its biological function and is strictly and precisely regulated at each stage of gene expression. Notably, protein abundance exhibits a strong correlation with its corresponding mRNA abundance, with approximately 40% of the variation in protein abundance explainable by mRNA abundance. The jasmonic acid signaling pathway regulates natural rubber biosynthesis in Hevea brasiliensis, yet the differences in expression abundance among related genes remain to be elucidated. This study compared the expression abundance differences of 15 rubber biosynthesis regulatory genes (HbCOI1, HbJAZ1, HbJAZ2, HbJAZ3, HbMYC1, HbMYC2, HbMYC3, HbMYC4, HbMYC5, HbGAPDH, HbHMGR1, HbSRPP, HbREF, HbHRT1, HbHRT2) and two commonly used reference genes (Hb18S, HbACTIN1) in the

latex of 10 rubber tree germplasms under the S/2D d/3 tapping system. The expression abundance of HbACTIN1 was set to 1, serving as the standard for calculating the abundance of other genes in each sample. The results revealed significant differences in transcriptional abundance among different genes within the same individual, and the ranking order of the same gene set varied among different individuals. The transcriptional abundance of the same gene also differed markedly across individuals. For these 16 genes, the maximum abundance was 9.43, 6.04, 10.02, 12.29, 18.82, 9.22, 38.46, 112.83, 121.36, 15.34, 19.09, 13.54, 10.05, 19.80, 24.83, and 11.82 times the minimum abundance, respectively. Their coefficients of variation were 73.05%, 55.19%, 69.09%, 67.37%, 66.59%, 53.87%, 83.25%, 122.02%, 166.34%, 59.89%, 70.59%, 75.67%, 74.20%, 68.34%, 84.23%, and 78.59%, respectively. Overall, at the population level, the transcriptional abundance of the 16 genes from highest to lowest was: 18S > SRPP > HMGR1 > REF > MYC2/HRT1 > COI1 > MYC1/MYC4 > GAPDH/JAZ1/MYC5 > JAZ2 > HRT2/MYC3/JAZ3. Their average abundances were 28382.26, 43.64, 11.39, 7.16, 5.47, 5.10, 1.07, 0.75, 0.74, 0.45, 0.42, 0.33, 0.12, 0.06, 0.06, and 0.04 times that of HbACTIN1, respectively. Notably, at both individual and population levels, Hb18S abundance was unequivocally the highest. Among mRNAs, HbSRPP showed the highest abundance, HbJAZ1 was greater than HbJAZ2 and HbJAZ3, HbMYC2 was greater than HbMYC1, HbMYC3, HbMYC4, and HbMYC5, and HbHRT1 was greater than HbHRT2. These results demonstrate that structural and functional genes exhibit higher abundance than regulatory genes. In gene relative expression analysis, normalization of target and reference genes often masks the true abundance differences between genes. Therefore, in gene expression analysis, attention should be paid not only to relative expression levels but also to inter-gene abundance differences, which facilitates a more comprehensive understanding of gene function.

Key words: Hevea brasiliensis, rubber biosynthesis regulation, gene abundance, comparison
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Introduction

Proteins are fundamental components of life systems and executors of most biological functions. Protein abundance is closely related to its biological function and is strictly and precisely regulated at each stage of gene expression. Among these regulatory mechanisms, mRNA abundance can explain the major portion of protein abundance variation.

Protein abundance exhibits a certain correlation with its corresponding mRNA abundance. Lu et al. (2007) quantified the proteomes of Escherichia coli and yeast cells, finding a high correlation between intracellular protein abundance and corresponding mRNA abundance ($R^2 = 0.47$ for E. coli, $R^2 = 0.73$ for yeast). Laurent et al. (2010) investigated protein and mRNA abundance across seven representative species, revealing positive correlations ranging from 0.36 to 0.70. Schwanhäusser et al. (2011) studied quantitative proteomes in mouse NIH3T3 cells and found a strong correlation between protein abundance and corresponding mRNA abundance ($R^2 = 0.41$). Marquerat et al. (2012) conducted quantitative proteome analysis of proliferating and quiescent fission yeast cells, observing a certain correlation between intracellular protein abundance and corresponding mRNA abundance ($R^2 = 0.55$). Collectively, these studies demonstrate that at the cellular population level, protein abundance exhibits a strong correlation with its corresponding mRNA abundance, with mRNA abundance explaining the major portion (approximately 40% or more) of protein abundance variation.

The jasmonic acid signaling pathway regulates rubber biosynthesis in Hevea brasiliensis (Deng et al., 2018), and rubber yield is positively correlated with the expression of key genes in the jasmonic acid signaling pathway and rubber biosynthetic enzyme genes (Yang et al., 2019a; Yang et al., 2019b). Current qPCR-based gene expression analysis primarily focuses on relative expression levels among genes, among sample tissues, or under different treatments, while rarely addressing abundance differences among functionally related genes. In relative expression analysis, normalization of target and reference genes often masks the true abundance differences between genes. Therefore, in gene expression analysis, attention should be paid not only to relative expression levels but also to inter-gene abundance differences, which facilitates a more comprehensive understanding of gene function. In this study, the abundance of HbACTIN1 in each sample was set to 1 to analyze the abundance differences among 15 rubber biosynthesis regulatory genes and the commonly used reference gene 18S, aiming to provide a more comprehensive understanding of the roles and significance of these genes in rubber biosynthesis regulation.

Materials and Methods

The experimental materials (Table 1) and experimental design were identical to those previously reported, which documented the relative expression differences of nine key jasmonic acid signaling pathway genes (HbCOI1, HbJAZ1, HbJAZ2, HbJAZ3, HbMYC1, HbMYC2, HbMYC3, HbMYC4, HbMYC5) and six rubber

biosynthetic enzyme genes (HbHRT2, HbSRPP, HbREF, HbHMGR1, HbHRT1, HbGAPDH) in these 10 rubber tree germplasms, as well as the expression correlations among these genes (Yang et al., 2019c). This study further utilized the qPCR results of these genes to analyze inter-gene abundance differences.

Table 1 Experimental materials
Plant material: PR107, RRIM600, Re ken 628, Re ken 525, Re ken 523, RO/CM/10 44/160, MT/IT/13 29/8, RO/C/8 24/104, RO/I/103 107, RO/CM/10 44/454

1.2 Methods

qPCR primers for HbACTIN1 were designed based on the full-length cDNA sequence from GenBank (JF775488): forward primer, GTTCTACAAGT-GCTTTGATGGCGA; reverse primer, GCAGCCATAACATGAAACG-CAATAG. The primer amplification efficiency was 92.7%, and the qPCR product size was 190 bp.

The abundance of each gene in each sample was calculated using the formula "A = 2^ΔCq = 2^(Actin1 Cq - Gene Cq)" , where the abundance of HbACTIN1 in each sample was set to 1 (A = 2^ΔCq = 2^(Actin1 Cq - Actin1 Cq) = 2^0 = 1).

1.3 Data Processing

GraphPad Prism 5 was used for graphing, and Duncan' s multiple range test in SPSS software was used for statistical analysis.

Results

2.1 Average Transcriptional Abundance of Genes

Overall, at the population level, the 16 genes exhibited substantial differences in transcriptional abundance (FIGURE:1). From highest to lowest, the ranking was: 18S > SRPP > HMGR1 > REF > MYC2/HRT1 > COI1 > MYC1/MYC4 > GAPDH/JAZ1/MYC5 > JAZ2 > HRT2/MYC3/JAZ3. Among these, the differences between MYC2/HRT1, MYC1/MYC4, GAPDH/JAZ1/MYC5, and HRT2/MYC3/JAZ3 were not significant ($P < 0.05$). The abundance of SRPP was extremely significantly higher than that of REF ($P < 0.01$). The abundance of HRT1 was extremely significantly higher than that of HRT2 ($P < 0.01$). Among the five MYC family members, the ranking was MYC2 > MYC1/MYC4 > MYC5 > MYC3 ($P < 0.01$). Among the three JAZ family members, the ranking was JAZ1 > JAZ2 > JAZ3 ($P < 0.01$).

Note: Data represent the mean ± standard deviation of transcriptional abundance for each gene across 30 samples. Genes are arranged from left to right in descending order of abundance. Different uppercase letters indicate extremely

significant differences between groups ($P < 0.01$), while different lowercase letters indicate significant differences ($P < 0.05$). The same notation applies below.

2.2 Expression Abundance of Different Genes in the Same Sample

At the individual level, different genes within the same sample showed significant differences in transcriptional abundance (FIGURE:2–FIGURE:6). For example, in samples 23 and 28, the abundance differences among all 16 genes reached significant levels ($P < 0.01$ or $P < 0.05$). The ranking order of the same gene set varied among different samples (FIGURE:2–FIGURE:6, Table 1). Across all samples, 18S and SRPP consistently ranked first and second, respectively. HMGR1 primarily ranked third (67%). REF primarily ranked fourth (53%). MYC2 primarily ranked fifth (60%). HRT1 primarily ranked sixth (57%). COI1 primarily ranked seventh and eighth (57%, 40%). MYC4 (30%) and GAPDH (30%) primarily ranked ninth. JAZ1 primarily ranked tenth and eleventh (47%, 30%). MYC4 (23%), MYC5 (17%), GAPDH (17%), JAZ2 (17%), and MYC3 (17%) primarily ranked twelfth. JAZ2 primarily ranked thirteenth (50%). JAZ3 primarily ranked fourteenth, fifteenth, and sixteenth (27%, 30%, 37%), with JAZ3 (37%) and MYC3 (33%) primarily ranking sixteenth. The ranking range of the same gene varied across samples; for instance, MYC2 showed three ranking positions across 30 samples, while MYC5 showed as many as nine ranking positions.

SRPP and REF are the two major proteins constituting rubber particles in rubber trees. In all samples of this study, the abundance of SRPP was extremely significantly higher than that of REF ($P < 0.01$). HRT1 and HRT2 are two members of the rubber transferase family in rubber trees. In all samples of this study, the abundance of HRT1 was extremely significantly higher than that of HRT2 ($P < 0.01$). Among the five MYC family members, MYC2 showed the highest abundance in all samples, with its abundance being extremely significantly higher than that of MYC1, MYC3, MYC4, and MYC5 ($P < 0.01$). Among the three JAZ family members, JAZ1 showed the highest abundance in all samples, with its abundance being extremely significantly higher than that of JAZ2 and JAZ3 ($P < 0.01$). In most samples (25 samples, 83.3%), JAZ2 abundance was greater than JAZ3; only in five samples (7, 8, 9, 15, 21; 16.7%) was JAZ3 abundance greater than (samples 7, 8, 9; 10%) or equivalent to (samples 15, 21; 6.7%) JAZ2.

2.3 Expression Abundance of the Same Gene in Different Samples

At the individual level, the transcriptional abundance of the same gene differed significantly among individuals, with coefficients of variation ranging from 53.87% to 166.34% (FIGURE:7–FIGURE:10). COI1 ranged from 3.9×10^{-1} to 3.7×10^{0}, with a coefficient of variation of 73.05% and inter-individual differences reaching one order of magnitude. JAZ1 ranged from 1.9×10^{-1} to 1.15×10^{0}, with a coefficient of variation of 55.19% and inter-individual differences reaching one order of magnitude. JAZ2 ranged from 3.0×10^{-2} to $3.0 \times$

10^{-1}, with a coefficient of variation of 69.09% and inter-individual differences reaching one order of magnitude. JAZ3 ranged from 1.0×10^{-2} to 1.3×10^{-1}, with a coefficient of variation of 67.37% and inter-individual differences reaching one order of magnitude. MYC1 ranged from 1.5×10^{-1} to 2.8×10^{0}, with a coefficient of variation of 66.59% and inter-individual differences reaching one order of magnitude. MYC2 ranged from 1.4×10^{0} to 1.24×10^{1}, with a coefficient of variation of 53.87% and inter-individual differences reaching one order of magnitude. MYC3 ranged from 4.5×10^{-3} to 1.7×10^{-1}, with a coefficient of variation of 83.25% and inter-individual differences reaching two orders of magnitude. MYC4 ranged from 4.0×10^{-2} to 4.4×10^{0}, with a coefficient of variation of 122.02% and inter-individual differences reaching two orders of magnitude. MYC5 ranged from 2.0×10^{-2} to 4.4×10^{0}, with a coefficient of variation of 166.34% and inter-individual differences reaching two orders of magnitude. GAPDH ranged from 8.0×10^{-2} to 1.2×10^{0}, with a coefficient of variation of 59.89% and inter-individual differences reaching two orders of magnitude. HMGR1 ranged from 1.5×10^{0} to 2.9×10^{1}, with a coefficient of variation of 70.59% and inter-individual differences reaching one order of magnitude. SRPP ranged from 1.2×10^{1} to 1.6×10^{2}, with a coefficient of variation of 75.67% and inter-individual differences reaching one order of magnitude. REF ranged from 2.8×10^{0} to 2.8×10^{1}, with a coefficient of variation of 74.20% and inter-individual differences reaching one order of magnitude. HRT1 ranged from 6.5×10^{-1} to 1.3×10^{1}, with a coefficient of variation of 68.34% and inter-individual differences reaching two orders of magnitude. HRT2 ranged from 1.1×10^{-2} to 2.8×10^{-1}, with a coefficient of variation of 84.23% and inter-individual differences reaching one order of magnitude. 18S ranged from 6.5×10^{3} to 7.7×10^{4}, with a coefficient of variation of 78.59% and inter-individual differences reaching one order of magnitude.

Discussion and Conclusion

The ribosome is the most ancient and sophisticated cellular organelle, with highly conserved structure and composition from prokaryotes to eukaryotes (Jin et al., 2018). Ribosomal RNA (rRNA) is the most abundant RNA in cells, accounting for approximately 50% of total RNA in eukaryotic cells (Su & Hong, 2009). rRNA is a major structural component of ribosomes, comprising 64.78% of the relative molecular weight of prokaryotic ribosomes and 58.72% of eukaryotic ribosomes (Liu, 2009). In this study, 18S showed the highest gene abundance, consistent with the general observation that structural proteins have higher abundance than regulatory proteins (Wang et al., 2017; Sato et al., 1999; Giegé & Brennicke, 1999; Lin et al., 1999), genes encoding highly expressed proteins tend to be evolutionarily conserved (Drummond et al., 2005; Drummond & Wilke, 2008), and primarily execute core cellular functions (Beck et al., 2011).

SRPP, HMGR1, REF, and HRT1 are key enzymes for rubber biosynthesis, with SRPP and REF being the two major proteins constituting rubber particles (Dennis & Light, 1989; Oh et al., 1999; Berthelot et al., 2014). COI1, JAZ1,

JAZ2, JAZ3, MYC1, MYC2, MYC3, MYC4, and MYC5 are key proteins in the jasmonic acid signaling pathway involved in regulating rubber biosynthesis (Deng et al., 2018). This study demonstrated that the gene abundance of SRPP, HMGR1, REF, and HRT1 was significantly higher than that of JAZs and MYCs family members, consistent with findings that functional/structural proteins generally have higher abundance than regulatory proteins (Ishihama et al., 2008; Beck et al., 2011; Nagaraj et al., 2011). HMGR1 is located upstream of multiple metabolic pathways, and cytoplasmic GAPDH is a key enzyme in glycolysis. Their higher gene abundance compared to JAZ2, JAZ3, and MYC3 aligns with the observation that proteins involved in fundamental "material flow"have higher abundance than those regulating precise "information flow" (Zhong et al., 2012).

In vitro analysis has shown that HRT2, rather than HRT1, is associated with rubber synthesis (Asawatreratanakul et al., 2003), which is consistent with the finding that HRT1 gene expression is more conserved than HRT2 across rubber tree germplasms with different yields (Yang et al., 2019a). However, the significantly higher abundance of HRT1 compared to HRT2 suggests that HRT1 may perform a more conserved function.

Draft genome sequence analysis indicates that the rubber tree genome contains 10 REF and 12 SRPP gene members (Rahman et al., 2013). These genes share similar genomic locations (Oh et al., 1999; Sookmark, 1999), and evolutionary analysis suggests that REF and SRPP are homologous proteins derived from a common ancestral gene, belonging to a large plant stress-related protein family (Karine et al., 2014). REF and SRPP mRNAs are highly expressed in laticifer cells (Ko et al., 2003; Chotigeat et al., 2010; Han et al., 2000; Chow et al., 2007; Tan et al., 2014), and this study obtained similar results. In latex, the REF family showed the highest transcriptional abundance (9.44%), followed by the SRPP family (1.21%) (Chotigeat et al., 2010). At the individual member level, SRPP abundance was greater than REF in this study.

MYC1, MYC2, and MYC3 are specifically expressed in latex, whereas MYC4 and MYC5 are primarily expressed in flowers (Zhao, 2011), which is consistent with the stronger correlation of the former with rubber yield compared to the latter (Yang et al., 2019b). However, the abundance of MYC4 and MYC5 in latex was still higher than that of MYC3, and MYC4 abundance was comparable to MYC1, indicating that MYC4 and MYC5 also function in latex metabolism.

Therefore, in gene expression analysis, attention should be paid not only to relative expression levels but also to inter-gene abundance differences, which facilitates a more comprehensive understanding of gene function.

The results of this study demonstrate significant differences in transcriptional abundance among rubber biosynthesis regulatory genes with different functions/pathways, and these differences are generally consistent across different rubber tree germplasms. Both within and among germplasms, the transcriptional levels of these genes exhibit certain fluctuations, with regulatory genes showing greater variation than functional and structural genes. This study

obtained gene transcriptional abundance data at 3 days after tapping. Since tapping significantly promotes rubber biosynthesis in rubber trees and involves both latex drainage and mechanical wounding effects, investigating the effects of wounding and latex drainage on the transcriptional abundance of related genes and systematically tracking the dynamic changes in transcriptional abundance of these genes after tapping will help refine the theoretical mechanisms of rubber biosynthesis regulation.

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Note: Figure translations are in progress. See original paper for figures.