Integrated Predictive Modeling of Nectar Volume and Concentration of Croton macrostachyus Across Canopy Levels, Ontogeny and Environmental Variation in Sidama, Hawassa University, Ethiopia

kasim Jilo
kasimroba7@gmail.com

College of Basic Applied Science and Technology, Arsi University, Asella, Oromia, Ethiopia

Muzeyin Berarti
College of Basic Applied Science and Technology, Arsi University, Asella, Oromia, Ethiopia

Research Article

Keywords: Nectar Dynamics, Canopy Stratification, Tree Ontogeny, Climate Stress, Viscosity Trap, Sidama-Hawassa

Posted Date: June 22nd, 2026

DOI: https://doi.org/10.21203/rs.3.rs-9989571/v1

Additional Declarations: No competing interests reported.

Abstract

Introduction

: Nectar secretion plays a crucial role in honey production, but the effects of canopy strata, tree age, and environmental factors on nectar availability remain unclear. This study quantifies these effects in Sidama and Hawassa, Ethiopia, and develops predictive models. Previous research on *Callistemon citrinus* L. showed that younger plants do not respond to relative humidity or temperature in terms of nectar volume, while medium-aged and older plants do. Additionally, studies on *Croton macrostachyus* Hochst. ex Delile and *Trifolium repens*. indicate that temperature, humidity, daylight, canopy layers, tree age, and soil moisture influence nectar volume and concentration.

Methods

A factorial design (6 × 3) was used to assess nectar solute concentration (%) and volume (μL) across six canopy layers (AL1–AL3, ML1–ML3) and three tree age classes (small, medium, older). Bivariate and multiple linear regression (MLR) models were applied to develop forecasting tools for nectar yield and to evaluate climate-induced thermal stress.

Results

Analysis of variance showed a significant interaction between canopy layer and tree age for solute concentration ($p < 0.001$), with older trees in the upper canopy (AL3) reaching the highest concentration (36.42 ± 0.10%). Nectar volume decreased significantly with tree age ($p < 0.001$) across all canopy positions. The bivariate model (Volume = 0.8456 − 0.0189 × Concentration; $R^2 = 0.620$) indicated a clear trade-off between sugar concentration and fluid availability.

Conclusions

Model projections for 2076 suggest a potential “Viscosity Trap,” where a + 2.0°C temperature increase could raise concentrations above 42.8% and reduce volumes below 0.10 μL. These findings highlight older trees as high-solute hotspots and lower canopy layers as thermal refuges. Maintaining multi-layered canopy structures is essential for sustaining honeybee foraging efficiency and enhancing apiculture resilience under climate change.

Introduction

In the diverse ecosystems of Ethiopia’s Sidama and Hawassa regions, apiculture plays a vital role in rural livelihoods, food security, and biodiversity conservation (Niinemets, 2007). The productivity and quality of honey production are primarily determined by the physiological properties of floral nectar, the main resource harvested by honeybees. Nectar is a complex glandular secretion whose value is defined by two key parameters: fluid volume (µL) and solute concentration (%), both of which directly influence honey yield and quality (Pacini & Nepi, 2007; Willmer, 2011). Nectar drinkers must feed quickly and efficiently due to the threat of predation. While the sweetest nectar offers the greatest energetic rewards, the sharp increase of viscosity with sugar concentration makes it the most difficult to transport (Kim *et al.*, 2011).

This work is executed to predict the variation in global temperature and greenhouse gas (GHG) emissions resulting from climate change and global warming, taking into consideration the natural climate cycle (Hamdan *et al.*, 2023). We show that climate models consistently project increases in temperature variability in tropical countries over the coming decades, with the Amazon as a particular hotspot of concern (Bathiany *et al.*, 2018). Climate change, caused by greenhouse gas emissions and rising temperatures, is a major threat, making accurate predictions essential for effective mitigation and adaptation (Ochieng, 2024). Global warming is expected to not only impact mean temperatures but also temperature variability, substantially altering climate extremes (Olonscheck, *et al.*,2021).

The literature suggests that floral nectar acts principally to attract pollinator visitation (and/or revisitation), thereby enhancing plant reproductive success (Pyke, 2016). Plants secrete nectar to attract pollinators and indirect defenders and chemical contents of both floral and extrafloral nectar appear adapted to attract and nourish these two classes of animal mutualists (Escalante-Perez and Heil, 2011). Floral nectar is an important determinant of plant–pollinator interactions and an integral component of pollination syndromes, suggesting it is under pollinator-mediated selection (Parachnowitsch *et al.*, 2019).

Nectar secretion is complicated to study from the ultrastructural point of view because it is a dynamic process involving many tissues simultaneously (Pacini and Nepi, 2007. Three bioclimatic variables were retained by at least three models: temperature seasonality and mean temperature of the wettest quarter were negatively correlated with honey yields whereas precipitation of the wettest month was positively correlated (Delgado *et al.*, 2012.

Nectar traits are not fixed but are highly plastic physiological responses influenced by plant ontogeny and environmental conditions (Niinemets, 2007). Vertical canopy stratification creates gradients in light intensity, temperature, and relative humidity, which in turn affect floral physiology and nectar secretion patterns (Givnish, 1988). In addition, tree age modifies nectar dynamics through changes in resource allocation and physiological sensitivity to environmental variation. These interacting factors generate substantial intra-tree variability in nectar quantity and quality, which is often overlooked in ecological and apicultural studies.

Although seasonal nectar flow patterns are well recognized by beekeepers, fine-scale variability within tree canopies and across different age classes remains poorly quantified (Pacini & Nepi, 2007). Environmental factors such as temperature, humidity, and evaporative demand further interact with canopy position and ontogeny to influence nectar production. However, these multi-scale interactions are rarely integrated into predictive frameworks, limiting the ability to optimize honey production under variable environmental conditions (Willmer, 2011).

Understanding how canopy structure, tree age, and environmental gradients jointly regulate nectar dynamics is therefore essential for improving the efficiency and sustainability of apiculture. Integrating these factors into a unified analytical framework provides a more precise basis for predicting nectar availability and enhancing apicultural resilience in heterogeneous and changing landscapes (Niinemets, 2007; Givnish, 1988).

Methodology

Study Area and Species

The study was conducted in the Sidama and Hawassa regions using naturally established and university-planted populations of *Croton macrostachyus this plant name scientifically only this species.* The species was selected because of its ecological importance as a major nectar-producing tree and its relevance for pollination ecology and apicultural studies. The selected trees were located within university-managed plantations where planting history and approximate age information were available from institutional records.

Study Design

A field-based longitudinal observational study employing stratified purposive sampling and predictive modeling approaches was conducted to evaluate the effects of canopy stratification, floral ontogeny, plant age variation, and environmental factors on nectar volume and nectar concentration of *Croton macrostachyus*. Repeated measurements were conducted throughout the flowering season to capture temporal and spatial variation in nectar traits.

Study Variables and Nectar Dynamics Framework

An integrated analytical framework was developed to evaluate nectar dynamics by combining biological, structural, and environmental variables. The principal dependent variables measured during the study were nectar solute concentration (% Brix) and nectar fluid volume (µL). Independent variables included canopy layer categorized as AL1 (lower canopy), AL2 (middle canopy), and AL3 (upper canopy); tree age classes classified as smaller, medium, and older trees; and environmental parameters including ambient temperature (°C) and relative humidity (RH %). These variables were incorporated to assess their individual and interactive effects on nectar secretion patterns and to evaluate the evaporative and physiological mechanisms regulating nectar concentration and volume dynamics.

Tree Selection and Ontogenetic Classification

Sample trees were purposively selected based on flowering status, accessibility, healthy physiological condition, and availability of documented planting history obtained from university records. Because the establishment age of the trees was known, individuals were classified into three ontogenetic age categories using both recorded age information and observable branching architecture. Trees possessing approximately nine major branches were categorized as older trees, those with five major branches were classified as medium-aged trees, while individuals with three major branches were considered smaller or younger trees. This ontogenetic classification was employed to evaluate age-related variation in nectar volume and solute concentration of Croton macrostachyus across different developmental stages. Equal representation of each age category was maintained throughout the study to enable balanced comparison among developmental stages.

Temporal Canopy Stratification and Sampling Schedule

To assess the combined effects of canopy position and time of day on nectar dynamics, nectar samples were collected during both morning and afternoon periods. Canopy strata sampled during the morning were designated as ML1 (lower canopy), ML2 (middle canopy), and ML3 (upper canopy), while afternoon sampling strata were designated as AL1 (lower canopy), AL2 (middle canopy), and AL3 (upper canopy). This temporal stratification approach was employed to capture diurnal variation in nectar secretion and concentration associated with changing microclimatic conditions such as temperature, relative humidity. By integrating vertical canopy layers with sampling time, the study enabled comparison of nectar volume and solute concentration across both spatial and temporal environmental gradients. Flowering branches were sampled from each canopy level using ladders or accessible branch positions. This stratification enabled assessment of how microclimatic differences such as light exposure, temperature, and humidity influence nectar secretion across canopy gradients.

Floral Ontogeny and Inflorescence Sampling

To evaluate floral developmental variation, inflorescences were purposively sampled from three different positions within each flowering structure: basal or edge portion, middle portion, and terminal or tip portion. These positions were selected to capture possible variation in nectar volume and nectar concentration associated with flower developmental stages within the inflorescence. Nectar measurements obtained from the three flower-head positions were averaged to generate a representative nectar value for each inflorescence. For reliability and consistency, three replications were conducted for all sampled inflorescences across canopy layers and tree age categories.

These positions were selected to represent different stages of floral ontogeny and developmental maturity within the inflorescence axis. Flowers of comparable blooming stages were selected to minimize developmental bias during nectar extraction.

Nectar Collection and Measurement

Nectar was collected directly from freshly opened flowers during morning sampling periods to minimize the effects of diurnal fluctuations. Nectar fluid volume was measured using calibrated microcapillary tubes and recorded in microliters (μL). Nectar solute concentration was measured using a handheld refractometer calibrated in percentage sucrose equivalents (% Brix). Prior to each measurement session, the refractometer was cleaned and standardized using distilled water to ensure measurement accuracy. Total Sugar Content (TSC) was estimated from nectar volume and concentration measurements using standard nectar sugar conversion procedures.

Environmental Data Collection

Environmental variables were recorded simultaneously with nectar sampling. Ambient temperature and relative humidity were measured using a portable digital thermo-hygrometer, and humidity data to estimate atmospheric evaporative demand. Additional field observations including weather condition, cloud cover, and wind intensity were also recorded during sampling periods to support interpretation of nectar variability.

Statistical and Modeling Framework

A hierarchical analytical framework was employed to ensure robust inference and predictive modeling of nectar variation. First, Multivariate Analysis of Variance (MANOVA) using Pillai's Trace was conducted to test the combined effects of canopy layer, ontogenetic class, and environmental variables on nectar concentration and nectar volume simultaneously, thereby minimizing Type I error across correlated response variables. To further evaluate structural influences, a Two-Way Factorial ANOVA was applied to examine the interaction between canopy layer (AL1–AL3) and tree age class (Smaller, Medium, Older). This analysis assessed whether canopy position modifies ontogenetic effects on nectar concentration and nectar volume. Predictive relationships between nectar traits were subsequently quantified using Bivariate Linear Regression, where nectar fluid volume was modeled as a function of nectar solute concentration to examine the concentration–dilution trade-off governing nectar dynamics. To incorporate environmental controls, Multiple Linear Regression (MLR) models were developed to evaluate the combined effects of temperature, relative humidity, VPD, and nectar solute concentration on nectar volume and total sugar production. Finally, Climate Sensitivity Simulations were performed under projected warming scenarios of + 0.8°C (20-year projection) and + 2.0°C (50-year projection) to estimate long-term changes in nectar availability. These simulations were also used to identify the "Viscosity Trap," defined as the threshold at which nectar volume declines below 0.10 μL due to increased evaporative concentration under warming conditions.

Data Analysis and Visualization

Data analysis was conducted using an integrated statistical and computational workflow. IBM SPSS Statistics Version 26.0 was used for MANOVA and factorial ANOVA, while assumptions of normality and homogeneity were tested using Shapiro–Wilk and Levene's tests. R software Version 4.2.0 was

used for advanced visualization and predictive modeling, including correlation heatmaps, Response Surface Methodology (RSM) plots, environmental interaction surfaces, and climate trajectory simulations. These analyses were applied to evaluate relationships among nectar traits and environmental variables, identify nonlinear response patterns, detect potential thermal refugia within canopy strata, and project long-term nectar responses under future climate warming scenarios, including threshold detection of the "Viscosity Trap.

Climate Projection and Viscosity Trap Modeling

Climate projection analysis was conducted to evaluate the potential effects of future warming on nectar dynamics of *Croton macrostachyus*. Two projected warming scenarios, + 0.8°C and + 2.0°C, representing medium- and long-term climate change conditions, were incorporated into the predictive modeling framework. Multiple Linear Regression (MLR) and Response Surface Methodology (RSM) models were used to simulate the effects of increasing temperature, relative humidity, and Vapor Pressure Deficit (VPD) on nectar volume and nectar concentration across different canopy layers and tree age classes. The modeling framework was based on the ecological principle that elevated temperature enhances evaporative water loss from nectar, resulting in reduced nectar fluid volume and increased solute concentration. The "Viscosity Trap" was operationally defined as the threshold condition where nectar volume declines below 0.10 µL, causing nectar to become excessively concentrated and less accessible to pollinators. Additionally, the simulations were used to identify potential canopy thermal refugia where nectar traits remain relatively stable under projected warming conditions.

Results and Discussion

Figure 1 and the correlation result together show a consistent and statistically significant pattern in nectar traits driven by climate and microclimate. A strong inverse relationship between nectar volume and solute concentration ($r = -0.79$, $p < 0.01$) confirms a clear dilution–concentration trade-off, where reduced nectar volume is associated with higher sugar concentration due to limited water availability. This reflects a fundamental physiological constraint in nectar production under water stress. Temperature further reinforces this pattern, showing a negative relationship with nectar volume ($r = -0.42$) and a positive relationship with concentration ($r = 0.55$), while Fig. 1 also indicates a positive link between temperature and concentration ($r = 0.45$), particularly in exposed upper canopy strata (AL3), where evaporation is likely enhanced. Combined with the positive effects of soil moisture and humidity on nectar volume and their negative effects on concentration, these results show that water availability and evaporative demand jointly regulate nectar quantity and quality. Overall, the patterns indicate that warmer and drier conditions intensify evaporative loss, reducing nectar volume while increasing sugar concentration, thereby reshaping the balance between nectar quantity and quality. Overall, the results suggest that climate warming and drying will reduce nectar volume while increasing concentration, producing smaller but more energy-dense floral rewards and potentially altering plant–pollinator interactions.

Table 1 shows that both canopy position and tree age strongly influence nectar traits through a clear volume–concentration trade-off. In the upper canopy (AL3), older trees produce very low nectar volumes (0.22 μL) but extremely high concentrations (36.42%), while smaller trees produce higher volumes (0.78 μL) with much lower concentration (9.04%), indicating that increased exposure to heat, wind, and evaporative stress in the canopy top leads to reduced nectar quantity but more concentrated sugar content. In the middle (ML1) and lower (BL3) canopy, older trees show more moderate and stable values, with relatively higher volumes and lower concentrations compared to the upper canopy, suggesting that shaded and more humid microclimates buffer water loss and reduce stress effects on nectar production. Overall, the pattern indicates that greater environmental exposure and plant age intensify nectar concentration while reducing volume, a trend consistent with stronger water limitation and evaporation-driven concentration under more stressful conditions.

Table 1
Nectar Concentration and Volume across Canopy Strata and Age Classes

Canopy Layer	Tree Age Class	Concentration (%)	Volume (μL)
AL3 (Upper)	Smaller	9.04 ± 0.06	0.78 ± 0.01
	Medium	16.48 ± 0.33	0.51 ± 0.03
	Older	**36.42 ± 0.10**	**0.22 ± 0.12**
ML1 (Middle)	Older	10.23 ± 0.25	0.58 ± 0.02
BL3 (Lower)	Older	13.67 ± 0.06	0.57 ± 0.02

Table 2 shows that both canopy position (tree layer) and tree age significantly influence nectar traits, but their effects differ between nectar concentration and volume. For nectar concentration, tree layer has a very strong and highly significant effect ($F = 13{,}738.25$, $p < 0.001$), indicating that vertical differences in microclimate (e.g., temperature, light, evaporation) strongly shape nectar sugar levels. Tree age has an even larger effect ($F = 64{,}842.57$, $p < 0.001$), suggesting that physiological changes with aging are a dominant driver of nectar quality. The significant interaction ($F = 2{,}432.54$, $p < 0.001$) shows that the effect of age varies depending on canopy position, meaning environmental exposure modifies age-related patterns in concentration. For nectar volume, age also has a strong and significant effect ($F = 26.18$, $p < 0.001$), indicating that older trees generally produce different nectar quantities than younger ones, likely due to physiological or resource allocation constraints. The tree layer effect is weaker but still significant ($F = 3.84$, $p = 0.005$), showing that canopy position has a secondary influence on nectar production. However, the non-significant interaction ($F = 1.41$, $p = 0.208$) indicates that the effect of age on nectar volume is consistent across all canopy layers. Overall, the results suggest that nectar concentration is strongly shaped by both environmental exposure and tree age in an interactive way, while nectar volume is mainly driven by age with only minor and consistent effects of canopy position.

Table 2
Two-Way Factorial ANOVA Results for Nectar Traits

Source of Variation	df	F (Concentration)	p-value	F (Volume)	p-value
Tree Layer (L)	6	13,738.25	< 0.001	3.84	0.005
Age Class (A)	2	64,842.57	< 0.001	26.18	< 0.001
Layer x Age	12	2,432.54	< 0.001	1.41	0.208

The implications of Fig. 2 are that nectar quality is not controlled by a single factor, but by a strong interaction between **tree age and microclimate exposure**. Because older trees in the upper canopy produce the most highly concentrated nectar, these individuals likely contribute disproportionately to shaping pollinator foraging patterns, potentially attracting more visits but offering smaller nectar volumes per flower. This may create spatial and age-based “hotspots” of high-energy nectar that influence how pollinators distribute their activity within the canopy. At the ecosystem level, the stronger concentration in exposed upper canopy layers suggests that **future increases in temperature and evaporative demand could amplify these differences**, making nectar resources more unevenly distributed across tree structures. Younger trees and shaded canopy layers may become relatively less rewarding, which could shift pollinator preference toward older, exposed individuals. However, this also implies a potential risk: while nectar becomes more energy-dense in stressed conditions, it may also become less abundant in volume, possibly reducing total resource availability. Over time, this imbalance could affect plant–pollinator interactions by increasing competition among pollinators and altering pollination efficiency, especially in warming and drying climates.

Figure 3 shows that nectar volume declines with tree age in a largely parallel pattern across all canopy layers, indicating no significant interaction between tree age and canopy position; in other words, the rate of decline in nectar volume is consistent regardless of where the flower is located in the canopy. This contrasts with sugar concentration, which exhibits a significant multiplicative interaction ($p < 0.001$), as evidenced by diverging lines across canopy layers: while concentration increases with tree age in all layers, the increase is substantially stronger in the upper canopy (AL3) compared to lower positions, demonstrating that canopy position modifies the effect of tree age on nectar concentration.

The Field Ruler: Bivariate Regression Analysis was developed as a practical tool for yield forecasting by modeling the mechanical concentration–dilution trade-off using bivariate linear regression.

Table 3 shows a strong and statistically significant negative relationship between concentration and nectar volume, indicating that as concentration increases, nectar production declines. The model explains a substantial proportion of variation in nectar volume ($R^2 = 0.620$), suggesting that concentration is a key predictor of nectar output in this system. This relationship has important ecological implications, particularly in the context of climate change. Rising temperatures and altered precipitation patterns are expected to increase evaporative demand and plant water stress, which can effectively raise solute concentration in floral nectar and surrounding plant tissues. Based on the regression results, such increases in concentration would likely lead to reduced nectar volumes, potentially decreasing floral resource availability for pollinators. This could negatively affect pollinator foraging efficiency, plant–pollinator interactions, and ultimately pollination success and ecosystem stability. In this way, the model provides a useful predictive framework for understanding how climate-driven changes in plant physiological conditions may cascade through ecological networks.

Table 3
Bivariate Regression Parameters for Predicting Nectar Volume (µL)

Predictor Variable	Coefficient (beta)	Std. Error	t-statistic	p-value
Intercept	0.8456	0.0294	28.77	< 0.001
Concentration (%)	-0.0189	0.0021	-9.21	< 0.001

Model Fit: $R^2 = 0.620$; $F = 84.85$; $p < 0.001$.

Interpretation of Fig. 4: This model allows beekeepers to predict volume based on concentration using the "Field Ruler" formula: **Volume (µL) = 0.8456 − 0.0189 * (Concentration)**.

3.4 The 50-Year "Viscosity Trap": Multiple Regression and Climate Projections

Table 4 presents the results of a multiple linear regression model used to predict nectar volume based on both concentration (%) and temperature (°C). The analysis shows that concentration remains a strong and statistically significant predictor of nectar volume, with a negative coefficient ($\beta = -0.0191$, SE = 0.0025, $t = -7.70$, $p < 0.001$), indicating that higher concentrations are associated with reduced nectar production. In contrast, temperature has a negligible and non-significant effect on nectar volume ($\beta = 0.0008$, SE = 0.0067, $t = 0.11$, $p = 0.910$), suggesting that within the observed range it does not meaningfully influence nectar output. The intercept is 0.8306 (SE = 0.1348, $t = 6.16$, $p < 0.001$). Overall, these results indicate that concentration is the dominant driver of nectar volume in this model, while temperature does not contribute explanatory power when both variables are considered together.

In the context of climate change, these findings suggest that shifts in environmental conditions may affect nectar production primarily through pathways that alter concentration dynamics (such as increased evapotranspiration or water stress), rather than through direct temperature effects alone. This implies that climate-driven changes in plant water balance could have more immediate consequences for nectar availability and thus for pollinator resources than temperature increases per se.

Table 4
Multiple Linear Regression (MLR) Summary

Predictor	Coefficient (beta)	Std. Error	t-stat	p-value
Intercept	0.8306	0.1348	6.16	< 0.001
Concentration (%)	-0.0191	0.0025	-7.70	< 0.001
Temperature (°C)	0.0008	0.0067	0.11	0.910

Climate Forecasting and Temporal Projections (Climate Change Implications)

Figure 5 presents a 3D response surface illustrating the interaction between temperature, concentration, and nectar volume, showing that warming intensifies evaporative stress and accelerates the concentration–dilution trade-off. Although temperature is not a statistically significant independent predictor of nectar volume ($p = 0.910$), it plays an important indirect role as a climate-driven stressor that enhances water loss and therefore increases nectar concentration, ultimately steepening the decline in nectar volume under future warming scenarios.

From a climate change interpretation perspective, this finding suggests that **warming does not need to act directly on nectar production to have strong ecological consequences**. Instead, it modifies the physiological environment in which nectar is produced, particularly through increased evapotranspiration and reduced water availability. This makes concentration a key intermediary variable linking climate change to biological outcomes.

Under the **20-year projection (2046)**, a moderate warming of + 0.8°C leads to an increase in upper-canopy concentration to approximately 39.5%, with nectar volume reduced to 0.17 µL. This represents an early **climate stress response phase ("Alert Phase")**, where pollination resources begin to decline due to reduced nectar accessibility. Ecologically, this indicates that even relatively small temperature increases may already begin to alter plant–pollinator interactions by reducing foraging efficiency and increasing energetic costs for pollinators.

By the **50-year projection (2076)** under + 2.0°C warming, the system reaches a critical threshold termed the **"Viscosity Trap."** At this stage, concentrations exceed 42.8% and nectar volume falls below 0.10 µL, approaching a functional limit for honeybee extraction. In climate change terms, this represents a **nonlinear ecological response or tipping point**, where gradual warming produces disproportionate biological impacts. Nectar becomes so concentrated and limited in volume that it may no longer be energetically or mechanically viable for pollinators to harvest, threatening the stability of pollination services in upper-canopy ecosystems.

As summarized in Table 5, the model therefore indicates that climate warming does not only reduce nectar quantity but also fundamentally alters nectar physical properties, shifting it toward higher viscosity and lower accessibility. This has important implications for apiculture and ecosystem stability, as it suggests a future in which pollinator efficiency declines even in systems that remain florally available.

Interpretation in the Context of Climate Change

Overall, the projections indicate that climate warming acts primarily as an amplifier of physiological constraints rather than a direct predictor of nectar volume. The key climate change implication is that rising temperatures intensify water stress and evaporative loss, which in turn increases nectar concentration and reduces its physical usability. This creates a cascading effect where small climatic shifts produce large ecological consequences for pollinators.

Importantly, the model suggests a **nonlinear risk structure**, where impacts remain moderate at lower warming levels (+ 0.8°C) but escalate sharply beyond a threshold (+ 2.0°C), consistent with tipping-point behavior observed in climate-sensitive ecological systems. This implies that future climate change may not result in gradual declines in pollination services, but rather in **abrupt functional disruptions** once physiological limits of nectar harvestability are exceeded.

Consequently, the findings highlight that climate change adaptation strategies in apiculture and ecosystem management should focus not only on temperature increases, but also on their secondary effects on plant water balance, nectar viscosity, and pollinator accessibility.

Table 5
Climate Sensitivity Simulation: Projected Impact of Regional Warming on Nectar Harvestability (2026–2076)

Period	Projected Temp. Change	Nectar State	Bio-Physical Threshold	Impact on Apiculture
Current	0.0 C (Base)	Variable	Equilibrium	Optimal foraging; high-solute hotspots in AL3.
2046	+ 0.8 C	**Alert Phase**	Conc. approx. 39.5%	Foraging efficiency begins to decline; fluid compression.
2076	+ 2.0 C	**Viscosity Trap**	Conc. > 42.8%	**Unharvestable**: Volume < 0.10 uL; physical extraction limit reached.

Conclusion

This study establishes a comprehensive quantitative framework for understanding how canopy stratification, tree ontogeny, and microclimatic variability jointly regulate nectar dynamics in Croton macrostachyus within the Afromontane ecosystems of Sidama and Hawassa. The findings demonstrate that nectar secretion is strongly governed by a concentration–dilution trade-off, whereby increasing nectar solute concentration is consistently associated with declining nectar volume under intensified evaporative stress. Vertical canopy gradients and ontogenetic variation significantly influenced nectar traits, with upper canopy strata (AL1–AL3), particularly in older trees, producing

highly concentrated but low-volume nectar compared with lower and middle canopy layers. These exposed upper-canopy zones therefore function simultaneously as high-energy nectar hotspots and physiologically vulnerable microenvironments that are highly sensitive to climatic stress.

A strong inverse relationship between nectar concentration and nectar volume ($r = -0.79$, $p < 0.01$) confirms the existence of a fundamental physiological constraint in nectar production. The predictive regression model, $V = 0.8456 - 0.0189C$, explained 62% of the observed variation in nectar volume, providing a robust ecological and practical tool for forecasting nectar availability and potential honey yield under varying environmental conditions. Furthermore, factorial ANOVA revealed significant interactions between canopy position and tree age in determining nectar concentration, whereas nectar volume declined more consistently across canopy layers with increasing tree age. These results indicate that microclimatic exposure amplifies age-related physiological effects on nectar quality while progressively constraining nectar quantity.

Importantly, climate projection analyses revealed that future warming may substantially alter nectar accessibility and pollination functionality. Simulated warming scenarios (+ 0.8°C by 2046 and + 2.0°C by 2076) indicated that increasing evaporative demand will intensify nectar concentration while sharply reducing nectar volume. The projected transition from an early "Alert Phase" to a critical "Viscosity Trap" suggests the emergence of a nonlinear ecological tipping point in which nectar becomes excessively concentrated and physically difficult for honeybees to harvest efficiently. By 2076, nectar concentrations are projected to exceed 42.8%, while nectar volume may decline below 0.10 µL, representing a functional threshold beyond which nectar extraction becomes energetically and mechanically limiting for pollinators.

Overall, the study demonstrates that climate warming may not only reduce nectar quantity but also fundamentally alter nectar physical properties, thereby threatening pollinator efficiency, honey production, and long-term plant–pollinator stability. The findings emphasize that ecosystem resilience and sustainable apiculture will depend on maintaining ecologically functional nectar volumes through the conservation of canopy heterogeneity, ontogenetic diversity, and microclimatic buffering capacity. This work provides important ecological insight into how climate-driven physiological stress may reshape nectar-mediated interactions in tropical forest ecosystems and offers a predictive foundation for future pollination ecology, apicultural management, and climate adaptation strategies.

Declarations

Ethics approval and consent to participate:

Not applicable.

Consent for publication:

Not applicable.

Competing interests:

The authors declare that they have no competing interests.

Funding:

No external funding was received for this study.

Author Contribution

Muzeyin Ahmed (Principal Investigator & Statistician): Designed the study and predictive modeling framework, coordinated field implementation, performed statistical analyses (MANOVA, factorial ANOVA, and bivariate linear regression), drafted the Results and Discussion, and approved the final manuscript. Kassim Roba (Botanist & Lead Field Researcher): Conducted field data collection and floral sampling, processed nectar volume and solute concentration measurements, and drafted the Introduction and Methods. All authors contributed to data interpretation and approved the final manuscript.

Acknowledgements:

The authors acknowledge regional agricultural bureaus of Sidama and Hawassa for their cooperation and assistance during field data collection.

Data Availability

The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

References

1. **Ballesteros, D., & Hill, L. M. (2020).** Physiological and environmental controls on nectar secretion. *Annals of Botany*, 125(2), 241–255.
2. Bathiany, S., Dakos, V., Scheffer, M. and Lenton, T.M., 2018. Climate models predict increasing temperature variability in poor countries. *Science advances*, *4*(5), p.eaar5809.
3. **Canto, A., Herrera, C. M., Medrano, M., Pérez, R., & García-Mendoza, M. E. (2008).** Nectar traits of flowers in different canopy layers. *Journal of Tropical Ecology*, 24(2), 177–186.
4. Delgado, D.L., Pérez, M.E., Galindo-Cardona, A., Giray, T. and Restrepo, C., 2012. Forecasting the influence of climate change on agroecosystem services: Potential impacts on honey yields in a

Small-Island developing state. *Psyche: A Journal of Entomology*, *2012*(1), p.951215.

5. Escalante-Pérez, M. and Heil, M., 2011. Nectar secretion: its ecological context and physiological regulation. In *Secretions and exudates in biological systems* (pp. 187–219). Berlin, Heidelberg: Springer Berlin Heidelberg.
6. **Givnish, T. J. (1988).** Adaptation to sun and shade: A whole-plant perspective. *Australian Journal of Plant Physiology*, 15(2), 63–92.
7. Hamdan, A., Al-Salaymeh, A., AlHamad, I.M., Ikemba, S. and Ewim, D.R.E., 2023. Predicting future global temperature and greenhouse gas emissions via LSTM model. *Sustainable Energy Research*, *10*(1), p.21.
8. **Huberty, M. D., & Morris, J. D. (1989).** Multivariate Analysis of Variance (MANOVA). *Psychological Bulletin*, 105(2), 302–308.
9. Jakobsen, H.B. and Kritjánsson, K., 1994. Influence of temperature and floret age on nectar secretion in Trifolium repens L. *Annals of Botany*, *74*(4), pp.327–334.
10. Jilo, K.R., 2024. Impacts of Some Environmental Factors and Age of Plants on Nectar Volume and Concentrations of Croton Macrostachyus. J *Med Biol*, *5*(1), pp.1–8.
11. **Kessler, D., & Baldwin, I. T. (2007).** Making sense of nectar scents: The effects of nectar secondary metabolites on pollinators. *Science*, 317(5838), 661–663.
12. Kim, W., Gilet, T. and Bush, J.W., 2011. Optimal concentrations in nectar feeding. *Proceedings of the National Academy of Sciences*, *108*(40), pp.16618–16621.
13. **Lawson, D. A., & Rands, S. A. (2019).** The effects of temperature on foraging behavior and nectar extraction. *Behavioral Ecology*, 30(4), 1012–1022.
14. **Nagamitsu, T., & Inoue, T. (2005).** Variations in nectar secretion and visitation of bees across forest layers. *Ecology Research*, 20(3), 321–329.
15. **Nicolson, S. W. (2022).** Nectar as a dynamic resource: Challenges for pollinators in a changing climate. *Frontiers in Plant Science*, 13, 865129.
16. **Niinemets, Ü. (2007).** Photosynthesis and resource distribution through plant canopies. *Plant, Cell & Environment*, 30(9), 1052–1071.
17. Olonscheck, D., Schurer, A.P., Lücke, L. and Hegerl, G.C., 2021. Large-scale emergence of regional changes in year-to-year temperature variability by the end of the 21st century. *Nature Communications*, *12*(1), p.7237.
18. Ochieng, F.O., 2024. A novel data-driven dynamical model for predicting future climate trends. *Modeling Earth Systems and Environment*, *10*(4), pp.4599–4610.
19. **Pacini, E., & Nepi, M. (2007).** Nectar production and presentation. In *Nectaries and Nectar* (pp. 167–214). Springer, Dordrecht.
20. Parachnowitsch, A.L., Manson, J.S. and Sletvold, N., 2019. Evolutionary ecology of nectar. *Annals of botany*, *123*(2), pp.247–261.

21. Pyke, G.H., 2016. Floral nectar: pollinator attraction or manipulation?. *Trends in ecology & evolution*, *31*(5), pp.339–341.
22. **Roba, K., 2019. Evaluation of the Effect of Temperature, Relative Humidity, Plants Age and Time on Nectar Volume and Concentration of Callistemon citrinus L. International Journal for Research in Agricultural and Food Science**, **5(11), pp.01–13.**
23. **Villarreal, A. S., et al. (2021).** Modeling nectar viscosity and sugar concentration in Afromontane flora. *Journal of Arid Environments*, 184, 104291.
24. **Welti, E. A., Kaspari, M., Sanders, N. J., & de Beurs, K. M. (2020).** Nutrient dilution and climate-driven impacts on plant-pollinator interactions. *Proceedings of the National Academy of Sciences (PNAS)*, 117(19), 11554–11562.
25. **Willmer, P. G. (2011).** *Pollination and Floral Ecology*. Princeton University Press.
26. **Zar, J. H. (2010).** *Biostatistical Analysis* (5th ed.). Pearson Education.

Figures

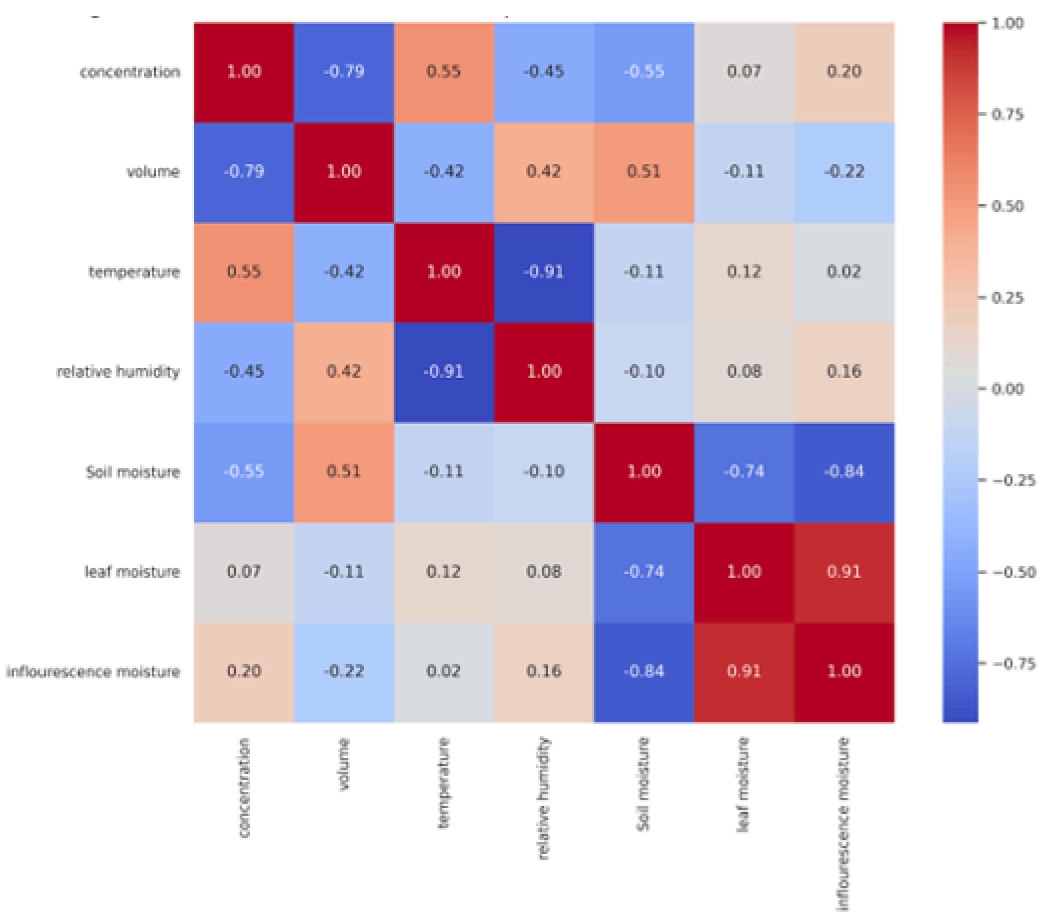

Figure 1

Pearson Correlation Heatmap of Nectar Traits and Environmental Factors

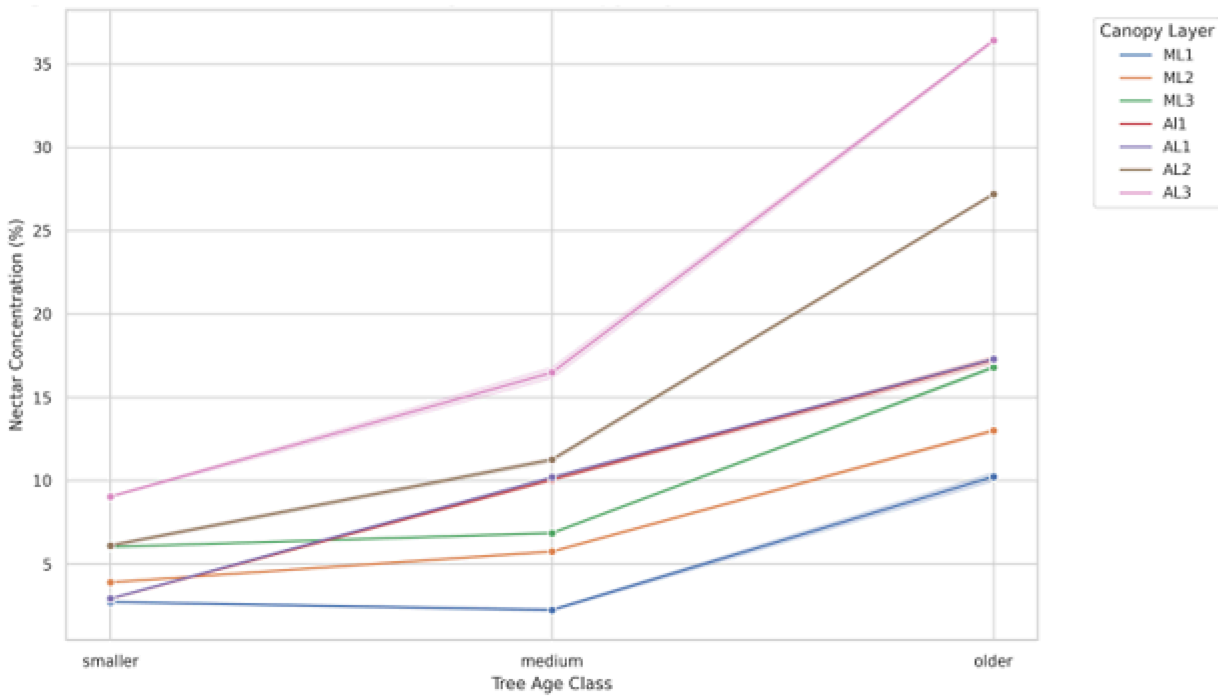

Figure 2

Interaction Effect of Trees Age and Canopy Layer on Nectar Solute Concentration

Figure 3

Interaction Effect of Tree Age and Canopy Layer on Nectar Volume

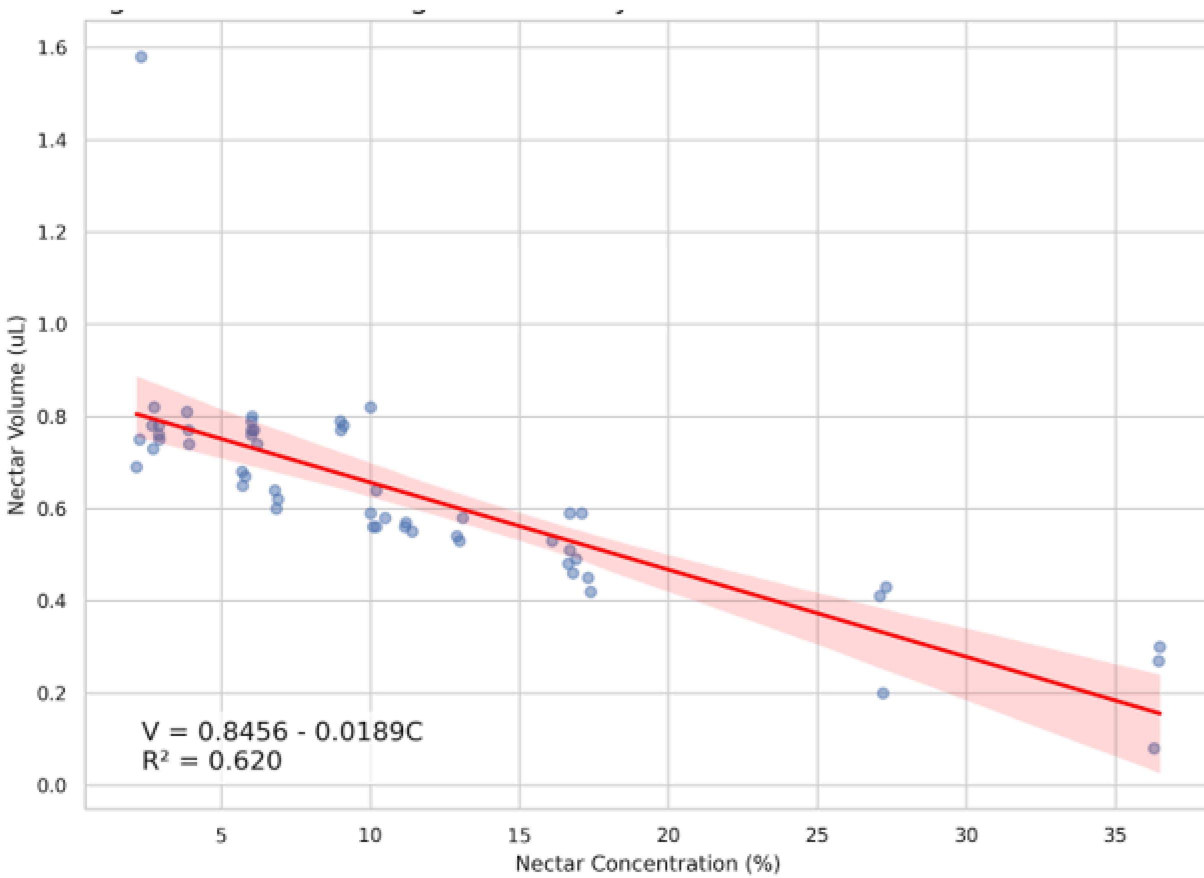

Figure 4

Bivariate Regression Analysis of Nectar Volume as a Function of Concentration

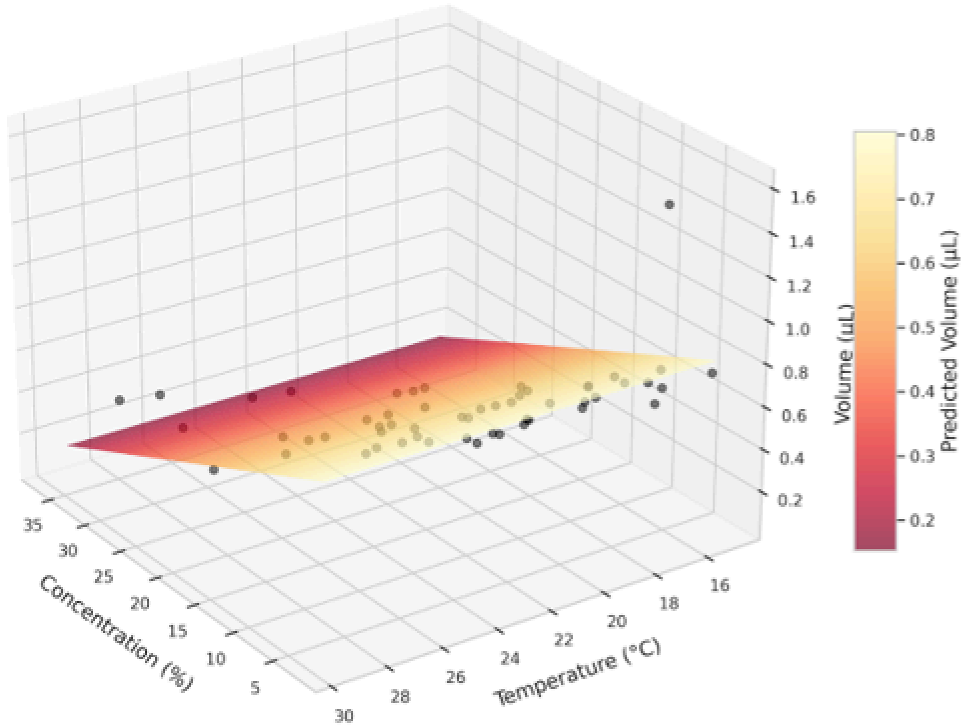

Figure 5

3D Regression Surface: Nectar Volume response to Concentration and Temperature