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Role of Transcription Factors in Banana Fruit Ripening: A Systematic Literature Review

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Abstract

Background: The development of edible fruit quality is a vital process. Banana fruit ripening is a complex biochemical and physiological process that causes physical changes such as softening. Fruit aging and ripening are greatly influenced by transcriptional regulation. Transcription factors also play an essential role in regulating various biological processes. Therefore, this study aimed to explore information about the role of transcription factors in banana fruit ripening. **Methods:** A systematic review was conducted by searching the Scopus database indexed Q1-Q4 through the Watase UAKE application from 2018 to 2023 to find relevant studies on the role of transcription factors in banana fruit ripening. **Results:** From the search results, 157 articles were found, which were then narrowed down to 11 articles by considering the established inclusion criteria. This study identified 11 transcription factors that have the potential for fruit ripening. **Conclusions:** The findings of this article review indicate that there are transcription factors, namely MYB, MaWRKY49, MabHLH7, MaNAC42, MaMADS36, bZIP21, MaMYB3, MabHLH, MaERF012, NAC, and WRKY. The role of transcription factors can control fruit quality in agricultural commodities that play genetics in molecular biology. These findings indicate that knowledge of the role of transcription factors can provide insight into the development of innovations in agriculture in the future.

Keywords: Banana fruit; Fruit ripening; Transcription factors

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Introduction

The fruit known as Banana (*Musa acuminata*) has an essential meaning as one of the most important fruit crops on a global scale. Banana is part of the climacteric fruit, which means it undergoes a rapid ripening process after harvesting, along with climacteric respiration, a significant increase in ethylene production, and changes in texture, color, nutritional components, and volatile compounds.

Developing edible fruit quality is a vital process that is very important (Yokphonchanachai et al., 2023), and overripe fruit causes a decrease in storage duration and selling price quality. Increasing the understanding of the fruit ripening and aging process will allow for adequate development to improve product quality and minimize losses (Yan et al., 2019)

Fruit ripening involves physiological and biochemical forms that directly or indirectly determine texture, appearance, taste, and nutritional quality, affecting shelf life and commodity value (Xiao et al., 2013; Ba et al., 2014).

Banana fruit ripening is a complex biochemical and physiological process that causes physical changes such as the appearance of aromatic substances, softening, and color changes (from green to yellow) (Xiao et al., 2018; Ringer et al., 2018). Fruit aging and ripening are greatly influenced by transcriptional regulation. The banana ripening regulatory network has shown the role of transcription factors (TFs).

Transcription factors (TFs) function as universal regulators of gene expression. This is because they scan and bind to specific DNA motifs. Transcription factors also play an essential role in regulating various biological processes (Zaret, 2020). Transcription factors (TFs) bind to target gene promoters to activate or repress expression. Still, TFs can also undergo post-translational modification (PTM) in response to developmental changes or environmental inputs (Skelly et al., 2016). The main targets of molecular breeding in plants and fruits are transcription factors (TFs). DNA Test Using bioinformatics tools and sequencing technology, 58 transcription factor families have been identified and characterized based on their plant DNA binding domains (Tian et al., 2020).

A common understanding has been achieved that different transcription factor variations can affect plant control. Based on molecular aspects, this shows an excellent potential for various transcription factors in banana fruit ripening. Therefore, a deep understanding of transcription factors can help facilitate the explanation of the banana fruit ripening process and its control.

Methods

Search Strategy

The type of research used is a systematic review based on a search for research articles from 2018 to 2023. A systematic review is a method for systematically identifying, evaluating, and synthesizing medical studies, providing a comprehensive understanding of a particular topic (Nundy et al., 2021). Systematic reviews can save time by presenting a concise summary of relevant scientific research, reducing bias and error, and guiding stakeholders in decision-making (Luchini et al., 2020; Mattos & Ruellas, 2015). The keywords in the literature search were fruit ripening transcription factors, banana ripening factors, the role of transcription factors in banana fruit ripening, banana ripening mechanism, and MYB transcription factors in bananas. The literature search was conducted using the Watase UAKE application. This application has various features, including systematic literature search using PRISMA, simple meta-analysis, article classification, and data visualization (Wahyudi et al., 2018).

Eligibility Criteria

The eligibility criteria for this study include: 1) References from literature in the form of journals and/or scientific proceedings, 2) Sources from Q1-Q4 indexed journals, 3) Journals and/or scientific proceedings that are open access, 4) Articles must be available in full text, 5) Journals and/or scientific proceedings that use English, 6) The year of publication of the journal and/or scientific proceedings is in the range of 2018-2023, 7) Discussions in journals and scientific proceedings must include transcription factors in banana fruit ripening, and 8) The research design must be experimental.

Article Selection

The research method used in the systematic literature review refers to the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA). This process was carried out carefully and systematically, following the appropriate research steps and protocols. The articles found were then filtered based on their relevance to the period and keywords used, primarily related to transcription factors in banana fruit ripening. Literature studies were excluded from the selection due to the emphasis on experimental research. Based on the search, 157 articles were found (Figure 1).

Data extraction

The selected articles were analyzed, and relevant information was extracted. Relevant information includes research details such as year of publication, title, methods used, and results achieved. The results will be evaluated to explore their relationship with transcription factors in banana fruit ripening.

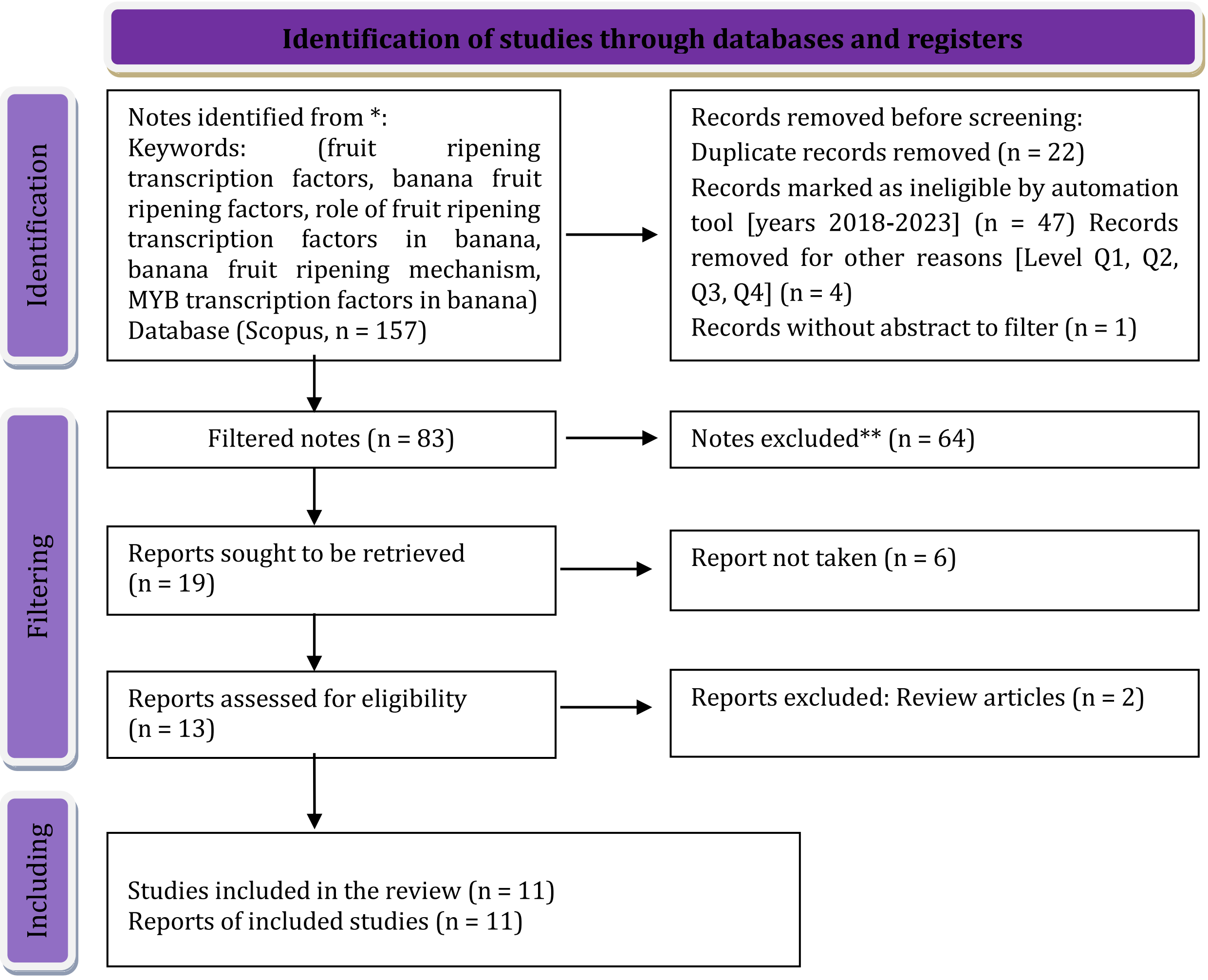

Figure 1. Systematic review flow chart using the PRISMA method
Source: processed by the author (2023)

Result

This systematic review details the role of transcription factors in banana fruit ripening. The review identifies possible influences of transcription factors that influence the banana fruit ripening process (Table 1).

Table 1. Summary description of data from included studies

No	Transcription Factor	Transcription Factor Location/Domain	Method	Result	Ref
1.	MYB	MYB transcription factors or MYB domains are located in the promoter region of target genes.	• RNA isolation, sequencing, and functional annotation • Differentially expressed genes (DEGs) analysis • Transcription factor binding site (TFBS) analysis RT-qPCR analysis	• 986 differentially expressed genes (DEGs) identified in banana fruit ripening • Nine low-temperature delays in fruit ripening characterize MYB genes and 32 ripening-related genes by affecting gene expression. • MYB regulates banana ripening through different pathways and has interconnections	(Yang et al., 2021)

				• MYB plays an essential role in fruit ripening under low temperatures.	
2.	MaWRKY49	The transcription factor MaWRKY49 has a WRKY domain that includes the conservative core sequence WRKYGQK	• Sequence analysis • RNA isolation and qRT-PCR analysis • Yeast one-hybrid (Y1H) assay • Subcellular localization analysis • Dual-luciferase reporter assay • Transient overexpression assay in banana fruit	• MaWRKY49 regulates banana fruit ripening by modulating the transcription of two PL genes. • The expression of mAWRKY49, MaPL3, and MaPL11 is induced by ethephon and inhibited by 1MCP. • MaWRKY49, MaPL3, and MaPL11 expression patterns are consistent with the fruit ripening process. • MaWRKY49 activates the transcription of MaPL3 and MaPL11 in response to ethephon treatment. • Overexpression of MaWRKY49 positively regulates the banana fruit ripening process.	(Liu et al., 2023)
3.	MabHLH7	The transcription factor or domain of MabHLH7 is located in the nucleus	• RNA extraction and qRT-PCR analysis • Subcellular location • Transcriptional activation assay in yeast cells • Cloning of MaXTH12, MaEXP2/21, MaPME4/5, MaPG4, MaPL1/2 promoters • Electrophoretic mobility shift assay (EMSA) • Transient dual-luciferase expression assay	• mABHLH7 is an ethylene-inducible transcription factor involved in the ripening of banana fruit. • mABHLH7 activates the promoters of cell wall modifier-related genes. • The expression of MaxTh12, MaExp2/21, MapMe4/5, MapG4, and MaPL1/2 is increased during ripening. • mABHLH7 acts as a positive regulator in banana fruit ripening.	(Song et al., 2020)
4.	MaNAC42	The transcription factor MaNAC42 is located in the nucleus	• RT-PCR and quantitative RT-PCR analysis • Subcellular localization Analysis • Transactivation assay for MaNAC42 in yeast • Purification of recombinant protein • SDS PAGE electrophoresis and western blotting • Electrophoretic mobility shift assay (EMSA) • Dual-luciferase reporter assay • Chromatin immunoprecipitation • Generation of transgenic Arabidopsis plants • Dark treatment and measurement of senescence parameters	• MaNAC42 is involved in the regulation of fruit ripening in bananas under oxidative stress. • MaNAC42 directly binds to the promoters of genes associated with oxidative stress and ripening. • Ectopic overexpression of MaNAC42 delays dark-induced senescence in leaves. • MaNAC42 is a target of MamSrb2, a methionine sulfoxide B reductase • Oxidation of methionine in MaNAC42 causes decreased DNA-binding capacity and transcriptional activity. • MamSrb2 can repair oxidized MaNAC42 and restore its DNA-binding capacity. • Sulfoxidation of	(Yan et al., 2024)

			• Site-directed mutagenesis of Met residues to glutamine • Bimolecular fluorescence complementation assay • Glutathione S-transferase pull-down assay • Oxidation and reduction of MaNAC42 and LC-MS/MS analysis	MaNAC42 decreases DNA-binding capacity and transcriptional regulatory activity. • Transcription of candidate genes regulated by MaNAC42 is up-regulated during natural maturation.	
5.	MaMADS36	The MaMADS36 domain is located in the G CA(r) box of the MaBAM9b promoter.	• Vector construction and banana transformation • Southern blot analysis • De novo RNA seq and transcriptome analysis • Construction of co-expression network • Prediction of promoter motifs and binding sites • B-Glucuronides histochemistry • Yeast one-hybrid assay • Electrophoretic mobility shift assay • Dual-luciferase reporting assay • GUS assay • Virus-induced gene silencing • RNA isolation and RT qPCR	• MamaDS36 regulates ethylene biosynthesis, starch degradation, softening, and sugar accumulation. • MamaDS36 interacts with 74 other proteins to form a co-expression network. • MamaDS36 directly binds to the Mabam9b promoter to enhance enzyme transcription and activity. • MamaDS36 can be applied to breeding programs to improve fruit shelf life.	(Liu et al. 2021)
6.	bZIP21	The transcription factor bZIP21 is located on the promoters of MabZIP21 and MaMPK6-3.	• In vitro phosphorylation assay using phos-tag technology sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS PAGE) • Yeast two-hybrid (Y2H) screening • Phosphoproteomic analysis and LC-MS/MS analysis • In vitro pull-down assay, BiFC assay, and co-immunoprecipitation (co IP) assay.	• The phosphoproteomic analysis identified 63 unique phosphopeptides corresponding to 49 proteins. • MabZip21 showed increased phosphorylation levels during banana ripening. • MabZip21 stimulated the transcription of ripening-related genes. • MabZip21 can be phosphorylated by mAMPK6-3, enhancing its transcriptional activation ability. • Transient overexpression of phosphomimetic MabZip21 accelerates the ripening of bananas.	(Wu et al., 2022)
7.	MaMYB3	The transcription factor MaMYB3 is located in the promoter of MaGWD1 and also in the promoters of 10 other starch degradation-related genes such as MaPWD1, MaSEX4, MaBAM7, MaBAM8, MaAMY2B,	• Y1H Screening • ChIP-qPCR Analysis	• MaMYB3 is a transcriptional repressor involved in banana fruit ripening. • MaMYB3 inhibits starch degradation by repressing starch degradation-related genes. • MaMYB3 also represses the activator of starch	(Fan et al., 2018)

		MaAMY3, MaAMY3A, MaAMY3C, MaMEX1, and MapGlcT2-1.		degradation-related genes, MabHLH6.	
8.	MabHLH	The MabHLH transcription factor is located on chromosome 11 in the Musa acuminata genome.	• Transcriptomic Analysis • Weighted Gene Co-expression Network Analysis • Quantitative RT-PCR Analysis	• 259 MabHLH TF genes were identified in the Musa acuminata genome • MabHLHs were classified into 23 subfamilies • Gene duplication and segmental duplication were involved in MabHLH expansion. • MabHLH expression profiles in fruit development, ripening, and stress were investigated. • The MabHLHS co-expression network was constructed to identify metabolic pathways. • MabHLHs involved in banana resistance to Foc TR4 infection were identified.	(Wang et al., 2020)
9.	MaERF012	Transcription factor MaERF012 is located in the cell nucleus	• RNA Extraction and Transcript Analysis • Subcellular Localization • Dual-Luciferase Transient Expression (DLR) • Yeast One-Hybrid (Y1H) • Electrophoretic Mobility Shift Assay (EMSA) • Transient Overexpression of MaERF012 in Banana 'Fenjiao' Fruit and RNA-Seq Assay	• MaErf012 is a transcriptional activator involved in fruit ripening. • MaERF012 activates the transcription of genes related to chlorophyll, starch, and cell wall degradation. • Overexpression of MaERF012 promotes fruit ripening by increasing the expression of these genes. • A high concentration of 1-MCP treatment represses the expression of MaERF012 and its target genes. • MaERF012 belongs to the AP2ERF transcription factor family and is in the cell nucleus.	(Chen et al., 2022)
10.	NAC	NAC is located at the N-terminal of the transcription factor NAC	BLAST P and mCScanx to analyze duplication events in the ManaC gene. • MapChart software to map the ManaC gene to the banana chromosomes.	• 181 banana NAC genes were identified • NAC genes in M. *acuminata*, Arabidopsis, and rice were clustered into 18 groups. • Segmental duplication events promoted ManaC gene evolution. • 10 ManaC genes were identified as associated with fruit ripening. • Selected MANACs were localized to the nucleus.	(Li et al., 2020)
11.	WRKY	Faktor transkripsi WRKY di bagian N-terminal, yang mengandung urutan inti yang sangat konservatif	• RNA sequencing. • Quantitative RT-PCR • GUS transactivation assay • Alignment and phylogenetic tree	• Some MAWRKY responds to abiotic stresses such as low temperature, drought, and salt stress. • MAWRKY is differentially expressed and	(Jia et al., 2022)

WRKYGQK	construction were used to compare WRKY protein sequences.	downregulated during the banana response to Foc TR4 infection • MaWRKY21 directly binds to the MAIC promoter to reduce MAIC transcription.

Discussion

Based on the review results of 11 kinds of literature, it is clear that the role of transcription factors has a significant impact on fruit ripening quality. Transcription factors, which usually consist of DNA binding domains, oligomerization domains, transcription regulation domains, and nuclear localization signals, regulate many critical biological processes by regulating the transcription of target genes underneath them (Li, 2019). Transcription factors play a key role in plant development and ripening by temporally and spatially regulating the transcription of their target genes (Wu et al., 2016).

MYB and MaMYB3 transcription factors are found in various types of bananas (Yang et al., 2021). Commonly found banana species include *Musa acuminata, Musa balbisiana*, and *Musa hybrids* (AAA, AAB, ABB, etc.) (Miao et al., 2020; Tan et al., 2020). The role of MYB is essential in the development, metabolism, and stimulus-response processes. The presence of MYB transcription factors in each variety has a different function. This is because their expression differs depending on genetic and environmental factors (Zhang et al., 2023).

WRKY and MaWRKY transcription factors are found in the Musa acuminata genome and play a role in fruit development, ripening, and stress resistance in this banana variety (Jia et al., 2022). The transcription factors MabHLH and MabHLH7 are abundant in Musa acuminata (Gudimella et al., 2018; Wang et al., 2020). The transcription factors NAC and MaNAC42 are found in Musa acuminata (Li et al., 2020). The transcription factor MaMADS36 is found in red bananas, which can regulate ethylene biosynthesis, softening, and sugar accumulation during fruit ripening (Liu et al., 2021). The following is an example of the banana ripening process.

MaMADS36 not only interacts with other MADS transcription factor boxes, but also interacts with other transcription factors or key genes related to ethylene biosynthesis, starch and sugar metabolism, and cell wall metabolism to regulate fruit ripening. The MaMADS36 domain is located in the G CA(r) box in the MaBAM9b promoter as shown in Figure 3. The G CA(r) box functions to bind transcription factors. The core sequence of CA/T(r) is CTTTTTTTTCCTG at position 608 (-).

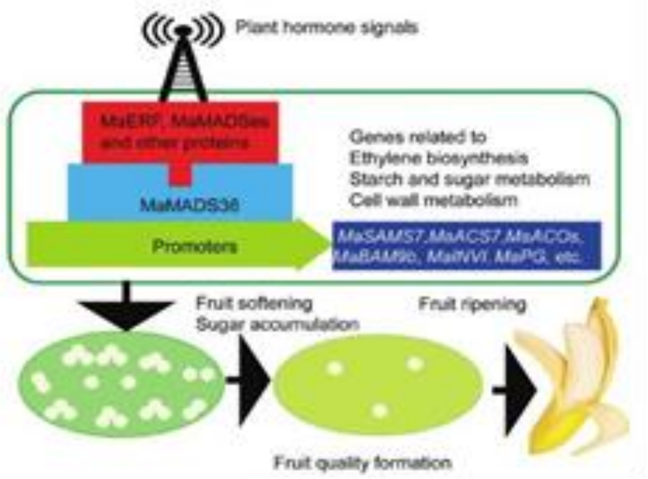

Figure 2. The role of MaMADS36 in regulating banana fruit ripening.

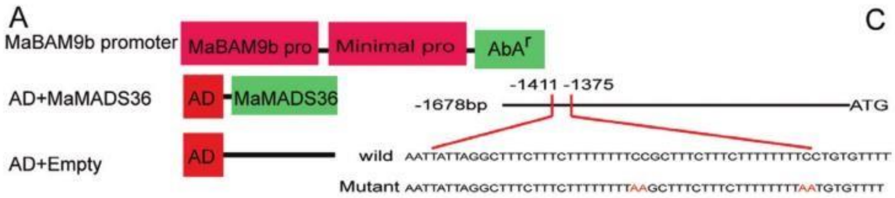

Figure 3. Binding process of MaMADS36 with the MaBAM9b promoter

Transcription factor MabZip21 was found in the genome database of banana (Musa spp.) cv Grand Naine (Shivani et al., 2017). Transcription factor MaERF012 was found in fenjiao banana and is associated with fruit ripening. MaERF012 was also found in Musa ABB Pisang Awak (Hu et al., 2016).

The quality of fruit ripening through transcription factors, especially regarding the influence of hormones on the fruit ripening process, is related to the agricultural sector. A study stated that the hormone ethylene can affect fruit quality by accelerating the storage period and ripening process (Mubarok et al., 2020). Fruit ripening requires transcription factors for its development and regulation (Chen et al., 2020). In addition to playing an essential role in fruit ripening, transcription factors also play a role in influencing color, sugar content, and cell wall breakdown (Sánchez-Gómez et al., 2022).

The regulation of various biological processes, including fruit ripening, is influenced by ethylene, which deciphers its genome sequence. Ethylene is a hormone that plays a central role in fruit ripening, and the expression of genes related to the production and response to ethylene can be regulated by transcription factors. Transcription factors regulating ethylene response can affect the expression of genes controlling the fruit ripening process. The MADS-Box gene family involves transcription factors that have been found to regulate fruit ripening in several plant species. These transcription factors can affect the expression of genes involved in the timing and process of fruit ripening. Several transcription factors from the NAC family have been identified as regulators in fruit ripening. They can affect gene expression in carbohydrate metabolism, color change, and fruit softening. Transcription factors from the MYB (v-my avian myeloblastosis viral oncogene homolog) and bHLH (basic helix-loop-helix) families can also play a role in fruit ripening. They are involved in regulating the biosynthesis of compounds such as fruit pigments.

According to Chen et al. (2020), WRKY TFs have different gene contents in plant species and have characteristics of growth, development, metabolism, and stimulation of environmental signals. WRKY TFs act as regulators of fruit ripening by activating the expression of genes related to fruit softening in bananas. Based on fruit transcriptome data, several WRKY genes are considered regulators during the postharvest ripening stage (Liu et al., 2023).

Environmental factors also affect the fruit ripening process. Ecological factors affecting fruit ripening include respiration rate, ethylene levels, storage temperature, nutrients, sunlight, water and humidity, and temperature. According to Yang et al. (2021), low temperatures affect the ripening and quality of harvested bananas. This is indicated by changes in skin color, ethylene production, and fruit hardness (Yang et al., 2021).

The mechanism of transcription factors in controlling fruit depends on the purpose of the study. However, the mechanism of banana fruit ripening with transcription factors is as follows: 1) RNA isolation and sequencing. Total RNA was extracted from banana samples using the borate heat method. The NanoDrop Spectrophotometer monitored the quality and integrity of total RNA. Then, the Illumina HiSeqTM platform for RNA-Seq analysis. 2) Quantitative RT-PCR analysis (Yang et al., 2021). RT-PCR (Reverse Transcription Polymerase Chain Reaction) analysis is a molecular technique used to detect and measure the relative amount of specific RNA in biological samples (Elfman & Li, 2020). Other methods are adjusted to the materials and research variables used.

Conclusions

The findings of this article review indicate that there are transcription factors, namely MYB, MaWRKY49, MabHLH7, MaNAC42, MaMADS36, bZIP21, MaMYB3, MabHLH, MaERF012, NAC, and WRKY. These transcription factors are present in banana fruit ripening and work specifically based on the research objectives. The role of transcription factors can control fruit quality in agricultural commodities that play genetics in molecular biology. These findings indicate that knowledge of the role of transcription factors can provide insight into the development of innovation in agriculture in the future.

Declaration statement

The authors reported no potential conflict of interest.

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