Vol. 14(1): 16-30, January 2026
DOI: https://doi.org/10.23960/jsl.v14i1.1250

Jurnal Sylva Lestari

P-ISSN: 2339-0913
E-ISSN: 2549-5747

Journal homepage: https://sylvalestari.fp.unila.ac.id

Full Length Research Article

Influence of Elevation on Growth Performance and Root Traits of 2-Year-Old *Terminalia copelandii* in Sukau, Kinabatangan, Sabah

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ARTICLE HISTORY:

Received: 15 August 2025
Peer review completed: 15 September 2025
Received in revised form: 1 October 2025
Accepted: 24 October 2025

KEYWORDS:

Fast growing species
Forest plantation
Root biomass
Root phenotyping
Terminalia copelandii

ABSTRACT

Terminalia copelandii is a native, fast-growing tree with potential for forest restoration and agroforestry in Sabah. There is a limited understanding of the effects of elevation on the growth and below-ground root strategies of smallholder farms. This paper examines growth patterns and underground structure of two-year-old *T. copelandii* grown at different altitudes in Sukau, Kinabatangan, Sabah. Tree height (TH) and diameter at breast height (DBH) were measured at a hilly site and a lowland site. A completely randomized design with three experimental units per site was used. Root traits assessed included specific root length (SRL), root length density (RLD), and root biomass (RB). Roots were extracted at soil depths of 25 cm, 75 cm, 125 cm, and 175 cm and analyzed using an independent t-test at a 5% significance level. Results showed significantly better growth at the lowland site (TH: 4.77 m; DBH: 12.58 cm) than the hilly site (TH: 1.87 m; DBH: 6.48 cm). SRL and RLD were similar at shallow depths but increased at 175 cm in the lowland site. The hilly site showed greater root biomass accumulation, although the difference was not statistically significant. These results demonstrate how elevation-induced environmental factors affect above-ground and below-ground performance, promoting forest restoration and agroforestry strategies for this valuable species.

1. Introduction

The introduction of plantations with advanced forestry systems aims to provide social, ecological, and economic benefits while promoting sustainable forestry. Typically, forest plantations, including both native and exotic species, have shorter rotation cycles than natural forests (Farooq et al. 2021). Forest plantations were not on a large scale until the 1960s. Deforestation rates were recorded globally due to agricultural activities, urbanization, and other land uses. There was an effort to meet the increasing global timber demand and satisfy the world's wood requirements, as noted by Ratnasing et al. (2020).

There is a recognition of forest plantation using native species. This is attributed to the fact that native species are evolutionarily adapted to the local ecosystem, are more resistant to pests, and are more accommodating of native biodiversity (Liebhold et al. 2017). Productivity is a crucial factor to be considered in forest production management (Attarik et al. 2024). *Terminalia copelandii* belongs to the Combretaceae family (Chakrabarty and Kumar 2023). In Malaysia, it was locally known as Talisai Sifaran Watershed Paya, and this species has great potential as a useful timber tree in freshwater swamp and floodplain environments. It is native to Sumatra, Borneo, Flores, the Moluccas, the Philippines, New Guinea and the Solomon Islands. In Sabah, it occurs in small natural colonies, primarily in seasonal freshwater swamp forests in the Kinabatangan (Sabah Forestry Department 2019). The species is also useful in Malaysia as both a timber resource and a smallholder planting crop, as well as for forest restoration, especially in Sabah, where it is locally marketed as Talisai Paya. It has a Least Concern conservation status, indicating its relatively extensive distribution (Malaysia Biodiversity Information System 2019).

Smallholder farms in Sukau (Lower Kinabatangan) comprise a fragmented mosaic of oil-palm plots and remnants of riparian forest, where local people practice agriculture, fishing, and ecotourism as their livelihood (Fletcher 2009). Timber species such as *T. copelandii* have been encouraged in the floodplain due to their flexibility in inundated soils and their potential to provide ecological and economic benefits through planting programs. Initial experiments in Kinabatangan demonstrated that *T. copelandii* is a promising light hardwood suitable for restoration and smallholder planting, as it can thrive in floodplain conditions (Steel 2000). These projects emphasise the integration of native species into smallholder systems in Sabah, with conservation and livelihood purposes.

Although *T. copelandii* has good potential for use in lowland swamp and floodplain reforestation (WWF-Malaysia 2020), little information is available on its growth behavior and adaptability, particularly in varying elevations. The specification database indicates that *T. copelandii* occurs naturally in lowland swamps to about 400 m above sea level. The information is very limited (Tropical Timber Information 2025), underscoring the importance of including altitude-range data in future ecological surveys of this species. Studying elevation reveals it as a significant factor in determining microclimate, soil characteristics, and hydrology, which, in turn, influence both above- and below-soil growth and root development in plants (Xie et al. 2023). Despite limited information for this species, in Malaysia, specifically in the Sabah district, the Sabah Forestry Department has planted more than 37,000 seedlings to 81 registered smallholders under the programme of the 12th Malaysia Plan, supporting planting of trees of Laran, Batai, Binuang, Eucalyptus, Mahogany, Acacia and Talisai Paya (International Tropical Timber Organization 2024). Forest plantations are constantly competing with external factors, such as market demand, pests, and diseases, to determine which species can be consistently used to produce timber. The epidemic of Ceratocystis in Acacia plantations in the region highlights the risk of excessive reliance on a single species. To address the growing wood needs, expand the species portfolio, conduct stringent species evaluations, and strategically implement them across the upstream and downstream parts of the timber value chain are urgently required (Sabah Forestry Department 2024).

Such a lack of site-specific data creates a significant gap, as elevation and soil conditions can substantially affect tree growth and root development, both of which are vital to the long-term success and sustainability of the plantation. Thus, this research aimed to determine the growth performance and root distribution of two-year-old *T. copelandii* trees on smallholder farms at different elevations in the Sukau area, Kinabatangan, Sabah. The results will be useful for providing practical guidance on improving the native species plantation approach in floodplain regions.

2. Materials and Methods

2.1. Site Description

The experiment was conducted at a smallholder farm in Sukau, Kinabatangan, Sabah (5.57946°N, 118.10480°E) (**Fig. 1**). The farm area is 200 ha, with 99 ha endowed with oil palm since 2013, and the remaining area is devoted to other crops, with a preference given to fast-growing tree species. The temperature and rainfall ranges in 2024 were 24–32°C and 135.2–35.9 mm, respectively (Jabatan Meteorologi Malaysia 2025). The pH value at the hilly site was 5.31, and at the lowland site it was slightly lower at 5.24. For moisture content, the value was slightly lower at the hilly site (26.71%) than at the lowland site (34.43%). The experimental plots can be categorized as humid tropical agricultural land based on field observations and soil moisture data. Therefore, the comparison between the two locations —a dry, hilly plantation area and a wetter, lowland plantation area —enables the assessment of the effects of soil hydrology on growth and root distribution in *T. copelandii*. The study was conducted from 30 June to 31 December 2024.

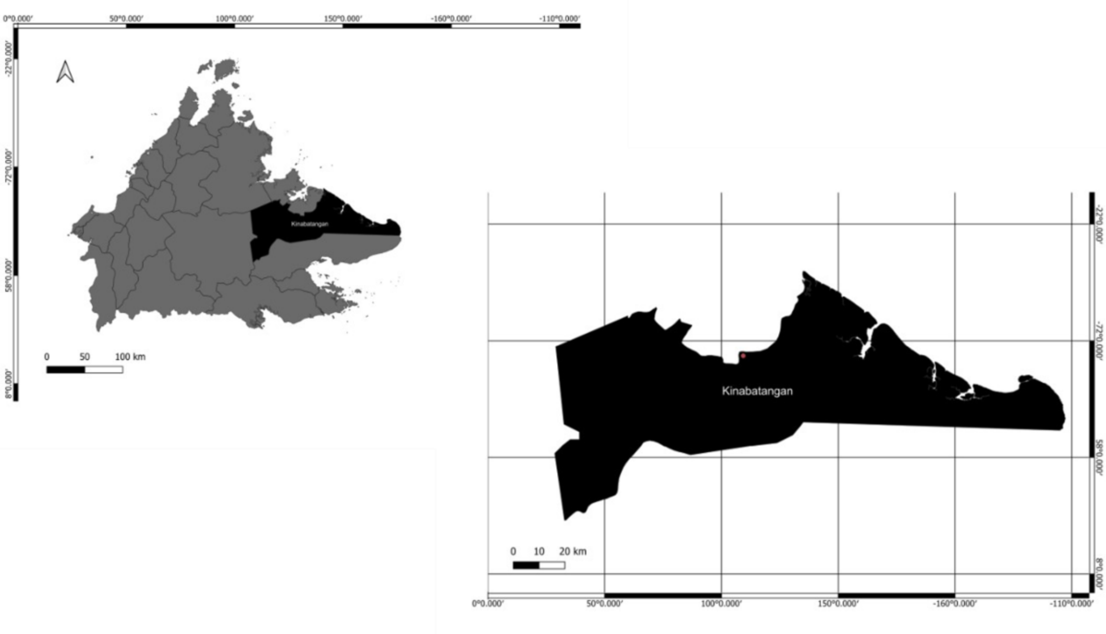

Fig. 1. Geographical location of the study site situated in Sukau, within the Kinabatangan district (JUPEM 2024).

2.2. Experimental Design

To compare the effects of above- and below-ground treatments on the selected parameters, the study employed a Completely Randomized Design (CRD). Based on standard topographical classification methods (United States Department of Agriculture 2010), the study sites are designated as the hilly site (site A, 41 m asl) and the lowland site (site B, 19 m asl). CRD was used because two elevation sites — hilly and lowland — are inherently different in terms of habitat type and should be blocked within the same landscape. Thus, the plots were randomly assigned to each elevation site and experimental unit three times to capture within-site variability.

Three experimental units (replicates) of 15 m × 15 m were set up on each site, with a tree spacing of 6 m × 6 m. This resulted in a single replicate yielding a total of six experimental units. Each experimental unit consisted of seven *T. copelandii* trees. In each experimental unit, seven *T. copelandii* trees were planted in a square plot design with a spacing of 6 m between individuals (i.e., a central tree with six trees at about equal spacing). The plots of 15 m × 15 m were sufficient for identifying early growth variation among trees and for ensuring that the trial was manageable, also serving as experimental units without the need to cover large areas of land (Harwood et al. 2024). This design will facilitate a rigorous comparison of the effects of elevation on root distribution and other variables of interest. Collected data systematically and analyzed following the CRD standards by adhering to the principles of experimental design that were set through statistical procedures (Ruíz et al. 2024). A 2-year-old culture of *T. copelandii* was selected for study of the early establishment stage. This is the stage at which the root structure is most dynamic and biomass allocation is most active. The pattern of early root development was frequently obscured by older age classes due to more secondary growth or root turnover (Behmen et al. 2022).

2.3. Data Collection

Data collection was conducted monthly. The experimental unit consisted of seven *T. copelandii* individuals, each providing 42 trees (21 per site). Three trees (one per site; three experimental units; three sites) were sampled (three trees/site across two sites), yielding six sites. The roots were randomly sampled on each experimental unit. All trees were measured above ground for growth parameters. The above-ground measurements were the total tree height and the tree's diameter. The diameter reading was taken at breast height (DBH, 1.3 m) (Ottmar 2020). A TruPulse laser rangefinder (Laser Technology, Inc.) was used to measure tree height, and a diameter tape was used to measure DBH. Growth measurements were taken over 6 months to emphasize the dynamic establishment phase. This period was insufficient to estimate the mean annual increment (MAI). However, short-term data are still useful for correlating shoot performance with initial root allocation patterns, as the initial stages of growth are known to be the most plastic in terms of biomass partitioning (Jaeger et al. 2024).

Below-ground sampling was conducted destructively. Roots were sampled with a cylindrical auger to a depth of 200 cm and stratified into four depths: 0 to 50 cm, 50 to 100 cm, 100 to 150 cm, and 150 to 200 cm. To describe the active root zone, soil cores were taken at a radial distance of approximately 1.0 m from the tree trunk, which is halfway between the canopy dripline and the trunk (Ryan et al. 2024). Soil samples were extracted and put into sealed plastic bags until the roots were washed out (Frasier et al. 2016). After harvesting, the samples were washed and stored in Eppendorf tubes with 50% ethanol in a refrigerated chamber at 5°C. The roots were extracted from the soil by running tap water through a 2.0 mm mesh sieve to clean off organic debris (Hassan et al. 2021). The roots were separated into secondary and tertiary roots. Separation of secondary and tertiary root classes based on root order and pattern branching. The morphometric method switches the direction of classification, with the first-order roots being those that end in a meristem; the second-order root is a root that is not affected at the junction with other first-order roots; the third-order root is a root formed at the junction of other second-order roots and so on (Freschet et al. 2021). Dry biomass (g) was then obtained by oven-drying the roots at 70°C for 48 hours (Hassan et al. 2020). Specific root length (SRL) was determined as the total root length divided by dry mass (Kramer-Walter et al. 2016), and root length density (RLD) was determined as the root length divided by the soil volume (Huot et al. 2020).

A total of 144 root samples were collected throughout the study using the coring method. Each sampled tree provided six cores at four depths, which equals 24 cores/tree, so that the total number of cores in the six sampled trees equals 144 cores (6 trees × 24 = 144). The cylindrical earth auger used in this study had a cup with a diameter of 7.92 cm, a radius of 3.96 cm, and a height of 16.5 cm, corresponding to a total volume of 812.87 cm^3.

2.4. Comparative Analysis

The statistical analysis of the data was performed using the most recent version of IBM SPSS Statistics (Version 28.0). The Shapiro-Wilk test was used at the 5% significance level to determine the normality of the data. An independent-samples t-test at the 5% significance level was used to compare two independent groups for all variables, including total height, diameter at breast height (DBH), dried root biomass (DRB), root length density (RLD), and specific root length (SRL). *T. copelandii* showed a response to above-ground growth in sites during the 6-month monitoring period. Mean height and DBH grew faster in lowland plots than in hilly plots, indicating greater resource availability in deeper soils, which is significant in the context of root development patterns.

3. Results and Discussion

3.1. Above-Ground Performance

3.1.1. Tree height

Based on **Fig. 2**, the mean tree height of the trees of *T. copelandii* at the lower site was significantly higher, with a mean of 4.77 m, compared to 1.87 m at the hilly site. The independent t-test showed significant differences. Elevation-related environmental factors significantly affect the growth performance of *T. copelandii* in the study area. Lowland sites generally have more fertile soil with higher nutrient levels and greater available soil moisture, due to better water retention, which directly promotes faster tree growth and biomass accumulation. A study by Zádorová et al. (2015) suggests that low-lying or colluvial sites are more fertile than uplands due to erosion of topsoil and organic matter, which is carried down the slope by runoff and sedimentation. Key climatic variables also influenced tree growth, clarifying how stand-level and individual-tree conditions responded to climate (Primicia et al. 2015). Although the upland areas are likely to experience shallower soils, greater compaction, and increased exposure to wind and temperature, the latter did not provide any laboratory soil analysis to support these assertions (Osman 2018). By contrast, a study by Jaffar et al. (2018) measured soil penetration resistance and found that surface soil compaction was a major constraint on root elongation, linked to lower above-ground expansion in forest species plantations in Sarawak. This suggests that our hypotheses are similar and that a similar mechanism may be operating in *T. copelandii* growing in upland versus lowland sites. In addition, microclimatic variations between lowland and hilly locations, especially in such variables as temperature, humidity, vapor pressure deficit, and soil moisture, may have an impact on plant physiological functions, including photosynthesis and transpiration, which, in turn, affect the growth of tree height (McNichol et al. 2024). The slowed height growth of trees in hilly locations suggests that *T. copelandii* may be adjusting to the adverse environment, where root interactions with changing temperatures can alter plant growth (Luo et al. 2020).

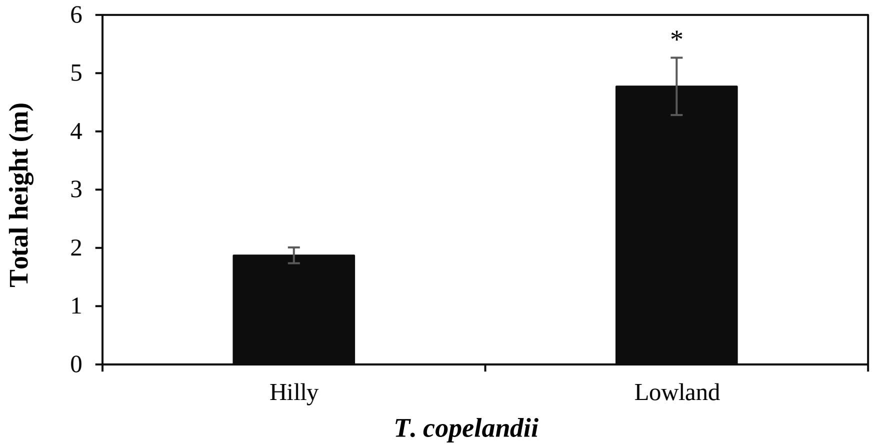

Fig. 2. Mean of the total height of 2-year-old *T. copelandii* trees at the hilly and lowland sites. The error bars show standard deviation, and an asterisk (*) shows statistical significance. Independent t-test results showed a significant difference ($t_{calculated}$ = -9.84, t_{table} = ± 2.78).

3.1.2. Diameter at breast height (DBH)

Fig. 3 shows the mean DBH of trees in the lowland sites, which were significantly higher, averaging around 12–13 cm, compared to approximately 6–7 cm in the hilly site. The independent t-test results showed that altitude differences influence the stem diameter of *T. copelandii* trees.

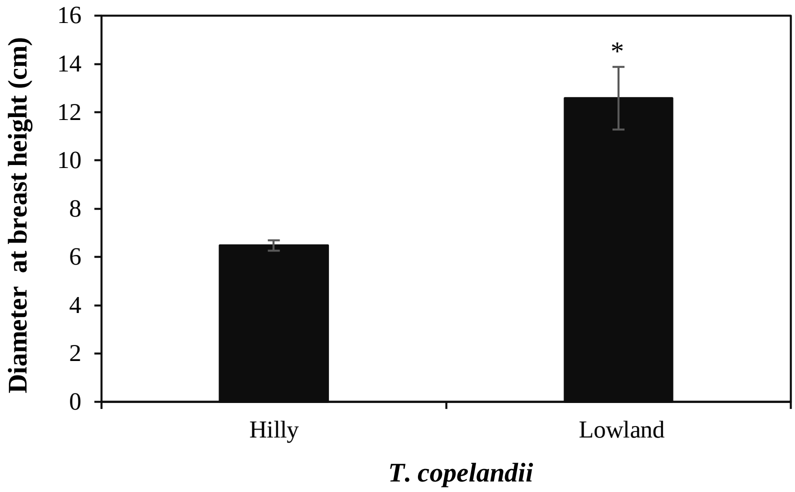

Fig. 3. Mean of the diameter at breast height (DBH) of 2-year-old *T. copelandii* trees at the hilly and lowland sites. The error bars show standard deviation, and an asterisk (*) shows statistical significance. Independent t-test results showed a significant difference ($t_{calculated}$ = -8.03, t_{table} = ± 2.78).

Diameter at breast height (DBH) and tree height remain the basic, commonly used measures of tree growth (Liu et al. 2018). The higher DBH values observed at the lowland site are likely associated with more favorable growing conditions, including increased nutrient availability, higher soil moisture, and reduced environmental stress (Prakash et al. 2025). Lowland sites usually receive sediment and nutrient-enriched topsoil washed down from the uplands, leading to the area (Li et al. 2024). Increased water availability influenced DBH through soil moisture, which affects diameter growth rates in tree species by alleviating water stress and allowing greater cell expansion (Ali et al. 2023). The regions are characterized by lowlands with higher water tables, which typically result in greater soil moisture availability, essential for plant development and agricultural yield (Zádorová et al. 2015). Moreover, the growth of secondary stems depends on microclimatic conditions, such as reduced wind exposure and higher humidity, which create a more favorable environment for cambial activity and xylem formation (Zhang et al. 2019).

The fact that *T. copelandii* grows to larger DBH and height in lowland plots is not unique, as preserved edaphic conditions (greater nutrient turnover, deeper soils) at lowland elevations have been shown to accelerate stem growth. Additionally, trees could alter biomass investment in response to elevation stress, balancing investment in survival and height enhancement—a trade-off mediated by the coordination of species-specific root and leaf traits—in both temperate forests and, over time, in tropical systems (Weemstra et al. 2021).

3.2. Below-Ground Performance

3.2.1. Specific root length (SRL)

Fig. 4 shows a bar graph of SRL (cm/g) for *T. copelandii* at the hilly and lowland sites across four depths. At a depth of 150 to 200 cm, the lowland site exhibits a notably higher SRL compared to the hilly site, with a statistically significant difference. However, despite no significant difference being recorded, *T. copelandii* was found in a hilly site.

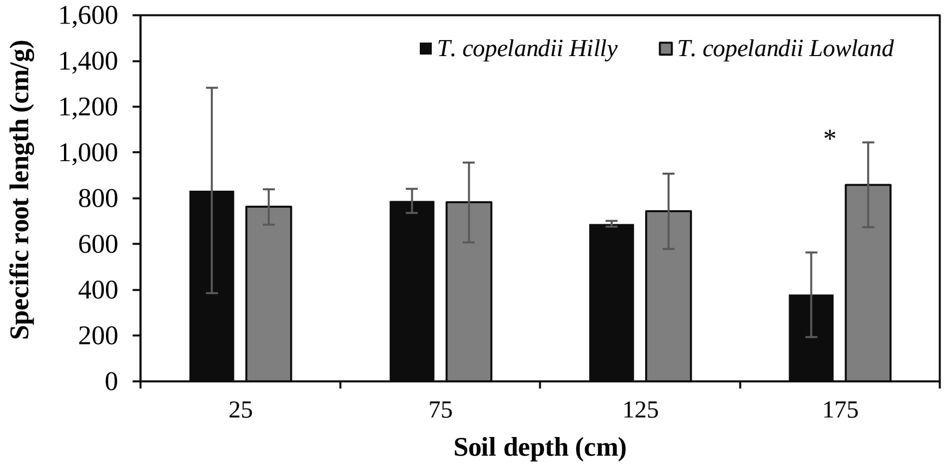

Fig. 4. Mean of the SRL (cm/g) of 2-year-old *T. copelandii* trees at the hilly and lowland sites. The error bars show standard deviation, and an asterisk (*) shows statistical significance. An independent t-test showed the $t_{calculated}$ value = −3.178 and t_{table} = ±2.776, df = 4, confirming a significant difference between the two sites.

Specific root length (SRL) is a functional character that combines the efficiency of plant resource acquisition, which is the capacity of a plant to obtain nutrients (Freschet et al. 2015). An increase in SRL typically implies that finer roots are produced, which are more effective in exploring the soil and finding nutrients and water; thus, it takes less biomass to acquire the resources efficiently (Weemstra et al. 2016). This is also supported by the fact that SRL means the roots are thinner and more efficiently exploited (Xu et al. 2012). At lowland sites, increased SRL at depth can be attributed to increased soil moisture and nutrient deposition, which stimulate root growth further into the soil to optimize resource uptake. This is a better predictor of fine root productivity (Huasco et al. 2021). Elevational gradients show that plants in nutrient-poor, high-elevation or slope conditions have thicker roots with lower SRL, a strategy for structural stability and conservative resource use rather than broad soil foraging (Weemstra et al. 2021). On hilly or upland locations, the plants are more invested in root strength than in the proliferation of finer roots (Fu et al. 2016).

3.2.2. Root length density (RLD)

As **Fig. 5** indicates, the root length density (RLD, cm/cm^3) of *T. copelandii* was greatest in the uppermost layer of the soil (0 to 50 cm) at the hilly site, indicating that the fine roots were concentrated close to the surface soils. On the contrary, the RLD values in the lowland site were more evenly distributed in the profile. The independent t-tests revealed significant site differences at deeper layers (100 cm to 150 cm and 150 cm to 200 cm), indicating that tree roots in hilly soils were more deeply rooted than in the lowland soils.

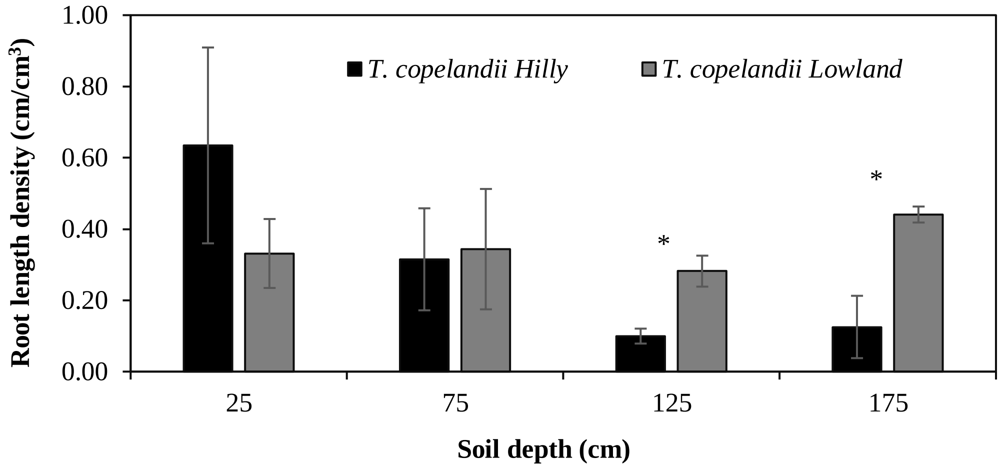

Fig. 5. Mean of the RLD (cm/cm^3) of 2-year-old *T. copelandii* trees at the hilly and lowland sites. The error bars show standard deviation, and an asterisk (*) shows statistical significance. The independent t-test showed the $t_{calculated}$ value = −6.54 and t_{table} = ± 2.78, df = 4, confirming a significant difference between the two sites.

The increased RLD in the upper soil layer at the hilly site may be attributed to a limited rooting depth and resource shortages in the deeper horizons. The soils of hilly landscapes are generally shallower, rockier, and more compacted, with lower nutrient levels, which require trees to develop a denser fine root system near the surface, where nutrients and water are more readily accessible (Campos-Cascaredo et al. 2021). Soil compaction and nutrient status are based on topographic context rather than direct measurement. Tropical landscapes are widely reported to have hillier soils, which are more compacted and less nutrient-rich than those in lowland areas (Jaffar et al. 2018; Osman 2018). These studies supported trends that justified our conclusion regarding observed site-specific differences in the growth and root distribution of *T. copelandii*, as part of the underlying edaphic differences. Conversely, the much higher RLD values in the deeper layers of the lowland site ($p < 0.05$) indicate that deeper soil, improved structure, and stable moisture conditions facilitate deeper root proliferation.

Lowland areas are generally characterized by deeper soils enriched with alluvial materials and runoff from higher altitudes, providing mechanical advantages for root penetration and supporting tree growth (Zimmer and Gannon 2018). This also provides more uniform access to subsoil water and nutrients, as flat areas are usually influenced by soil drainage. Poorly drained soils are usually flat and saturated due to water retention, which retards the formation of the soil profile. Conversely, well-drained soils can form E horizons over well-developed B horizons as clay is washed away at the top (Schoonover and Crim 2015). These findings indicate the adaptive plasticity of *T. copelandii* root systems in distributing growth across soil layers to maximize resource acquisition within site-specific constraints, as well as in soil-plant water interactions across geographical differences. In tropical environments, the RLD pattern of *T. copelandii* is influenced by soil and hydrology. In more nutrient-enriched lowland soils, roots do not need to penetrate deep, and in more leached hillside systems, deeper root penetration is beneficial. A pattern that is opposite to those typically reported in the xeric or temperate environment (Cusack et al. 2021).

3.2.3. Dried root biomass (DRB)

The bar graph in **Fig. 6** shows the mean of DRB of *T. copelandii*. The independent t-test revealed no significant differences. The highest mean recorded in the fourth layer of soil (150 to 200 cm) for *T. copelandii* in the hilly site (0.18 g) compared to the lowland site (0.04 g). However, in soil layer depth 1, both SRL and RLD were higher at the hilly site than at the lowland site.

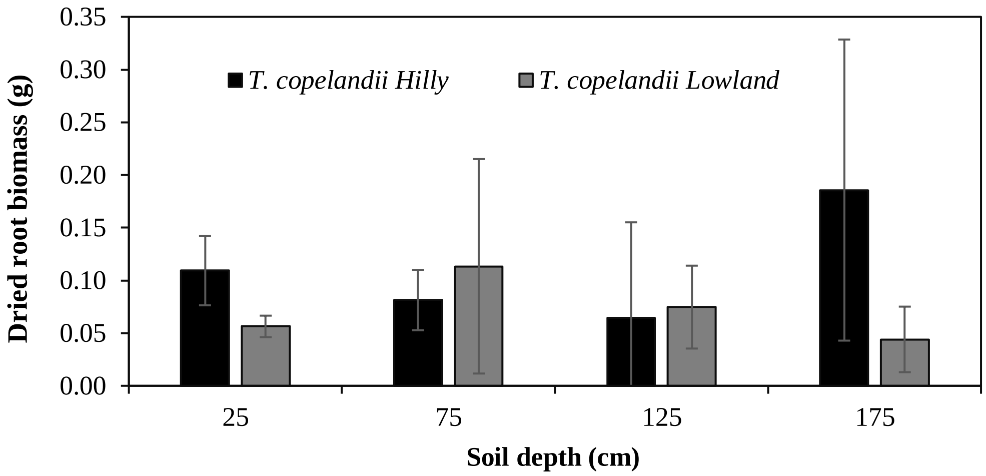

Fig. 6. Mean of the DRB (g) of 2-year-old *T. copelandii* trees at the hilly and lowland sites (the error bars show standard deviation).

Variations in DRB between hilly and lowland sites can be interpreted in the context of root system adaptation. The increase in DRB at deeper soil depths on the hilly site could be a compensatory mechanism to address shallow topsoil nutrient constraints by allocating biomass to structural and transport roots in subsoil layers. This increased investment in biomass can enhance access to more secure water resources and potentially stabilize trees in more unstable, steep landscapes (Mihrete and Mihretu 2025). According to a study by Goyo et al. (2025), the water absorption rate increases with increasing root biomass. Interestingly, the increasing SRL and RLD in the surface layer of the hilly site suggest a two-tier approach, which fine roots in the topsoil to take up the nutrients through litter decomposition quickly (Martins et al. 2021), and the coarse, more biomass-intensive roots in the subsoil to provide water and mechanical support (Koch et al. 2021). Such a functional differentiation of root characteristics among soil layers is a response to the heterogeneous distribution of resources in the environment (Burton et al. 2020).

In contrast, lower DRB in the deep layers of the lowland site could be associated with improved nutrient availability (Khadiza et al. 2025) and water retention at shallower depths, thereby minimizing the need for heavy structural root investment below 150 cm. This shallower rooting approach enables the tree to invest in more fine, absorptive roots (Sanaei et al. 2025) rather than large-diameter structural roots, maximizing carbon investment in resource capture efficiency (Valverde-Barrantes et al. 2015) rather than mechanical anchorage or deep water foraging. The plasticity in biomass allocation of this species is central to its productivity and resilience in response to topographical and edaphic constraints.

4. Conclusions

The growth performance analysis showed a significant difference between the trees at the the hilly and lowland sites, indicating that the lower-elevation site is more favorable for tree growth. Such conditions can include increased nutrient availability, which is likely the factor driving increased growth. In terms of root distribution, variation in root biomass and distribution across depths indicates that soil properties, including compaction and water availability, differ with elevation and affect root growth strategies in *T. copelandii*. These results indicate that the species exhibits adaptive responses to site-specific environmental gradients. Additional studies are needed to conduct long-term monitoring, capture stand-level growth curves, combine soil nutrient and physical analyses to make comparisons more robust, and increase trials to larger elevations. In practice, these findings can inform stakeholders, including farmers and forestry agencies, to focus on lowland locations for biomass production, and conservation groups can focus on hilly locations to restore them with deep roots, thereby improving soil stabilization.

Acknowledgements

The authors sincerely thank all those who contributed to the completion of this research, and the Faculty of Tropical Forestry at Universiti Malaysia Sabah for providing the necessary facilities. The authors also appreciate the support from smallholder farms under the Forest Research Centre (FRC) for its outstanding assistance during the study conducted, including technical support and sponsorship of the plant material.

Author Contribution

A.N.M.K.: Methodology, Software, Investigation, Resources, Data Curation, Writing—Original Draft Preparation; A.S.Q.A.N.: Methodology, Software, Investigation, Writing—Original Draft Preparation; H.D.: Methodology, Software, Investigation; T.A.T.: Formal Analysis, Resources, Writing—Review and Editing; N.F.W.: Software, Validation, Writing—Review and Editing, Data Curation; K.P.K.N.: Validation, Resources; S.C.: Formal Analysis; R.T.: Formal Analysis; A.H.: Conceptualization, Methodology, Software, Validation, Resources, Data Curation, Supervision, Funding Acquisition.

Conflict of Interest

The authors declare no conflict of interest.

Declaration of Generative AI and AI-Assisted Technologies in the Manuscript Preparation

Not applicable.

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