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Genetic Basis of Tree Size and Fruit Yield in Durian Roles of Auxin and Cytokinin Signaling Pathways

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Abstract Durian (*Durio zibethinus*), widely known as the "King of Fruits", holds significant economic and cultural value across Southeast Asia. The size of its trees and fruit yield are critical agronomic traits, directly affecting cultivation efficiency and commercial viability. Despite their importance, the genetic underpinnings of these traits remain insufficiently understood. This study explores the influence of auxin and cytokinin signaling pathways in shaping durian tree architecture and determining fruit productivity. Auxin primarily regulates apical dominance and cell elongation, influencing overall tree morphology, while cytokinin drives branch differentiation and canopy expansion. During fruit development, auxin plays a crucial role in fruit set and expansion, whereas cytokinin modulates fruit number and size by controlling cell division rates. The balance between these two plant hormones is essential for optimizing durian growth and yield. Advancements in molecular breeding technologies, such as genetic modification and marker-assisted selection, present new opportunities for durian productivity enhancement. Understanding the intricate interactions between auxin and cytokinin at the genetic level will not only deepen our comprehension of durian growth and fruiting but also provide valuable insights for precision breeding and improved orchard management.

Keywords Durian (*Durio zibethinus*); Auxin signaling pathway; Cytokinin regulation; Tree architecture; Fruit yield optimization

1 Introduction

Durian (*Durio zibethinus*), known as the "King of Fruits", is a highly valuable tropical fruit crop cultivated primarily in Southeast Asia. Its economic significance is driven by increasing global demand, yet its cultivation is challenged by long juvenile phases, variable fruit yields, and large tree size, which complicates orchard management. Understanding the genetic basis of tree size and fruit yield in durian is crucial for improving productivity and optimizing breeding strategies. Among the key regulators of plant growth and fruit production, plant hormones- particularly auxin and cytokinin- play fundamental roles in shaping tree architecture and determining fruit yield potential. Recent advances in molecular biology and genomics provide new opportunities to explore the genetic mechanisms underlying auxin and cytokinin signaling in durian, offering insights for targeted breeding and cultivation improvements (Khaksar and Sirikantaramas, 2020).

Tree size and fruit yield are critical agronomic traits that significantly impact durian cultivation and commercial viability. Durian trees are naturally large, with some varieties reaching heights of over 40 meters, making harvesting and maintenance labor-intensive (Immanen et al., 2016). Reducing tree size through genetic or agronomic interventions can enhance orchard efficiency, enabling higher planting densities and improved resource utilization. Additionally, fruit yield varies widely among cultivars and environmental conditions, affecting profitability. Optimizing yield-related traits through genetic improvement can help stabilize fruit production and meet market demands. Therefore, understanding the genetic factors that regulate tree growth and fruit set is essential for enhancing durian cultivation efficiency (Iqbal et al., 2021).

Plant hormones are key regulators of growth and development, orchestrating various physiological processes that shape tree morphology and fruit characteristics. Among them, auxin and cytokinin are central to the regulation of vegetative growth and reproductive development. Auxin influences apical dominance, root formation, and fruit initiation, while cytokinin controls cell division, shoot branching, and sink-source dynamics (Khaksar et al., 2019).

The interplay between these hormones determines the overall architecture of the durian tree, affecting branching patterns, canopy density, and ultimately fruit-bearing capacity. In fruit development, auxin promotes ovary expansion and fruit set, while cytokinin plays a role in nutrient allocation and fruit size determination. A deeper understanding of auxin and cytokinin interactions will provide new insights into improving tree growth regulation and optimizing fruit yield in durian (Suntichaikamolkul et al., 2021).

Despite the recognized importance of auxin and cytokinin in plant growth, their specific regulatory mechanisms in durian remain largely unexplored. This research aims to investigate the genetic basis of tree size and fruit yield by focusing on auxin and cytokinin signaling pathways. By identifying key genes involved in hormonal regulation, we can develop strategies to modulate tree architecture and improve yield efficiency. Recent advances in durian genomics, transcriptomics, and functional studies provide an opportunity to dissect the molecular interactions between auxin and cytokinin, leading to potential applications in precision breeding. This research will contribute to a better understanding of durian's growth dynamics and offer new approaches to optimizing its cultivation through genetic and hormonal interventions.

2 Genetic Regulation of Tree Size in Durian

2.1 Key genes involved in tree height and canopy development

The genetic factors controlling durian tree size are linked to several key genes that influence height and canopy growth. While specific genes directly affecting tree height in durian remain under investigation, transcription factors such as Dof proteins, known for their role in various plant growth processes, present promising candidates. These proteins regulate auxin biosynthesis, which is essential for plant development and plays a key role in determining tree size (He et al., 2018).

2.2 Influence of auxin signaling pathway on tree morphology

Auxin is a crucial plant hormone that significantly affects tree morphology, including height and canopy structure. In durian, auxin signaling is mediated by auxin response factors (ARFs), such as DzARF2A, which have been identified for their role in fruit ripening via ethylene biosynthesis regulation (Liu et al., 2018a). Although auxin's direct effects on durian tree morphology remain unclear, its well-documented influence on plant growth suggests it plays an important role in shaping tree structure (Liu et al., 2018b).

2.3 Role of cytokinin in shoot differentiation and growth

Cytokinin is another essential phytohormone that regulates shoot differentiation and overall tree growth. While specific data on cytokinin's role in durian tree development is limited, its well-established function in promoting cell division and shoot formation in other plants highlights its significance in determining tree architecture (He and Yamamuro, 2022). The dynamic interaction between cytokinin and auxin is critical for balancing root and shoot growth, ultimately influencing tree size and productivity.

2.4 Interaction between auxin and cytokinin in tree development

The interplay between auxin and cytokinin is a fundamental aspect of plant development, affecting multiple growth processes. In durian, auxin-ethylene crosstalk, regulated by DzARF2A, demonstrates the complex hormonal interactions that drive growth and structural changes. Although specific auxin-cytokinin interactions in durian tree development remain underexplored, their well-established synergistic and antagonistic relationships in other plant species suggest that similar regulatory mechanisms may influence durian tree morphology (Reyes-Olalde et al., 2017). Understanding these interactions will provide valuable insights for optimizing durian tree architecture and improving orchard management strategies.

3 Genetic Control of Fruit Yield in Durian

3.1 Genetic regulatory mechanisms affecting flowering and fruiting

The regulation of flowering and fruiting in durian is influenced by complex interactions between plant hormones and transcription factors. Auxin response factors (ARFs) play a critical role in fruit development and ripening by acting as key regulators in hormone-dependent pathways, impacting fruit size, yield, and quality. Additionally, MADS-box transcription factors are involved in modulating cytokinin levels, which are essential for fruit growth

and development. These genetic regulators collectively influence flowering timing and fruit production, ultimately shaping yield outcomes (Zhao et al., 2023). The weight of a durian fruit is determined by multiple components, including pulp, peel, and seed (Figure 1) (Khaksar et al., 2024).

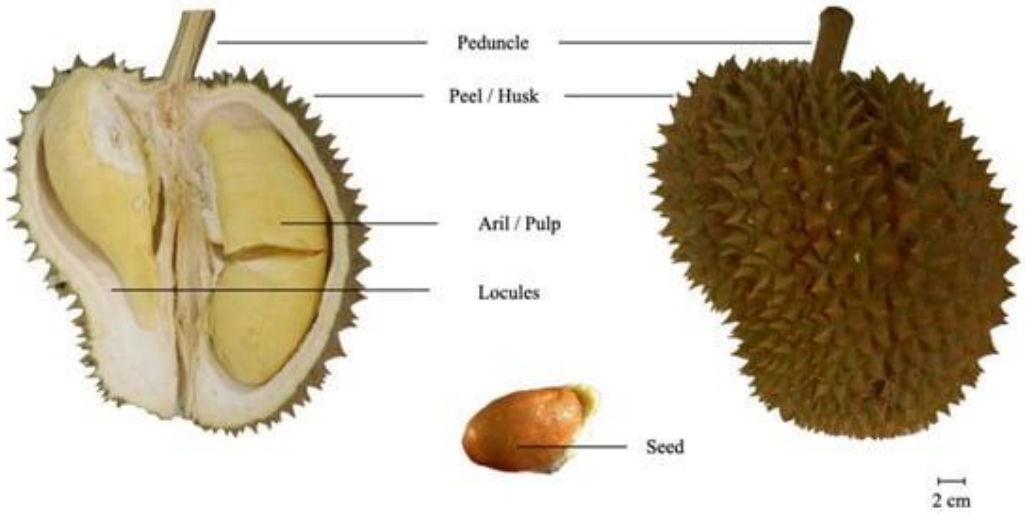

Figure 1 Images of durian (*Durio zibethinus* L.) fruit: peduncle, peel (husk), aril (pulp), locules, and seed (Adopted from Khaksar et al., 2024)

3.2 Role of auxin in fruit set and expansion

Auxin is a primary hormone governing fruit set and expansion. It promotes both cell division and enlargement, which are vital processes in early fruit development. In durian, auxin levels rise during post-harvest ripening, indicating its role in enhancing fruit size and quality through ethylene biosynthesis regulation. Auxin also interacts with gibberellic acid (GA) to further support fruit enlargement by coordinating cell growth and expansion. Its impact on fruit size has been observed in various plant species, where it influences endoreduplication-related cell expansion, leading to larger fruit (Su et al., 2014).

3.3 Influence of cytokinin on fruit number and size

Cytokinin also plays a key role in determining fruit number and size. It regulates cell division and expansion, both of which contribute to overall fruit growth (Li et al., 2024). However, cytokinin levels must be carefully balanced, as excessive amounts can negatively impact cell expansion and hinder fruit development. In durian, cytokinin signaling likely interacts with other hormonal pathways to influence fruit yield, similar to other species where cytokinin oxidase/dehydrogenase (*CKX*) genes regulate fruit size (Di Marzo et al., 2020).

3.4 Potential genetic markers for high-yield durian varieties

Identifying genetic markers associated with high-yield durian varieties can enhance breeding programs. Auxin response factors, such as DzARF2A, have been identified as potential markers due to their role in regulating ethylene biosynthesis and fruit ripening. Additionally, genes involved in cytokinin degradation, such as CKX, may serve as useful markers for selecting varieties with optimal fruit size and yield. Incorporating these genetic markers into breeding strategies could lead to the development of durian varieties with improved fruit yield and quality (Zhao et al., 2021).

4 Synergistic Role of Auxin and Cytokinin in Durian Growth and Yield

4.1 Hormonal balance in tree growth regulation

Maintaining a balance between auxin and cytokinin is essential for durian tree growth. Auxin promotes cell elongation and division, while cytokinin regulates cell differentiation and organ formation. Their interaction helps coordinate tree growth, with auxin driving shoot and root elongation and cytokinin stimulating new shoot formation (Sharif et al., 2022). A well-maintained hormonal balance supports tree structure and health, ultimately influencing fruit production (Teh et al., 2017).

4.2 Synergistic and antagonistic effects during fruit development

Auxin and cytokinin interact in both cooperative and opposing ways during fruit development. Auxin plays a central role in the early stages, driving cell division and expansion, which are critical for fruit set and growth (Huang and Hong, 2024). Cytokinin becomes more influential in later stages, affecting nutrient distribution and fruit maturation. The relationship between these hormones is complex- auxin enhances ethylene biosynthesis, which accelerates ripening, as seen in the fast-ripening durian cultivar Chanee (Figure 2) (Hurny et al., 2020; Suntichaikamolkul et al., 2021). While auxin speeds up ripening, cytokinin is more involved in maintaining fruit quality and size.

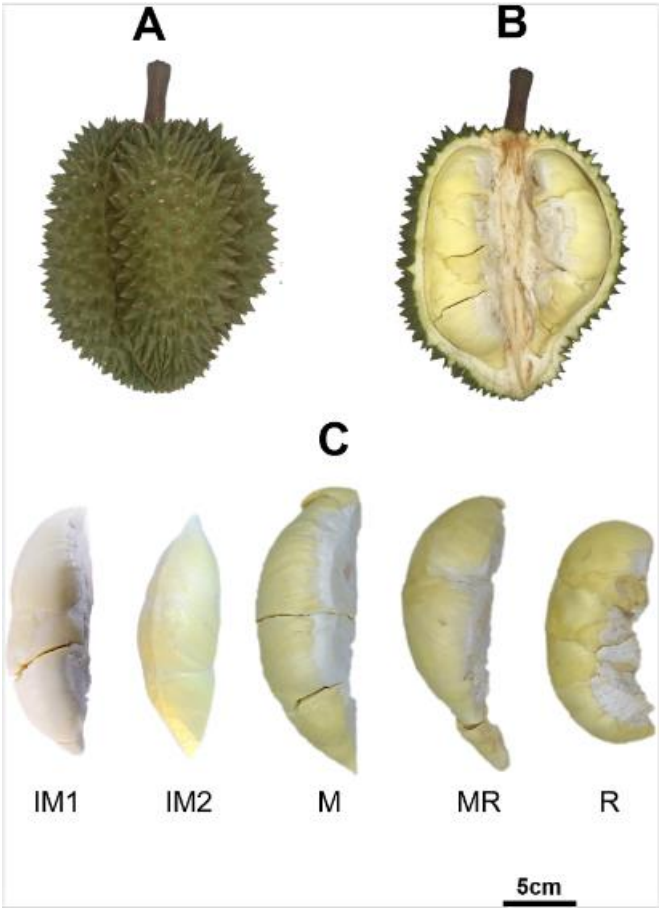

Figure 2 Fruit morphology during fruit development (Adopted from Suntichaikamolkul et al., 2021)

Image caption: (A) whole fruit. (B) peeled fruit. (C) Arils across five developmental and ripening stages. Stage abbreviations: IM1, immature 1; IM2, immature 2; M, mature; MR, mid-ripe; R, ripe (Adopted from Suntichaikamolkul et al., 2021)

4.3 Environmental and genotypic effects on hormonal regulation

Both environmental factors and genetic variations play a role in the hormonal regulation of durian growth and yield. Different durian cultivars display variations in auxin and cytokinin levels, influencing their growth and fruiting patterns (Fenn and Giovannoni, 2020). For instance, the Chanee cultivar has higher auxin levels during ripening compared to Monthong, contributing to its faster ripening process. Environmental elements such as temperature, sunlight, and soil conditions also impact hormone activity, ultimately affecting tree growth and fruit yield. Understanding these genetic and environmental influences is crucial for refining durian cultivation practices and boosting production efficiency (Cao et al., 2020).

5 Applications in Durian Breeding and Agricultural Production

5.1 Genetic improvement strategies for optimizing tree structure and yield

Understanding the roles of auxin and cytokinin in durian growth offers opportunities to enhance breeding strategies. Identifying key auxin response factors (ARFs), such as DzARF2A, which regulate ethylene biosynthesis, allows for targeted genetic modifications to improve fruit ripening and overall yield (Khaksar et al.,

2024). Selecting cultivars with elevated DzARF2A expression could lead to varieties that ripen more quickly and produce higher yields, as observed in the fast-ripening Chanee compared to the slower-ripening Monthong. Additionally, the differential expression of Dof transcription factors (DzDofs) during fruit development suggests potential targets for enhancing auxin biosynthesis and fruit yield (Nawae et al., 2023).

5.2 Application of hormonal regulation techniques in yield enhancement

Modulating key phytohormones, including auxin and ethylene, provides another approach to increasing durian yields. The upregulation of DzARF2A and its role in activating ethylene biosynthesis genes highlight the potential of applying exogenous auxin to accelerate fruit ripening and enhance production (Husin et al., 2018). This technique could be particularly effective in fast-ripening cultivars like Chanee, where higher auxin levels correlate with increased DzARF2A expression. Similarly, enhancing DzDof2.2 expression, which is associated with auxin biosynthesis, may further boost auxin levels and initiate the ethylene response earlier, potentially improving fruit yield and consistency (Santoso et al., 2017).

5.3 Future prospects for molecular breeding in durian

The integration of genomic and transcriptomic data is paving the way for advanced molecular breeding in durian. The identification of regulatory genes such as *DzARF2A* and *DzDof2.2*, both of which play essential roles in auxin and ethylene signaling, provides opportunities for developing improved durian cultivars with enhanced fruit quality and yield (Huang, 2024). With advancements in gene-editing tools like CRISPR/Cas9, targeted modifications to these genes could lead to varieties with optimized ripening characteristics and greater resistance to environmental stress. As research continues to uncover the genetic foundations of tree size and fruit yield, breeders will be better equipped to cultivate high-yielding, resilient durian varieties suited to both producer needs and consumer preferences (Huy et al., 2023).

6 Future Research Directions

6.1 Further elucidation of auxin and cytokinin regulatory networks in durian

Auxin and cytokinin play essential roles in durian tree development and fruit ripening, but their precise regulatory mechanisms remain insufficiently understood. Research has linked auxin response factors (ARFs), particularly DzARF2A, to ethylene biosynthesis, which accelerates ripening in some cultivars. Future studies should focus on mapping the complete auxin and cytokinin signaling pathways and their interactions, which could reveal new targets for genetic improvement aimed at optimizing fruit yield and quality (Lin, 2020).

6.2 Advances in durian genomics and precision breeding technologies

The identification of key transcription factors, such as DzDofs, associated with auxin biosynthesis and cultivar-specific ripening characteristics, underscores the potential of genomic research in durian breeding. With developments in genomic tools like CRISPR/Cas9, researchers have the opportunity to create improved durian varieties with enhanced traits (Cheng et al., 2021). Future efforts should focus on integrating genomic data with phenotypic traits to refine breeding strategies, ultimately leading to cultivars with higher yields and improved fruit quality (Tang et al., 2024).

6.3 Strategies for enhancing durian yield and quality by hormonal balance regulation

Achieving a balance between auxin and cytokinin is crucial for maximizing durian fruit yield and quality. Auxin-ethylene crosstalk, as demonstrated by the role of DzARF2A in ethylene biosynthesis regulation, offers a framework for adjusting hormonal pathways to control ripening and enhance fruit development (Desta and Amare, 2021). Future research should explore genetic and agronomic techniques to fine-tune hormonal levels, aiming for an optimal balance that improves yield consistency while preserving fruit quality (Ngoc et al., 2024).

7 Concluding Remarks

The genetic factors influencing durian tree size and fruit yield are closely tied to hormonal signaling pathways, particularly those involving auxin and cytokinin. Auxin plays a fundamental role in fruit ripening, as indicated by the identification of auxin response factors (ARFs) that regulate ethylene biosynthesis, a key hormone in the ripening of climacteric fruits. Specifically, DzARF2A has been found to upregulate ethylene biosynthetic genes,

leading to a faster ripening process in cultivars such as Chanee compared to the slower-ripening Monthong. Additionally, the involvement of Dof transcription factors, particularly DzDof2.2, in auxin biosynthesis further supports the link between auxin and ethylene in fruit ripening.

Despite recent progress in understanding the hormonal regulation of fruit ripening in durian, there are still several knowledge gaps. The exact mechanisms through which auxin and cytokinin interact to regulate tree size and fruit yield remain unclear. Additionally, the variation in hormone responses among different cultivars suggests a more complex genetic basis that requires further exploration. The interplay of other phytohormones with auxin and cytokinin in shaping these traits also warrants more investigation. Furthermore, environmental factors influencing hormonal pathways in durian need to be studied in greater detail to optimize fruit production and quality.

Gaining deeper insights into the hormonal regulation of durian growth and fruiting presents significant opportunities for improving cultivation practices and breeding strategies. By targeting genes such as *DzARF2A* and *DzDof2.2*, it may be possible to enhance fruit yield and accelerate ripening in commercial durian varieties. This could contribute to the development of new cultivars with traits like faster ripening and larger fruit size, aligning with market demands. Moreover, understanding hormonal interactions could guide breeding programs aimed at enhancing stress resilience and refining growth conditions for durian trees, ultimately supporting more efficient and sustainable production.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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