Mesopotamia Journal of Agriculture

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LEAF BIOCHEMICAL TRAITS IN LOCAL DUKU (Lansium domesticum Corr.) TREES UNDER ROOT-ASSOCIATED DECLINE

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Article information
Article history:
Received: 12/2/2026
Accepted: 22 /6/2026
Available: 30/6/2026

Keywords:
Flavonoids, oxidative indicator, phenylpropanoids, tannins.

DOI:
https://doi.org/10.33899/magrj.v54i2.61449

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ABSTRACT

Root-associated decline, suspected to involve *Phytophthora* species, is considered one of the major constraints to duku (*Lansium domesticum* Corr.) production in Indonesia. Although the disease primarily affects roots and basal stem tissues, prolonged stress may also influence physiological processes in leaves. This study examined whether several leaf biochemical parameters associated with antioxidant and phenylpropanoid metabolism could differentiate healthy and diseased duku trees under orchard conditions. Guaiacol-reactive POD-like oxidative activity, total flavonoid content, and tannin levels were analyzed in leaf samples collected from healthy and diseased trees using spectrophotometric methods. Statistical analyses showed no significant differences between the two health categories for all measured parameters ($p > 0.05$). Health categories were defined based on field-observed root-associated decline symptoms, and pathogen identity was not directly confirmed in the present study. Considerable overlap among individual samples was also observed. The POD-related measurement should be interpreted as an exploratory guaiacol-reactive oxidative indicator rather than as a direct estimate of native POD enzyme activity. The results suggest that leaf biochemical responses remained relatively stable despite prolonged root-associated stress. Under field conditions, these parameters were not sufficiently sensitive to distinguish between healthy and diseased trees when measured at a single sampling period. The findings suggest phenylpropanoid-related compounds in duku leaves mainly reflect long-term physiological adjustment rather than short-term inducible defense responses. Consequently, single-time-point biochemical measurements in leaves have limited value for diagnosing prolonged root-associated decline in perennial fruit trees.

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INTRODUCTION

Duku (*Lansium domesticum* Corr.) is an important tropical fruit tree cultivated in many parts of Southeast Asia. In Indonesia, orchard productivity is often reduced by a prolonged decline disorder that gradually weakens tree vigor and reduces long-term orchard performance (Figure 1). Typical symptoms observed in affected trees include canopy thinning, branch dieback, and lesions around the base of the trunk. In many orchards, these visible symptoms are commonly used by growers to assess tree condition, although their physiological basis is not always clearly understood.

In Jambi Province, Indonesia, symptoms of decline in duku orchards have previously been associated with root and basal stem disorders suspected to involve *Phytophthora* species. In addition, Phytophthora palmivora has been reported as a pathogen associated with stem canker and root-associated disease in duku-growing areas of Jambi Province (Hayati et al., 2019a, 2019b). Earlier local observations have also linked decline symptoms with Phytophthora-like disorders. Similar Phytophthora-associated decline disorders have been reported in several perennial crops and woody plant species, where root impairment usually develops slowly and leads to long-term physiological stress rather than rapid tissue collapse (Jung et al., 2016; Hardham & Blackman, 2018). Chronic root dysfunction can alter water and nutrient acquisition and trigger systemic signalling pathways that influence physiological and biochemical processes in aboveground tissues (Hilleary & Gilroy, 2018; Reverchon & Méndez-Bravo, 2021). However, pathogen isolation or molecular confirmation was not conducted in the present study; the disease condition is referred to here as field-observed root-associated decline.

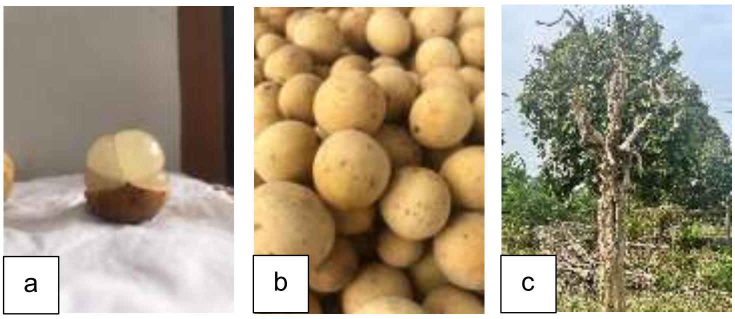

Figure (1). Field observations and fruit characteristics of local duku (*Lansium domesticum* Corr.) collected from the same orchard environment. (a) Duku fruit revealing translucent, segmented aril tissues enclosed by the peel, representing the edible portion. (b) External fruit morphology of mature duku is characterized by a pale yellow to light brown peel with naturally occurring surface markings. (c) Healthy and diseased trees growing under comparable site conditions, illustrating contrasting canopy status. Diseased trees show evident branch dieback and reduced canopy density, whereas healthy trees retain structurally intact branches and foliage.

Root infections can interfere with water uptake, nutrient transport, and overall plant metabolism. As the stress progresses, physiological responses may extend beyond the infected tissues and influence aerial organs such as leaves. Systemic communication between roots and shoots involves hydraulic, hormonal, and redox-related pathways that coordinate whole-plant responses to stress (Passardi *et al.*, 2005; Waszczak *et al.*, 2018; Farmer *et al.*, 2020; Reverchon & Méndez-Bravo, 2021). However, in perennial trees, leaf biochemical responses may not directly reflect the intensity of root or basal stem damage because long-term physiological adjustment can buffer biochemical fluctuations in distal tissues (Herms & Mattson, 1992; Walters, 2011; Hardham & Blackman, 2018; Hilleary & Gilroy, 2018; Mittler et al., 2022; Sood, 2025).

Plant defense responses are closely associated with reactive oxygen species (ROS) metabolism and the activation of antioxidant systems. Peroxidases (PODs) are important enzymes involved in ROS detoxification, lignin formation, and cell wall strengthening (Passardi *et al.*, 2005; Mittler *et al.*, 2022). In addition, phenylpropanoid-derived compounds such as flavonoids and tannins contribute to antioxidant protection, antimicrobial activity, and structural defense functions (Treutter, 2005; Agati *et al.*, 2012; Sharma *et al.*, 2019; Ortiz & Sansinenea, 2023).

Recent reviews have further emphasized the central role of phenylpropanoid metabolism in plant development, stress adaptation, antimicrobial defense, and lignification-related structural protection (Li *et al.*, 2024; Singh, 2025).

In long-lived perennial species, many defense-related compounds are maintained at relatively stable levels as part of constitutive protection mechanisms (Herms & Mattson, 1992; Walters, 2011). During prolonged stress exposure, biochemical traits in leaves may therefore reflect long-term physiological adjustment rather than rapid inducible defense responses. As a result, differences between healthy and diseased plants can become difficult to detect, particularly under variable field conditions.

Understanding these physiological patterns is important for improving disease assessment in perennial fruit crops. If leaf biochemical traits are weakly associated with disease status, their use as field diagnostic indicators may be limited. Therefore, this study evaluated guaiacol-reactive POD-like oxidative activity, total flavonoid content, and tannin levels in leaves of healthy and diseased duku trees growing under orchard conditions. The study also aimed to examine the relevance of these biochemical traits as indicators of prolonged root-associated decline.

MATERIALS AND METHODS

Plant material and experimental design

All laboratory procedures, including extraction and biochemical analyses, were carried out at the Integrated Laboratory Academic Support Unit of Jambi University and the Analytical Laboratory, Faculty of Animal Science, Jambi University.

Leaf samples were collected from healthy (SH) and diseased (SK) duku trees growing under comparable orchard conditions. Diseased trees were identified based on consistent field-observed symptoms associated with root-associated decline, including basal stem canker, canopy thinning, and progressive shoot dieback. Healthy trees showed no visible basal stem lesions, severe canopy thinning, or progressive shoot dieback at the time of sampling. In this study, tree condition was treated as a categorical health status variable (healthy versus diseased), rather than as a quantitative disease severity gradient. A formal Disease Severity Index was not recorded during field sampling.

Five healthy and five diseased trees were used as biological replicates. For each tree, mature leaves were pooled into a single composite sample. Guaiacol-reactive POD-like oxidative activity was measured in technical triplicate, and the resulting values were averaged before statistical analysis. After leaf collection, leaves were washed with distilled water, dried in a forced-air oven at 40–45 °C until they achieved constant weight. The dried material was ground into powder and stored in airtight containers before analysis.

Sample extraction

Phenolic compounds were extracted following a solvent extraction procedure. Approximately 0.5 g of powdered leaf material was mixed with 70% ethanol at a 1:10 (w/v) ratio. The mixture was shaken at room temperature for 24 h to facilitate extraction. After filtration, the solvent was removed under reduced pressure at temperatures below 40 °C to avoid thermal degradation. The concentrated extracts were stored at 4 °C before analysis.

Guaiacol-reactive POD-like oxidative activity

A guaiacol-based oxidation assay was conducted as an exploratory POD-related measurement using the available processed leaf material. Because the extraction and sample-processing conditions were not optimized for preservation of native enzyme activity, this measurement was interpreted cautiously as guaiacol-reactive POD-like oxidative activity rather than as a definitive estimate of native peroxidase enzyme activity. Absorbance changes were recorded at 470 nm for up to three minutes using a microplate spectrophotometer. Technical readings were averaged for each tree before statistical analysis, and the tree was retained as the biological replication unit.

Determination of flavonoid and tannin contents

Total flavonoid content was determined using an aluminum chloride colorimetric assay with quercetin as the standard, following previously reported $AlCl_3$-based colorimetric methods with slight modification (Chang *et al.*, 2002; Shraim *et al.*, 2021). Absorbance was recorded at 370 nm and corrected using a reference measurement at 435 nm according to the analytical laboratory protocol. The wavelength selection followed the laboratory protocol used for this analysis and was considered a modified measurement condition of the aluminum chloride-based colorimetric assay. Flavonoid concentration was calculated from a quercetin standard curve and expressed as mg quercetin equivalents (QE) g^{-1} dry weight.

Total tannin content was determined using a ferric chloride iron-complexation colorimetric assay, following tannin quantification procedures for tree and shrub foliage with slight modification (Makkar, 2003). Briefly, 0.5 mL of leaf extract was mixed with 1 mL of 1% $FeCl_3$ solution and incubated for 15 min at room temperature. Absorbance was recorded at 510 nm, with a reference reading at 770 nm for background correction. Tannin concentration was calculated from a tannic acid standard curve and expressed as mg tannic acid equivalents (TAE) g^{-1} dry weight.

Data handling and statistical analysis

For all biochemical parameters, each tree was considered the biological replication unit ($n = 5$ trees per health category). For guaiacol-reactive POD-like analysis, each leaf extract was measured in triplicate, and technical replicate values were averaged before statistical analysis. Flavonoid and tannin contents were likewise calculated at the tree level and analyzed using five biological replicates per group.

Data are presented as mean ± standard deviation (SD). Because of the limited sample size, both parametric and non-parametric approaches were considered during exploratory analysis. Differences between healthy and diseased trees were evaluated using Welch's t-test, which does not assume equal variances between groups. For completeness, Mann–Whitney U tests were also performed as a sensitivity analysis and yielded similar conclusions. Statistical significance was accepted at $p < 0.05$.

To assess analytical precision, approximately 10% of samples were reanalyzed in duplicate. Standard reference solutions were included in each analytical batch.

Duplicate measurements showed close agreement with the original values, indicating acceptable analytical precision

RESULTS AND DISCUSSION

Guaiacol-reactive POD-like oxidative activity

Guaiacol-reactive POD-like oxidative activity averaged 0.327 ± 0.122 ΔA_{470} min^{-1} in healthy trees and 0.361 ± 0.123 ΔA_{470} min^{-1} in diseased trees. The difference between groups was not statistically significant based on Welch's t-test, t(8.00) = -.439, p = 0.672, with a small effect size (Hedges' g = -0.251). The 95% confidence interval for the mean difference ranged from -0.213 to 0.145. Several diseased samples showed relatively higher values, although substantial overlap between groups remained evident (Figure 2).

Because this measurement was not based on a cold, non-denaturing aqueous enzyme extraction optimized to preserve native peroxidase activity, the result was interpreted with caution as an exploratory guaiacol-reactive oxidative indicator rather than as a definitive estimate of native POD activity.

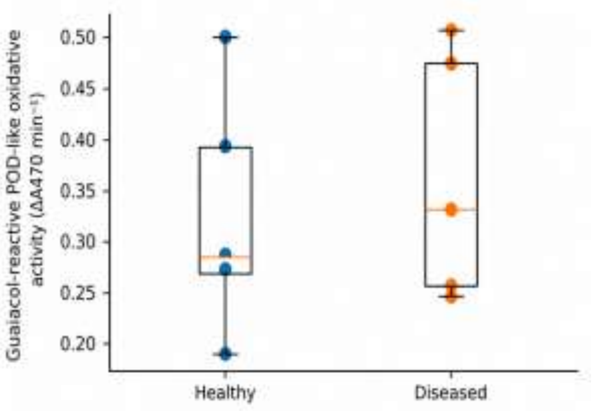

Figure (2). Guaiacol-reactive POD-like oxidative activity in leaves of healthy and diseased duku (Lansium domesticum Corr.) trees affected by root-associated decline. Values are expressed as ΔA_{470} min^{-1}. Boxes represent the interquartile range with median values indicated by horizontal lines, while individual points represent tree-level biological replicates (n = 5 trees per group). Technical readings were averaged for each tree before statistical analysis. No significant difference was detected between healthy and diseased trees (Welch's t-test, t(8.00) = -0.439, p = 0.672).

Total flavonoid content

Total flavonoid content averaged 8.560 ± 5.617 mg QE g^{-1} dry weight in healthy trees and 9.778 ± 5.126 mg QE g^{-1} dry weight in diseased trees. The difference was not significant based on Welch's t-test, t(7.93) = -0.358, p = 0.730, with a small effect size (Hedges' g = -0.205). The 95% confidence interval for the mean difference ranged from -9.071 to 6.635. A Mann–Whitney sensitivity analysis gave a similar result (U = 13.0, p = 1.000) (Figure 3).

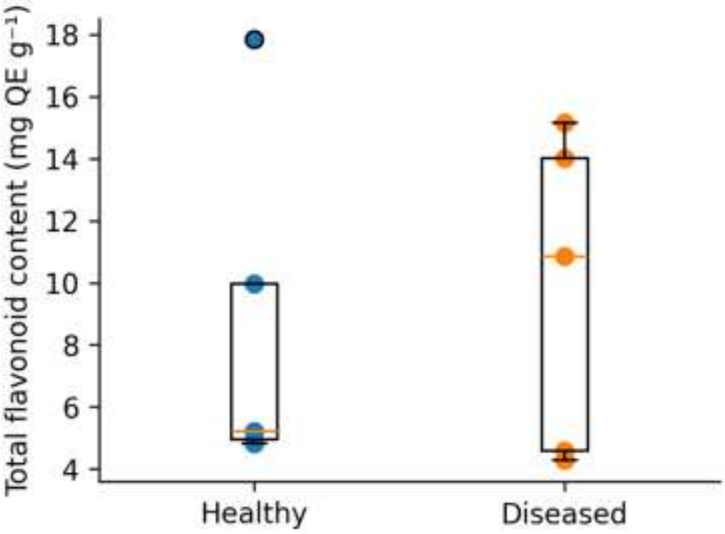

Figure (3). Total flavonoid content in leaves of healthy and diseased duku (*Lansium domesticum* Corr.) trees affected by root-associated decline. Values are expressed as mg quercetin equivalents (QE) g^{-1} dry weight. Boxes represent the interquartile range with median values indicated by horizontal lines, while individual points represent tree-level biological replicates (n = 5 trees per group). No significant difference was detected between healthy and diseased trees (Welch's t-test, t(7.93) = -0.358, p = 0.730).

Total tannin content

Total tannin content averaged 549.078 ± 77.689 mg TAE g^{-1} dry weight in healthy trees and 453.711 ± 130.601 mg TAE g^{-1} dry weight in diseased trees. Although the mean value was higher in healthy trees, the difference was not significant based on Welch's t-test, t(6.72) = 1.404, p = 0.205, with a moderate effect size (Hedges' g = 0.803). The 95% confidence interval for the mean difference ranged from -65.792 to 256.526. A Mann–Whitney sensitivity analysis gave a similar result (U = 18.0, p = 0.222) (Figure 4).

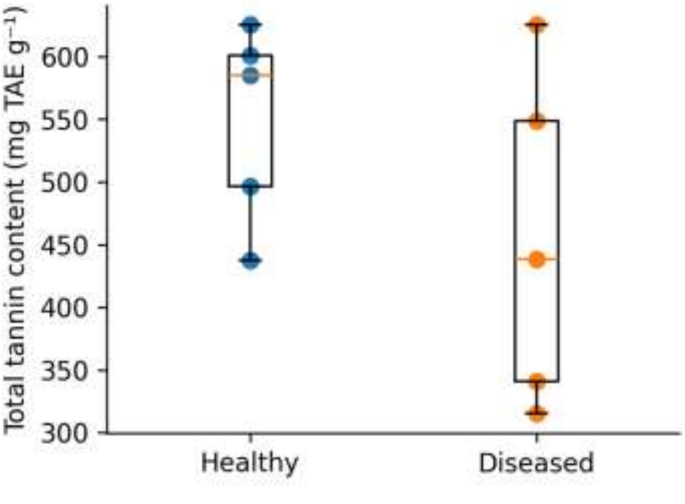

Figure (4). Total tannin content in leaves of healthy and diseased duku (Lansium domesticum Corr.) trees affected by root-associated decline. Values are expressed as mg tannic acid equivalents (TAE) g^{-1} dry weight. Boxes represent the interquartile range with median values indicated by horizontal lines, while individual points represent tree-level biological replicates (n = 5 trees per group). No significant difference was detected between healthy and diseased trees (Welch's t-test, t(6.72) = 1.404, p = 0.205).

Guaiacol-reactive POD-like oxidative activity

Guaiacol-reactive POD-like oxidative activity did not differ significantly between healthy and diseased duku trees. Although several diseased samples showed relatively higher values, the broad overlap between health categories indicates that this parameter had limited ability to distinguish field-defined tree health status under orchard conditions. This pattern supports the overall interpretation that leaf-level oxidative and phenylpropanoid-related traits may remain relatively stable during prolonged root-associated stress.

Peroxidases are involved in oxidative balance, lignification, and cell wall-related defense processes in plants (Passardi et al., 2005). However, in the present study, the POD-related measurement should not be interpreted as a definitive estimate of native peroxidase enzyme activity because the assay was not based on a cold, non-denaturing aqueous extraction procedure specifically optimized for enzyme preservation. Therefore, the measured response is described as guaiacol-reactive POD-like oxidative activity and is treated only as an exploratory oxidative indicator. Reactive oxygen species (ROS) are central components of plant stress signalling and redox regulation, integrating stress perception, acclimation, and defense-related responses across plant tissues (Passardi *et al.,* 2005; Waszczak et al., 2018; Mittler *et al*., 2022; Fedoreyeva *et al*., 2024; Sood, 2025). Under prolonged root-associated stress, systemic redox regulation may contribute to physiological stabilization in leaves, thereby reducing the likelihood of detecting clear differences between healthy and diseased trees at a single sampling time. Accordingly, stronger emphasis is placed on total flavonoid and tannin contents, which are more directly compatible with ethanolic extraction of phenylpropanoid-related compounds.

Total flavonoid content

Flavonoids play multiple roles in plant defense, including antioxidant protection, redox regulation, and antimicrobial activity (Agati *et al*., 2012; Sharma *et al.*, 2019). However, in perennial species, flavonoid accumulation is often maintained constitutively as part of long-term protection strategies. The broad overlap observed between healthy and diseased trees suggests that flavonoid metabolism in duku leaves was not strongly altered by prolonged root-associated decline. Similar conditions have been described in other woody plants, where long-term stress tends to promote metabolic stabilization rather than sharp increases in secondary metabolites (Eyles et al., 2010; Franceschi et al., 2005).

Environmental conditions, developmental stage, and long-term physiological adaptation may also influence flavonoid levels, making disease-related differences difficult to distinguish under field conditions (Lavola & Julkunen-Tiitto, 1994; Singh *et al*., 2023).

Overall, the findings indicate that flavonoid content in duku leaves is more closely associated with constitutive biochemical protection than with rapid inducible responses to root infection.

Total tannin content

Tannins are widely recognized as defensive phenolic compounds in woody plants. They contribute to antimicrobial activity and herbivore deterrence and are often associated with constitutive defense systems maintained over long periods (Herms & Mattson, 1992; Walters, 2011).

Although healthy trees tended to show slightly higher tannin levels, the difference was not statistically significant. This pattern suggests that tannin accumulation in leaves remained relatively stable regardless of disease status. Previous studies in perennial trees have shown that tannin production is often regulated over extended physiological timescales rather than through rapid localized induction (Franceschi et al., 2005; Bonello & Blodgett, 2003). During prolonged stress conditions, defense responses may become spatially compartmentalized, with stronger biochemical changes occurring in roots or basal stem tissues rather than in leaves. Consequently, tannin levels in leaves may reflect long-term physiological balance more than the immediate intensity of disease symptoms.

Integrated interpretation

Overall, the measured biochemical traits showed limited ability to differentiate healthy and diseased duku trees under orchard conditions. Guaiacol-reactive POD-like oxidative activity, total flavonoid content, and tannin levels all exhibited broad overlap between the two health categories. However, because the POD-related measurement was interpreted only as an exploratory oxidative indicator, the main biochemical interpretation of this study is based primarily on phenylpropanoid-related compounds, particularly flavonoids and tannins.

The results suggest that defense-related biochemical traits in perennial fruit trees may remain relatively stable during prolonged stress exposure, rather than showing strong inducible changes at a single sampling time. Long-lived species commonly maintain relatively stable antioxidant and phenylpropanoid-related defenses under continuous environmental and biotic stress. During long-term root-associated stress, localized responses may remain confined to roots and basal stem tissues, whereas leaf biochemical profiles mainly reflect systemic responses.

In perennial plants, recent studies have highlighted that reactive oxygen species (ROS)-driven systemic signalling integrates stress perception, acclimation, and redox regulation across different plant organs, thereby contributing to the stabilization of physiological responses in distal tissues (Myers et al., 2024). In the present study, the exploratory POD-like oxidative measurement and phenylpropanoid-related traits were not sufficiently sensitive to indicate disease status at a single sampling time. Future studies involving fresh or frozen tissues, cold non-denaturing enzyme extraction, repeated sampling, and direct analysis of root tissues may provide a clearer understanding of the relationship between oxidative responses, phenylpropanoid metabolism, and disease progression.

From an applied perspective, these findings indicate that leaf-level antioxidant and phenylpropanoid traits should be interpreted with caution when used as diagnostic indicators for prolonged root-associated decline in perennial fruit trees. Under orchard conditions, systemic physiological balance may mask disease-related variation at the leaf level, emphasizing the need for integrated temporal and tissue-specific assessment strategies.

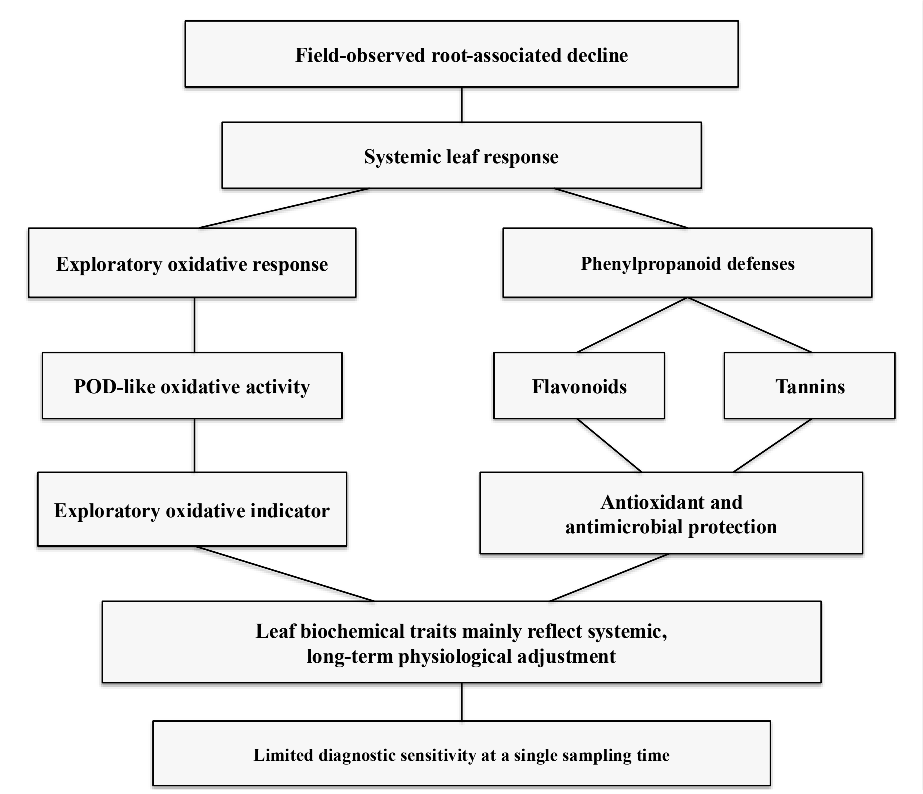

Figure (5). Conceptual model of integrated leaf biochemical responses in duku (*Lansium domesticum* Corr.) under root-associated decline. Root-associated decline may be associated with systemic leaf responses involving an exploratory oxidative branch and phenylpropanoid defenses. The POD-related branch is interpreted as exploratory guaiacol-reactive POD-like oxidative activity, whereas flavonoids and tannins represent phenylpropanoid-related compounds associated with antioxidant and antimicrobial protection. Overall, the measured leaf biochemical traits mainly reflect long-term systemic physiological adjustment and therefore show limited diagnostic sensitivity at a single sampling time.

The absence of significant biochemical differentiation between healthy and diseased trees may also reflect temporal variability in defense metabolism. Defense reactions occurring in affected root tissues may not be fully represented in the measured leaf biochemical traits. The interpretation presented here should be considered within the context of field-observed root-associated decline symptoms, as pathogen identity was not directly confirmed in the present study.

Because a formal Disease Severity Index and direct pathogen confirmation were not included in the present study, the results should be interpreted as a comparison between field-defined health categories rather than as a quantitative assessment of disease progression. Future studies should combine biochemical analyses with pathogen confirmation and severity scoring to better evaluate the relationship between disease progression and systemic leaf responses.

CONCLUSIONS

Guaiacol-reactive POD-like oxidative activity, total flavonoid content, and tannin levels in leaves of duku (*Lansium domesticu*m Corr.) did not differ significantly between healthy and diseased trees affected by root-associated decline under orchard conditions. The strong overlap observed among samples indicates that the measured leaf biochemical traits remained relatively stable despite prolonged root-associated stress. However, the POD-related measurement should be interpreted only as an exploratory oxidative indicator because the extraction and sample-processing conditions were not optimized for preservation of native peroxidase enzyme activity. Therefore, the main biochemical interpretation of this study is based primarily on phenylpropanoid-related compounds, particularly flavonoids and tannins. Overall, the findings suggest that these leaf biochemical traits mainly reflect long-term physiological adjustment rather than short-term inducible defense responses. Consequently, single-time-point leaf biochemical measurements have limited sensitivity for distinguishing disease status in perennial fruit trees affected by prolonged root-associated disorders. These findings provide additional insight into the limitations of leaf biochemical traits as indicators of field-observed root-associated decline in duku. Future studies should include pathogen confirmation, disease severity scoring, repeated temporal sampling, and tissue-specific analyses using fresh or frozen tissues to better evaluate the relationship between disease progression, oxidative responses, and phenylpropanoid metabolism in duku.

ACKNOWLEDGMENT

The authors gratefully acknowledge Universitas Jambi for financial support through the internal research grant program No. 1717/UN21/PT/2025 and Research Contract No. 630/UN21.11/PT.01.05/SPK/2025. The authors also thank the UNJA Integrated Laboratory Academic Support Unit and the Analytical Laboratory, Faculty of Animal Science, Universitas Jambi, for laboratory facilities and technical assistance during this study.

CONFLICT OF INTEREST

The authors state that there is no conflict of interest.

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