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EDITED BY

Luis Raul Comolli,
Independent researcher, Basel,
Switzerland

REVIEWED BY

Lieslea Magaliao Wagayen,
Don Mariano Marcos Memorial State
University, Philippines
Ricardo Borjas,
Universidad Nacional Agraria La Molina,
Peru

*CORRESPONDENCE

Stéphane Saj
✉ stephane.saj@fibl.org

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Unravelling the link between tree architecture and production potential in *Theobroma cacao*: implications for pruning strategies

Stéphane Saj^{1*}, Thomas Wibaux^{2,3}, Sam Wallner^{1,4},
Lucia Descarpontrie⁵, Consuelo Campos⁵, Ruben Humerez⁶,
Johanna Rüegg¹ and Pierre-Eric Lauri²

¹Department of International Cooperation, Research Institute of Organic Agriculture (FiBL),
Frick, Switzerland, ²ABSys, CIRAD, INRAE, Institut Agro, Université de Montpellier, Montpellier, France,
³CIRAD, UMR ABSys, Montpellier, France, ⁴Haute École du paysage, d'ingénierie et d'architecture
(HEPIA), Geneva, Switzerland, ⁵Ecotop Foundation, La Paz, Bolivia, ⁶PIAF-El Ceibo Foundation, La
Paz, Bolivia

Current pruning recommendations for clonal cacao (*Theobroma cacao*) lack scientific support regarding tree architectural development. This study investigates the relationship between tree architecture and production potential using data from a long-term trial in Bolivia. We measured architectural and production traits on 331 seventeen-year-old grafted trees across five cropping systems, ranging from conventional monocultures to input-free dynamic agroforestry, and four genotypes. We differentiated the productive “leafless zone” from the “leafy crown,” measuring branch orders, diameters, lengths in the former, and crown geometry traits in the latter. Results demonstrate that, while cropping systems and genotypes significantly influence vegetative biomass, the structural drivers of pod production remain consistent. Production was strongly related to the vigor (diameter) and number of low-order scaffold branches (orders 1 and 2) after accounting for cropping system type and genotype. Modelling confirmed that trees with complex scaffold structures and thicker 1st-order branches produced significantly more pods and beans than those with simple structures, with crown projected surface and foliage height further enhancing production potential. These findings challenge standard pruning recommendations focusing mainly on leafy crown management. We conclude that production potential is determined by the development of scaffold branches in combination with effective crown management. Consequently, pruning strategies should evolve from simple canopy control toward preserving vigorous scaffold branches and optimizing the tree’s physiological capacity for fruit production. To support this shift, we propose an architectural typology based on the branching structure of the leafless zone in grafted cacao trees to assess production potential and guide pruning decisions.

KEYWORDS

agroforestry, cropping systems, genotype, pruning strategies, *Theobroma cacao*, tree architecture, yield components

1 Introduction

Cacao (*Theobroma cacao*) is a species native to the Neotropics of Central and South America, with its domestication process traced to the Amazon basin, suggesting origins at least 5,000 years ago (Lanaud et al., 2024; Motamayor et al., 2008). It is a small evergreen tree with multiple trunks that can grow to between 10 and 15 meters tall in the wild. As a shade-tolerant species, it usually thrives in the understory with high air moisture. A distinctive feature of cacao is its production of flowers directly on the trunk and large branches (a trait known as cauliflory), where small flowers appear in clusters called floral cushions. In the wild, most trees are self-incompatible, meaning that fertilization requires pollen from genetically distinct individuals. Due to this self-incompatibility system, a high proportion of flowers abort and only a small percentage develop into fruit, called pod. Seed dispersal is mainly attributed to animal activity, as ripe pods fall to the forest floor where rodents and other fauna distribute seeds, allowing seedlings to establish in suitable microhabitats (Lanaud et al., 2017).

The cacao vegetative development follows the “Nozeran’s architectural model”, characterized by a dimorphic branching system. The main sympodial trunk is articulated into modules of successive orthotropic axes, each terminated by a crown of leafy plagiotropic branches (Bell and Bryan, 2008; Hallé et al., 1978). The foliage is produced rhythmically on plagiotropic branches of this leafy crown, and new modules of trunks and crowns are also rhythmically produced from the base or top of established orthotropic axes. When cultivated, cacao is usually restrained from its natural vegetative development through pruning and the removal of supernumerary trunks and orthotropic shoots. In most extensive management schemes, such as the agroforests of Central Cameroon, cacao is grown from seeds and allowed to develop for two or more successive modules, left to grow up to 8–10 m height. In that case, the most important management intervention consists in the removal of new orthotropic shoots (suckers) on or next to the 1st trunk (Jagoret et al., 2017). In more technical management schemes, cacao is cultivated with clones of selected genotypes, produced from scions collected on plagiotropic branches and usually grafted onto rootstocks grown from seed (Waldburger et al., 2019). These grafted trees are therefore composed almost entirely of plagiotropic branches, apart from the remaining portion of the rootstock, and they lose the dimorphic growth habit characteristic of seed-grown cacao. The resulting grafted tree develops a shrub-like architecture, with the lowest, defoliated plagiotropic axes serving as scaffold branches, that support a pseudo-crown of dense foliage (called hereafter “leafy crown”), and which rarely exceeds 5 m in height.

Surprisingly, pruning recommendations for cacao did not evolve much despite the tree’s long history of cultivation (Braudeau, 1969). This may be because relatively little research has examined cacao responses to pruning, with most studies focusing on pruning intensity (i.e., the proportion of foliage removed) rather than on the branching structures resulting from pruning and their effects on yield components (Tosto et al., 2022; Thomas and Balasimha, 1992; Susanti et al., 2017; Villamar-Torres and Jazayeri, 2022). The pruning recommendations for cacao are based on a set of fundamental principles that are widely applied in all technical manuals: (i) maintain a canopy height to a defined maximum, (ii) avoid branch overlap between neighbor cacaos, (iii) maintain an “open” canopy in order to promote light penetration

within the (leafy-)crown, (iv) eliminate suckers, low-hanging and/or diseased shoots, (v) align pruning schedule to local cacao phenological cycle. Even though these rules follow a certain logic, they lack scientific support and are rarely adapted to the specific conditions of different orchard types, which limits their adoption in many regions (Obeng Adomaa et al., 2022).

In particular, we lack evidence-based guidelines for pruning in the specific context of clonal cacao, where the dimorphic architectural model no longer applies and tree architecture is strongly dependent on the tree training and pruning strategy. This contrasts with the pruning principles based on tree architecture and physiology that have been meticulously developed for other fruit-tree species and with high adoption rates, such as mango (Normand and Lauri, 2018) or apple (Lauri and Simon, 2019). Furthermore, cacao exhibits a specific reproductive habit known as cauliflory, which implies a particularly strong relationship between the tree architecture of trunks and older branches, where reproductive sites are located (Wibaux et al., 2025). It is also well established that the vegetative development and yield of cacao are tightly linked (Pang and Lockwood, 2008; Yapp and Hadley, 1994) and strongly modulated by genotype (Daymond et al., 2002; Ofori et al., 2016), cropping system (Armengot et al., 2023; Efron et al., 2005), and propagation mode (i.e., trees planted from seed or cloned through grafting or rooted cuttings (Armengot et al., 2023)). However, it is surprising how few studies have examined how architectural traits affect flowering and pod production in cacao, and how genotype and cropping system modulate this relationship.

Based on existing knowledge of how architectural traits influence the number and activity of flowering sites in relation to genotype (Wibaux et al., 2025), and how management practices such as agroforestry impact the tree biomass, carbon assimilation, and yield of cacao (Krause et al., 2025; Somarriba et al., 2023; Suárez Salazar et al., 2018), we hypothesize that genotype and cropping system shape cacao architecture, which in turn affects its productivity. To test this hypothesis and address the current lack of architecture-based pruning frameworks for cacao, we develop and evaluate a practical architectural typology for grafted cacao trees and assess its ability to explain variation in production potential across genotypes and cropping systems.

Using the SysCom Bolivia long-term trial, which compares the performance of different clones in various cropping systems, we aimed to provide the first comprehensive assessment of this topic. We aimed to answer the following questions: (i) Are there any effects of the cropping system or clone on the vegetative development and flowering and fruiting characteristics of cacao? (ii) Are there any tree architectural traits that favor pod production potential for specific genotype and/or cropping system? (iii) If the answers to the first two questions are positive, what would be the technical applications for cacao pruning?

2 Material and methods

2.1 Research site and trial description

The SysCom long-term trial is located at the Sara Ana Centre for Research and Training in the Alto Beni region of the La Paz department, Bolivia. It is situated on an alluvial terrace of the Alto

Beni River on the north-eastern side of the Andes, at an altitude of approximately 380–400 m a.s.l. (15°27'36.60''S, 67°28'20.65''W). The soils are classified as Lixisols and Luvisols according to the FAO system [Schneider et al. \(2016\)](#). The climate of the area is humid tropical with a unimodal rainfall pattern. The dry season, defined by months with less than 100 mm of rainfall, generally lasts from May to October, while the rainy season occurs between November and April. The mean annual temperature is about 26–27 °C, with recorded extremes ranging from 9 °C (June 2022) to 42 °C (November 2020). Mean annual rainfall is 1635 ± 83 mm based on records from 2013–2022, with most of the precipitation falling between October/November and March/April.

The Bolivian long-term trial is part of the international Farming Systems Comparison in the Tropics (SysCom) program, which investigates the performance of organic and conventional agriculture in the tropics. Established in 2008, the trial compares five cacao cropping systems: conventional monoculture (MC), organic monoculture (MO), conventional agroforestry (AFC), organic agroforestry (AFO), and dynamic agroforestry without external inputs (DAF). This gradient of management intensity - from input-based monocultures to diverse, agroecological systems - provides data on sustainable production strategies. The trial follows a randomized complete block design with four replications. Each plot measures 48 × 48 m, with a central net plot for data collection and border trees to reduce edge effects. Cacao is planted at 4 × 4 m spacing (625 trees ha⁻¹), with 12 genotypes of locally selected or international clones, or full-sib hybrid families. Trees of poorly performing full-sib families were grafted in 2018 with best-yielding individuals of the same family from the trial. The AFO and AFC systems feature permanent shade from leguminous (e.g., *Erythrina* spp, *Inga* spp), timber (*Swietenia macrophylla*), and fruit trees (*Theobroma grandiflorum*) interplanted with cacao, totaling about 200 trees ha⁻¹ in 2024. The DAF system includes these species plus additional crops (e.g., ginger, curcuma), trees (e.g., peach palm), and naturally regenerated species totaling about 440 trees ha⁻¹ in 2024. For more information on: management practices and agroforestry designs, please refer to [Rüegg et al. \(2025\)](#); cacao genotypes, please refer to [Armengot et al. \(2023\)](#); associated tree pruning, please refer to [Saj et al. \(2025\)](#).

In the trial, similar cacao pruning calendar and methods are used across all cropping systems and cacao genotypes. Two types of pruning are applied, maintenance and thinning. Maintenance pruning is carried out once a year, when the peak fruit harvest is declining, typically from mid-August to mid-September, just after fertilizer application in fertilized cropping systems. It involves cutting all branches and shoots that cause excessive shade, as well as suckers, basal and vertically growing branches, and that interfere with the tree scaffold branches and consequently the basic tree structure. Its objective is to improve air circulation and light distribution within the tree as well as to promote new branch sprouting to renew the leafy crown. The pruning height is kept between 3.5 and 4 meters for easier harvesting and phytosanitary control. Thinning pruning is a lighter pruning operation, usually done twice a year, in January-February and April-May, timed according to the cacao's production cycle and weather. It focuses on removing intertwined branches and the branches expanding to neighbors, suckers, aiming to optimize light exposure and aeration

for better flowering and fruit setting. In both types of pruning, visibly damaged or diseased branches are systematically removed.

2.2 Cacao characterization

Not all genotypes included in the trial could be evaluated because of the time required for field measurements, and four genotypes were selected based on the results of [Armengot et al. \(2023\)](#). The two best yielding local clones Ila22 (n=78) and Ila58 (n=79), the best yielding international clone ICS1 (n=94) and clones of the best yielding full-sib family ICS1 × IMC67 (n=80) were selected for the study, totalizing 331 trees. They will be hereafter called genotypes for simplicity.

Cocoa yields, expressed as average yearly pod production [Av. pods per year] and fresh bean weight [Av. beans per year (kg)], were measured for each cacao tree by counting all harvested pods and weighting their contents in fresh beans over three years (2022, 2023 and 2024). The dry weight of the branches was calculated using their approximate volume (see below) multiplied by a 0,43 factor ([Chave et al., 2006](#)).

Cacao branches were characterized between June and July 2024, with the objective to use simple measurements of the tree architecture, that directly reflect the tree's photosynthetic and productive potential as well as biomass. To document the appearance of the tree at the time of measurement, two photographs were taken per tree from different viewpoints to capture the overall architecture as clearly as possible.

We identified two distinct zones within the aerial parts of the cacaos ([Figure 1](#)). The first zone is the “leafy crown” of the tree. It comprises the young branches bearing leaves where carbon fixation and primary growth occur ([Figure 1a](#)). The horizontal projected area of each tree's leafy crown (“projected crown surface”) was estimated by measuring two perpendicular leafy-crown diameters, oriented parallel to the plot boundaries. Measurements were taken using the outermost leaves as reference points, and the estimated crown area was calculated as the surface of an ellipse, following usual calculation methods for tree species ([Röhle and Huber, 1985](#)). A 4-meter marked pole was used to record the height of the lowest and highest leafy branch respectively, representing crown base and maximum height, respectively. When a branch extended far beyond the overall shape, or when one branch emerged much lower than the others, more representative branches were selected to obtain average values for crown dimensions. The measurements of the crown were used to estimate the maximum volume of the crown, calculated as the volume of the ellipse formed by the two horizontal measurements and the vertical crown height.

The second is the “leafless zone”, located beneath the leafy crown. It comprises the main scaffold branches and older leafless sections of the branches, where most of the flowers and pods are set ([Figure 1a](#)). It is therefore the zone where the production potential lies, and it has long been recognized that the vigor of branches/trunks (i.e. their cross sectional area, or diameter) in this lower part of the tree is closely related to this potential ([Pang and Lockwood, 2008](#)).

All branches with an insertion diameter greater than or equal to 3 cm, located between the ground and the base of the leafy crown,

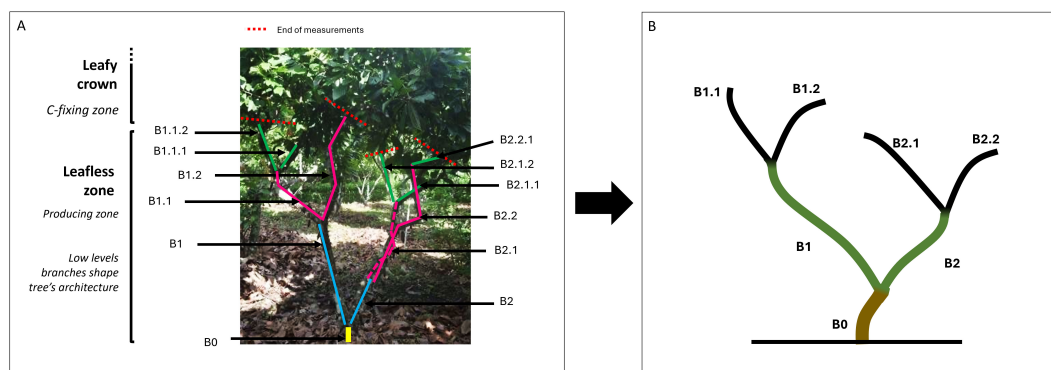


FIGURE 1

(a) Branch coding used for the study. B stands for “branch”. First number after B stands for 1st order number of the branch. Second number after B stands for the 2nd order number of the branch etc. Branch/trunk of order 0: yellow lines. Branch of order 1: blue lines. Branch of order 2: pink (full or dotted) lines. Branch of order 3: green lines. End of measurements: red dotted lines. (b) Representation of the branches chosen for building cacao architectural types.

were counted and measured. The 3 cm threshold was chosen to include the structural branches bearing most flower cushions and pods, while excluding the smaller shoots resulting from late branching in the leafless zone, which are typically removed during maintenance pruning. Each branch section was assigned a “branching order”, distinguishing different levels of branches within the trees, determined by branching whether natural or provoked (by pruning or breakage: Figures 1a, b). We called these levels “order”, even though they do not necessarily correspond to “ramification order” *per se*. We assigned the original trunk or the initial graft point as order 0, with subsequent branching orders increasing at each ramification node, when the branched axis shows a reduced diameter compared to parent axis. For each tree, the length of branches in the leafless zone were measured and summed for each branching order. For higher-order branches, length was measured from the base to the tip or to the start of the leafy crown, unless growth was interrupted by a dead terminal bud, a diameter change, pruning, or breakage. Branch diameters were measured at two points to obtain representative values and averaged for branches of a same branching order. For the order 0, two measurements were taken at different positions, avoiding graft swellings when possible; if this was not feasible, the diameter was noted as not applicable. For higher-order branches, locations of measurement were chosen according to the shape of the branch to reflect an accurate mean diameter.

Flower-cushion density was evaluated on all branches within leafless zones by counting all floral sites (single or merged cushions) within the first 50 cm from the branch insertion point. Only observable floral sites before, during, or after fruiting were recorded, and counts were averaged for branches of the same branching order. Measurements were restricted to the proximal 50 cm of each branch and therefore do not characterize flower-cushion density along the entire branch. This section was selected because cacao flowers develop on persistent flower cushions borne on ageing woody tissues, typically located on trunks and older branches after leaf fall, where reproductive structures are concentrated (Alvim, 1986; Wibaux et al., 2025).

2.3 Building an architectural typology

The typology was built to be practical in nature and describe the basic architectural structure of cacao in a concise manner. It was based on visual observations of the leafless zone under the leafy crown. We used the number of branches found in orders 1 and 2 because these are the thickest branches of the tree and can also be considered as scaffold branches (Figure 1b). We constructed seven architectural types applying this strategy (Figure 2). Type 1x (n=30) corresponds to trees with complete or partial removal of the original scion and bearing a single productive branch of order 1. Type 2 trees are trees with their original scion where two branches of order 1 developed. The subtypes studied correspond to tree with differing numbers of branches of order 2. Type 24- corresponds to trees that have three or less branches of order 2 (n=58). Type 24 corresponds to trees that have 4 branches of order 2 (n=100). Type 24+ corresponds to trees that have more than 4 branches of order 2. Type 3 trees are trees with their original scion where three branches of order 1 developed. The studied subtypes correspond to trees with differing numbers of branches of order 2. Type 35- corresponds to trees that have five or less branches of order 2 (n=48). Type 35+ corresponds to trees that have six or more branches of order 3 (n=35). Finally, type 4x gathers all trees with four productive branches of order 1 (n=18).

2.4 Statistical analyses and modelling

2.4.1 Effect of the cropping system and clone on tree features

We analyzed the effect of each experimental factor on the different branch architecture and crown geometry traits. The set of studied variables included crown geometry (foliage minimum and maximum heights, foliage maximum thickness, projected leafy crown surface, crown volume), branch architecture measurements (numbers, diameters and lengths of orders 0–5; total branch length and total number of branches), and reproductive indicators (flower

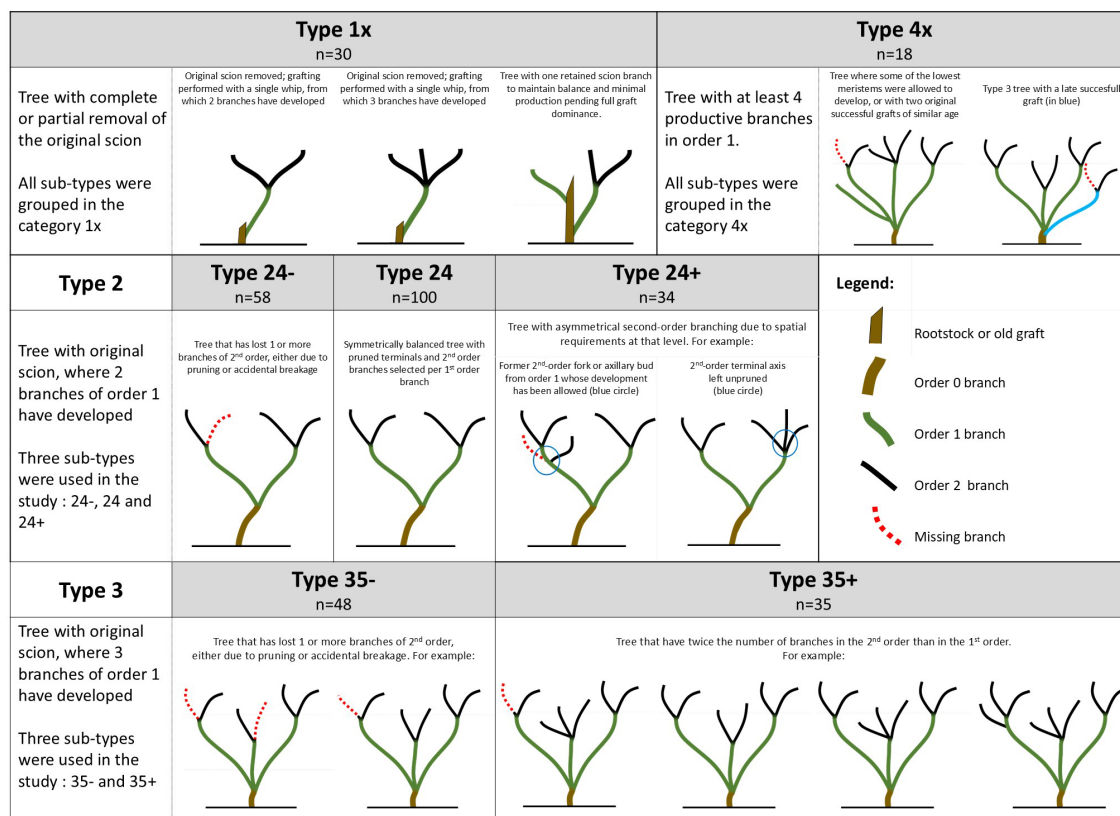


FIGURE 2

Architectural typology of cacao trees used in the study. The first number indicates the number of 1st-order scaffold branches, while the second number indicates the number of 2nd-order branches. For example, Type 1x corresponds to trees bearing a single productive 1st-order branch, Type 24- corresponds to trees with two 1st-order branches and three or fewer 2nd-order branches, and Type 35+ corresponds to trees with three 1st-order branches and six or more 2nd-order branches.

cushion density; averaged number of pods and fresh bean weight per year, average number of pods per linear meter of branch). The set of experimental factors included the system (MC, MO, AFC, AFO, DAF), genotype (Ila22, Ila58, ICS1 and ICS1 × IMC67), Bloc (4), and plot (20), all encoded as categorical. For each quantitative trait, we fitted a linear mixed-effects model with fixed effects for system, genotype, and their interaction, a fixed effect for block, to test the potential effect of the pruning operator, and a random intercept for plot: Trait ~ system × genotype + block + (1|plot). Fixed-effect significance was assessed with Type-III ANOVA F-tests for the main effects and the interaction. *Post-hoc* pairwise comparisons between systems and between genotypes across systems were assessed using the Šidák adjustment, to control for multiple independent families of comparisons.

2.4.2 Relationships between branch architecture, crown and production traits to guide crop management

To study the relationship between branch architecture and pod production, we modelled average yearly pod production (Av. pods per year) with generalized linear mixed-effects models (GLMM). The models were constructed using architectural traits, with a random intercept for plot, and genotype and system were treated as either random or fixed effects. When the models included

interaction between factors, the traits were z-scored prior to modelling. To reduce the number of variables and avoid multicollinearity, we screened the candidate architectural and crown variables using Spearman's rank correlation across all pairs of quantitative traits. Where correlations were high (>0.80), we selected a single trait, favoring variables that were easier to measure and retaining lower-order branch metrics when adjacent orders were highly correlated.

To test the relative importance of the different traits measured on branches of increasing order (from 0 to 5) on pod production, we compared “full models”, which included fine architectural measurements on branches of orders 0–5, with “simple models”, which used only easily measured subsets of traits on branches of orders 0, 1, 2 or 3, either individually or in combination. In these models, genotype and system were set as random factors.

To test whether our typology captures architecture–yield information, we contrasted the ‘full model’ with typology-based models that comprised either typology only or typology and other easily measurable traits (branch length and diameter up to order 3, i.e. ‘typology models’).

To enable comparison between models built using measurements of branches up to the fifth branching order, we employed a reduced dataset comprising only individuals with at least one branch at the fifth branching order. We used AIC (Akaike Information Criterion) to assess the goodness of fit of the models

and marginal or conditional R^2 to interpret the variance explained by the fixed factors, with or without random effects. Likelihood-ratio tests between nested models were used to determine whether adding or removing certain traits significantly altered the fit ($\alpha = 0.05$). The effect sizes of model factors on pod production were reported by exponentiating the coefficients of the model (log link).

The best “typology model” was then fitted to the full dataset, with genotype and systems as fixed factors, with or without interaction, in order to test its suitability for predicting and comparing tree production across systems and varieties. To make adjusted comparisons between typologies, we fitted the model with genotype and system set as fixed effects for interpretability and plot as a random intercept to account for field-level heterogeneity. We then tested whether responses to the typology differed by genotype or system via an interaction model. This model was used to identify typologies associated with higher production within each genotype and system by estimating marginal means and conducting Tukey or Sidak adjusted pairwise contrasts among typologies within genotypes and systems. The combinations of typology and system or genotype were only tested for pairwise contrasts when the combinations showed at least five occurrences in our data.

Finally, to account for the potential moderating effect of crown traits on the model, we tested, for different crown geometry trait, i.e. “projected crown surface”, “minimum foliage height”, “foliage thickness” (difference between foliage maximum and minimum height) and “crown volume”: (i) its additive contribution to the previously selected architectural model, by comparing models with and without the crown trait using likelihood-ratio tests ($\alpha = 0.05$) and changes in marginal and conditional R^2 ; (ii) its moderation effect, by testing the interaction between the crown trait and the average diameter of 1st-order branches, and examining whether these effects varied among architectural typologies; (iii) the existence of thresholds or plateau in the hypothesis of non-linear relationship between the crown trait and its effect on production, with the use of gamma-log generalized additive models (GAMs), to capture non-linear dependencies between each crown trait and pod production.

All analyses were performed using R Statistical Software (version 4.4.1; R Core Team 2024). Linear mixed-effects models were fitted with the ‘lme4’ package for most architecture and crown geometry traits (version 1.1-37; Bates et al., 2015) or using Gamma (log) generalized linear mixed models from glmmTMB package (version 1.1.11; McGillicuddy et al., 2025), to account for the right-skewed nature of production variables. Fixed-effects were retrieved using F-tests from the ‘lmerTest’ package (version 3.1-3; Kuznetsova et al., 2017). Spearman’s rank correlation tests were conducted using ‘stats’ package (version 4.4.1; R Core Team 2024) and all *post-hoc* comparisons were performed using the ‘emmeans’ package (version 1.11.2; Lenth and Piaskowski, 2025). GAMs were fitted using ‘mgcv’ package (version -1.9-3; Wood et al., 2016). The schematic workflow of the modelling strategy is presented in the Supplementary Materials (Supplementary Figure 1).

3 Results

3.1 Analyses of the cropping system and clone effects on architecture, crown and production traits

General linear mixed models were fitted for each architectural type and for each crown and production trait. The additive and interaction effects of the genotype, cropping system, and block are presented in Table 1. Table 2 contains details of the average values and standard deviation for the main architectural, crown, and production variables, as well as the pairwise comparisons between cropping systems and between genotypes within each cropping system. The average values for a selected number of variables for each genotype and systems are provided in Supplementary Material (Supplementary Tables 1–4).

The effects of the cropping system were significant for total branch count, total branch length, and branch counts and lengths at orders 3–5. The system also influenced the average diameter of branches across orders 0–4 and crown geometry, including projected crown surface, crown volume, pod and bean productions (Table 1). The most notable effect was that the conventional monoculture (MC) system had higher counts of high-order branches (third, fourth, and fifth order) and crown volume compared to the dynamic agroforestry (DAF) system (Tables 1, 2). Additionally, the two monocultures (MC and MO) exhibited significantly larger diameters of 1st- to 3rd-order branches and higher values of branch weights, pod production, and bean production compared to agroforestry systems (AFC, AFO, and DAF). Trees in the DAF system yielded the least among all systems (Table 2; Figure 3).

Genotype had strong effects on all architectural traits, including the number, average diameter and sum of branch lengths up to the fourth’s branching order, as well as every crown measurement and pod or bean productions (Table 1). Genotype “ICS1 x IMC67” in particular showed significantly lower vigor and branching development as compared to every other genotype, across all systems (Table 2; Figure 3). This genotype also showed lowest pod and bean productions, although differences with other genotypes were more significant under full sun than under agroforestry (Table 2; Figure 3). Beyond the main effects, several traits showed genotype-specific responses to cropping system: branch numbers count at orders 2–3, total branch count, total branch length, average diameters at orders 1–4, projected crown surface, yearly pod and bean productions and average number of pods per meter of branch, indicating that genotypes differed in how architecture and production responded to management context (Table 1). Block effects were observed on architectural traits (e.g., counts of branches at order 3–4; average length of order-4 branches and total branch length; diameter of order-2 branches), as well as crown volume traits, although without effect on pod and bean productions.

TABLE 1 Effects of experimental factors and the interaction between system and genotype on every architecture, crown and production trait.

Trait	Cropping system	Genotype	System vs. genotype	Block
Architecture				
Branch count o0	—	***	—	—
Branch count o1	—	***	**	—
Branch count o2	**	***	**	—
Branch count o3	**	***	—	**
Branch count o4	*	***	—	*
Branch count o5	—	—	—	—
Total branch count o0-o5	***	***	***	**
Sum branch length o0	—	***	—	—
Sum branch length o1	—	***	—	—
Sum branch length o2	—	***	*	—
Sum branch length o3	**	***	—	—
Sum branch length o4	***	***	—	***
Sum branch length o5	*	**	—	—
Total branch length o0-o5	***	***	**	*
Av. diam. branch o0	***	***	—	—
Av. diam. branch o1	***	***	*	—
Av. diam. branch o2	***	***	*	*
Av. diam. branch o3	***	***	**	—
Av. diam. branch o4	***	***	*	—
Av. diam. branch o5	—	—	—	—
Flowering				
Est. flower cushion density o0	—	***	—	—
Est. flower cushion density o1	—	***	—	—
Est. flower cushion density o2	—	***	***	*
Est. flower cushion density o3	—	***	***	—
Est. flower cushion density o4	—	***	*	**
Est. flower cushion density o5	—	***	—	*
Crown geometry				
Max. height	*	***	—	**
Max. thickness	*	***	—	***
Min. height	—	***	*	*
Projected crown surface	**	***	**	—
Max. crown volume	**	***	—	***
Crown thickness/max. height	—	***	—	***
Production				
Av. pods per year	***	***	***	—
Av. beans per year	***	***	***	—
Av. pods per m of branch	***	***	***	—

Branching order from 0 to 5 is abbreviated as o0 to o5. *p < 0.05; **p < 0.01; ***p < 0.001. Av., average; Est., estimated; Max., maximum.

Overall, genotype showed important effects on architecture, crown traits, and pod and fresh bean yearly productions, while the cropping system added further substantial variation. Such results suggest that both factors should be included in all

subsequent models and comparisons, and block effect should be considered for all models that include crown traits, to account for the putative effect of the pruning operator (one per block).

TABLE 2 Mean values and standard error (in brackets) of major architecture, crown and production traits of cacao for each cropping system (bold lines) and genotype within each system.

System and genotype	Count branches	Sum branch length (m)	Sum branch weight (kg)	Av. diam. 1 st order branches (cm)	Proj. crown surface (m ²)	Crown thick. / max. height	Average pods per year	Av. fresh beans per year (kg)	Av. pods per m of branch
MC	25.6 (8,9)^c	19.1 (6,2)^c	39.0 (18,1)^b	11.5 (2,5)^b	13.5 (3,4)^c	0.41 (0,07)^a	74.3 (35,9)^c	2.9 (1,4)^c	3.9 (1,57)^d
ICS 1	26.8 (7,5) ^b	22.8 (5,3) ^b	48.1 (15,0) ^b	11.9 (2,1) ^b	14.6 (2,9) ^b	0.40 (0,06) ^a	62.4 (21,0) ^b	2.3 (0,8,0) ^b	2.7 (0,80) ^a
ICS 1 x IMC 67	15.5 (4,7) ^a	10.4 (3,3) ^a	16.0 (8,0) ^a	8.8 (2,6) ^a	9.1 (2,6) ^a	0.46 (0,10) ^b	37.7 (16,9) ^a	1.6 (0,8) ^a	3.6 (1,23) ^b
lla 22	25.6 (3,6) ^b	20.6 (2,9) ^b	44.3 (13,8) ^b	12.4 (1,9) ^b	15.1 (2,2) ^b	0.40 (0,08) ^{ab}	119.1 (25,4) ^c	4.4 (0,9) ^d	5.8 (1,27) ^c
lla 58	34.0 (8,6) ^c	20.9 (4,2) ^b	43.9 (14,9) ^b	12.8 (1,6) ^b	14.5 (2,3) ^b	0.40 (0,04) ^{ab}	75.8 (18,9) ^b	3.5 (0,9) ^c	3.7 (0,80) ^b
MO	22.1 (9,6)^{bc}	16.8 (6,3)^{bc}	35.5 (16,6)^b	11.4 (2,9)^b	12.3 (3,4)^{bc}	0.43 (0,07)^a	61.4 (29,8)^c	2.6 (1,2)^c	3.7 (1,36)^{cd}
ICS 1	26.2 (8,1) ^c	20.9 (4,1) ^b	47.3 (13,6) ^b	13.0 (2,2) ^b	14.6 (1,4) ^b	0.42 (0,06) ^a	59.9 (19,7) ^b	2.4 (0,7) ^b	2.9 (1,01) ^a
ICS 1 x IMC 67	12.3 (5,7) ^a	8.6 (3,3) ^a	15.5 (9,5) ^a	7.9 (2,3) ^a	8.0 (2,5) ^a	0.50 (0,08) ^b	30.7 (17,8) ^a	1.5 (1,0) ^a	3.4 (1,18) ^a
lla 22	20.0 (6,3) ^b	17.6 (3,9) ^b	38.1 (10,2) ^b	12.6 (1,7) ^b	13.3 (2,4) ^b	0.42 (0,04) ^a	91.9 (27,9) ^c	3.4 (1,0) ^c	5.3 (1,47) ^b
lla 58	29.5 (7,3) ^c	20.1 (4,2) ^b	41.4 (10,6) ^b	12.2 (1,5) ^b	13.6 (2,3) ^b	0.38 (0,03) ^a	70.6 (19,2) ^b	3.3 (0,9) ^c	3.5 (0,68) ^a
AFC	20.0 (6,0)^{ab}	14.6 (4,8)^{ab}	22.1 (9,3)^a	9.5 (1,8)^a	11.5 (2,9)^{ab}	0.41 (0,06)^a	40.0 (15,3)^{ab}	1.7 (0,6)^{ab}	2.8 (0,83)^{ab}
ICS 1	23.2 (4,7) ^b	18.5 (3,1) ^c	30.3 (7,3) ^c	10.1 (1,5) ^b	13.6 (2,2) ^c	0.41 (0,06) ^a	40.2 (13,3) ^a	1.6 (0,6) ^{ab}	2.2 (0,58) ^a
ICS 1 x IMC 67	13.6 (4,6) ^a	9.0 (3,6) ^a	12.1 (5,7) ^a	7.9 (2,2) ^a	8.8 (2,6) ^a	0.43 (0,07) ^a	27.4 (12,9) ^a	1.2 (0,4) ^a	3.0 (0,4) ^b
lla 22	19.5 (5,2) ^b	15.0 (3,1) ^b	20.2 (4,8) ^{ab}	9.6 (1,5) ^b	11.7 (2,2) ^b	0.40 (0,06) ^a	55.4 (9,9) ^b	2.2 (0,5) ^b	3.8 (0,77) ^c
lla 58	22.6 (4,7) ^b	14.9 (3,7) ^b	23.0 (7,6) ^{bc}	10.1 (1,4) ^b	11.3 (2,2) ^b	0.40 (0,07) ^a	37.7 (12,1) ^a	1.9 (0,6) ^b	2.5 (0,51) ^{ab}
AFO	19.4 (6,8)^{ab}	14.1 (4,9)^{ab}	22.2 (10,3)^a	9.3 (2,1)^a	11.0 (2,7)^{ab}	0.41 (0,08)^a	42.5 (17,9)^b	1.8 (0,7)^b	3.1 (0,93)^{bc}
ICS 1	22.8 (4,8) ^b	18.0 (3,2) ^c	29.8 (8,1) ^c	10.3 (1,7) ^b	12.9 (2,0) ^c	0.39 (0,06) ^a	45.1 (12,7) ^a	1.9 (0,5) ^{ab}	2.5 (0,62) ^a
ICS 1 x IMC 67	13.4 (5,2) ^a	9.6 (3,7) ^a	13.9 (9,8) ^a	7.4 (2,0) ^a	8.7 (1,9) ^a	0.43 (0,06) ^a	31.7 (17) ^a	1.3 (0,6) ^a	3.3 (0,90) ^{bc}
lla 22	21.1 (6,0) ^b	15.8 (3,5) ^{bc}	24.7 (5,7) ^{bc}	10.2 (1,5) ^b	12.3 (1,8) ^{bc}	0.41 (0,10) ^a	60.1 (13,2) ^b	2.4 (0,6) ^b	3.9 (0,91) ^c
lla 58	20.4 (7,1) ^b	13.1 (4,9) ^b	20.4 (9,8) ^{ab}	9.4 (2,0) ^b	10.3 (2,8) ^{ab}	0.41 (0,09) ^a	34.3 (14,2) ^a	1.7 (0,6) ^a	2.7 (0,59) ^{ab}
DAF	17.5 (6,3)^a	12.9 (4,5)^a	17.4 (8,7)^a	8.4 (1,9)^a	10.4 (2,7)^a	0.40 (0,1)^a	28.7 (11,8)^a	1.3 (0,5)^a	2.3 (0,70)^a
ICS 1	20.5 (5,5) ^b	15.8 (3,7) ^b	23.7 (10,4) ^b	9.0 (1,7) ^b	11.4 (2,5) ^b	0.41 (0,09) ^a	27.3 (9,0) ^{ab}	1.2 (0,4) ^{ab}	1.8 (0,50) ^a
ICS 1 x IMC 67	9.9 (2,6) ^a	7.2 (1,6) ^a	8.5 (2,8) ^a	6.2 (1,4) ^a	8.0 (2,0) ^a	0.44 (0,12) ^a	18.2 (6,0) ^a	0.8 (0,2) ^a	2.5 (0,41) ^b
lla 22	19.1 (6,0) ^b	14.2 (3,5) ^b	16.3 (4,4) ^{ab}	8.5 (1,4) ^b	11.0 (2,6) ^b	0.38 (0,06) ^a	38.8 (12,0) ^b	1.6 (0,5) ^b	2.8 (0,72) ^b
lla 58	19.1 (3,9) ^b	13.1 (3,2) ^b	18.6 (4,8) ^b	9.6 (0,9) ^b	10.8 (2,0) ^b	0.38 (0,11) ^a	29.8 (10,0) ^{ab}	1.6 (0,5) ^b	2.3 (0,68) ^{ab}

MC, conventional monoculture; MO, organic monoculture; AFC, conventional agroforestry; AFO, organic agroforestry; DAF, dynamic agroforestry. Values followed by identical letters are not significantly different between cropping systems (bold lines) and between genotypes within each system (Šidák-adjusted *post-hoc* tests, $p < 0.05$). Av.: average; Proj.: projected; thick.: thickness; max.: maximum.

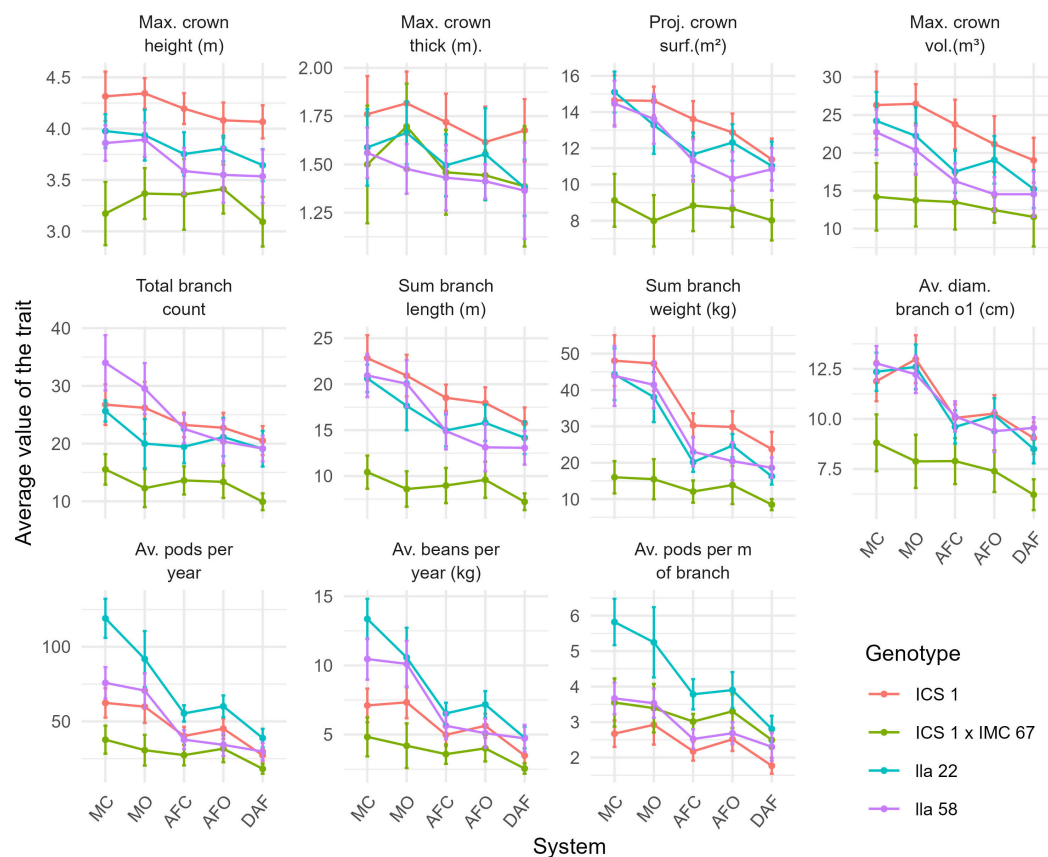


FIGURE 3

Mean values of major architectural, crown, and production traits across cropping systems and genotypes. Error bars represent 95% confidence intervals. MC, conventional monoculture; MO, organic monoculture; AFC, conventional agroforestry; AFO, organic agroforestry; DAF, dynamic agroforestry.

3.2 Analysis of relationships between architecture measurements and pod production

The screening of candidate traits used for modelling pod production as a function of architectural and crown traits revealed many strong correlations between branch counts and lengths for a given branching-order: for each order the number of branches correlated tightly with the summed length of branches of the same order (Spearman $r > 0.8$ across orders; Figure 4). This redundancy supports a parsimonious choice to retain branch counts, which is a discrete measure that also aligns with our typology, over lengths measurements in subsequent models. We also found high correlations among average diameters across orders: average 1st-order branch diameter was strongly correlated with 2nd- and 3rd-order average branch diameters (Spearman $r = 0.89$ and 0.82 , respectively, Figure 4). These results indicate that measuring 1st-order diameter alone captures much of the information conveyed by higher-order diameters, justifying its use as the primary diameter predictor in our parsimonious modelling.

In response to these results, we chose to test the effects of combinations of counts, average length and average diameter measurements of branches at different orders, on the average yearly pod production of the trees. A first mixed-effects model

(“Complete model”, Table 3) was constructed with pod production as the response variable, genotype and plot as random effects (plot accounting for the nesting of cropping system within block), and all measurements of branch counts, lengths, and diameters at orders 0 to 5 included as fixed effects without interactions. The model achieved a conditional R^2 of 0.85, indicating a strong association between architectural traits and pod production in cacao trees, when accounting for genotype, block and systems effects. Moderate collinearity was detected among variables measured at branching orders 4–5, and among diameters at orders 1–2, as expected. Consequently, significant predictors of production were limited to measurements from order 0–2 branches. This pattern is consistent with the observed collinearity structure and supports the strategy of focusing on architectural measurements from the lowest branching orders.

Building on the results from the “complete model,” we adopted a stepwise strategy to evaluate a series of increasingly parsimonious models, with the aim of maximizing predictive performance while minimizing measurement requirements. In this procedure, we first excluded measurements of average branch length and average diameter from the highest branching orders, and then progressively removed diameter measurements from successive lower orders. At each simplification step, we monitored changes in model performance using goodness-of-fit criteria (AIC) and explained variance

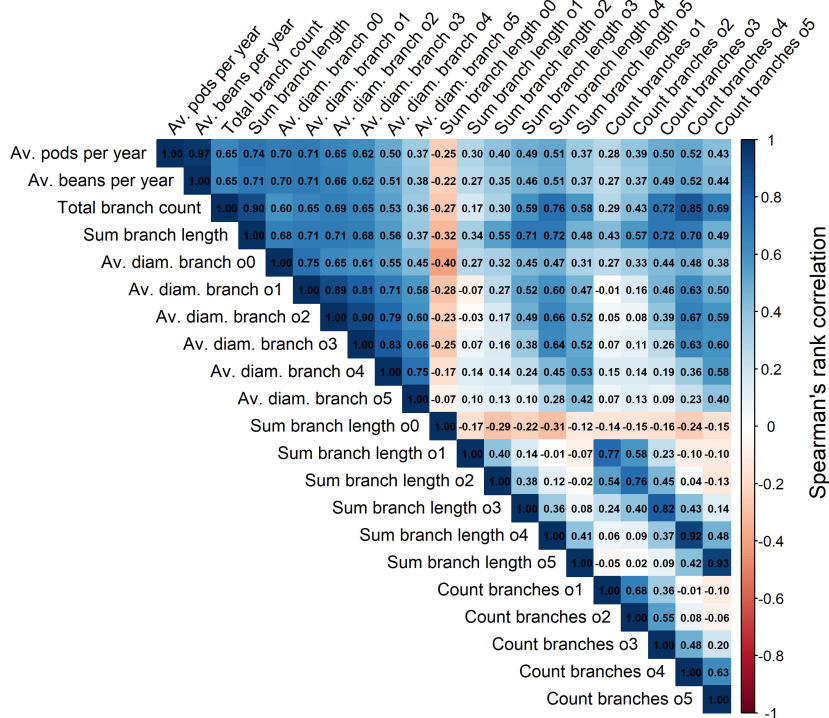


FIGURE 4

Correlation matrix between production and architectural variables of reproductive zone. Color scale shows the values of Spearman's rank correlations. Branching order from 0 to 5 is abbreviated as o0 to o5.

(marginal and conditional R^2). The structure of each model considered in the stepwise procedure, along with the corresponding performance indicators, are presented in Table 3.

The stepwise analysis revealed only a modest decrease in predictive performance when progressively excluding length measurements, branch counts, and average diameters from higher branching orders. The conditional R^2 decreased from 0.85 in the complete model to 0.81 when retaining only branch counts and average diameters up to the 2nd-order, and 0.79 when using branch counts up to the 2nd-order combined with average diameter measured only on 1st-order branches. In contrast, a substantial loss of predictive power occurred when the average diameter of 1st order branches was removed, highlighting the importance of

this variable. Overall, these results suggest that the most efficient predictive model, balancing explanatory power with minimal data collection and an acceptable loss of fit ($\Delta AIC < 25$), relies on branch counts at orders 1 and 2, together with the average diameter of 1st-order branches. In this model, the fixed effects contribute substantially to explaining variation in pod production (marginal $R^2 = 0.53$), while including plot and genotype effects increases the total explained variance to 79% (conditional $R^2 = 0.79$). All in all, these results showed that the architectural typology based on counts of axes at branching orders 0–2 was associated with differences in the measured traits. Variations were also observed according to 1st-order branch diameter, genotype, and crop management.

TABLE 3 Details of structure and performance of the generalized mixed-effect models built in the stepwise approach, with yearly average pod production as response variable, genotype and plot set as random factors.

Model	Av. lengths Order	Counts Order	Av. diameters Order	Df	R^2 m	R^2 c	AIC	ΔAIC
Complete model	0-5	0-5	0-5	20	0.61	0.85	1454	0
Counts (0-3) + Diam (0-3)	–	0-3	0-3	11	0.58	0.83	1457	3
Counts (0-2) + Diam (0-2)	–	0-2	0-2	9	0.55	0.81	1468	15
Counts (0-2) + Diam (1)	–	0-2	1	8	0.53	0.79	1475	21
Counts (0-2) + Diam (0-1)	–	0-2	0-1	9	0.53	0.78	1477	23
Counts (0-2) + Diam (0)	–	–	0	8	0.25	0.67	1535	81
Counts only	–	0-3	–	7	0.08	0.71	1554	101

n = 184. R^2 m = marginal coefficient of determination; R^2 c = conditional coefficient of determination. AIC, Akaike Information Criterion. Bold = chosen model.

3.3 Assessment of the value of the architectural typology

We assessed the predictive value of the architectural typology by comparing the complete model and the parsimonious model, with generalized mixed-effects models that included either the typology alone or the typology combined with the average diameter of 1st-order branches. In all models, genotype and cropping system were included as fixed effects to explicitly account for their influence on the relationship between architectural traits and annual pod production. Model structures and performance indicators are presented in Table 4. In this configuration, because genotype and cropping system explained most of the experimental variation in pod production, the remaining plot-level variability was minimal (random-effect variance < 0.01), indicating very limited unexplained differences among plots.

When genotype and cropping system information were combined with the full set of architectural measurements describing the leafless zone of cacao trees (branch counts, lengths, and diameters for orders 0-5), the model explained 83% of the between-tree variation in annual pod production. Replacing these detailed measurements with the architectural typology and the mean diameter of 1st order branches led to only a small reduction in model performance, corresponding to a 3% decrease in predictive power relative to the approach with complete geometry measurements. This indicates that, once genotype and system are accounted for, the combination of the typology with a single average measurement of 1st order branch diameter is sufficient to explain approximately 80% of the variation in yearly pod production among trees.

A final model was then fitted with the same structure as the selected parsimonious model, i.e. including architectural typology, the mean diameter of 1st-order branches, genotype and cropping system as fixed effects, and plot as a random effect, but this time using the full dataset of 318 trees, including individuals for which branches of order > 3 were not measured. To assess whether trees of different genotypes or grown under different cropping systems responded differently depending on their architectural type, we also tested the interaction effects among typology, genotype and system. The interaction terms did not improve model fit compared with the additive formulation, indicating that the effects of architectural typology and average 1st-order branch diameter were consistent across all genotypes and systems. The additive model retained high predictive performance (marginal $R^2 = 0.78$). The

TABLE 4 Performance comparison of complete model with best model selected from the stepwise approach and built with architectural typology, with and without average measurement of diameter of 1st order branches with yearly average pod production as response variable, genotype and plot set as random factors.

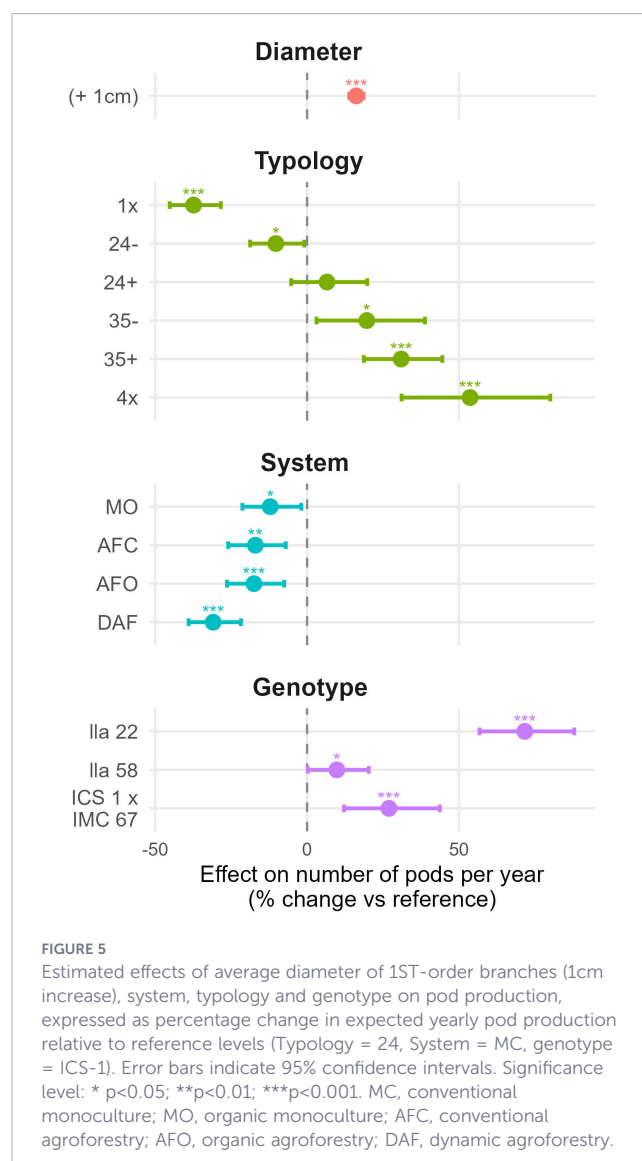
Model	df	R^2 m	R^2 c	AIC	Δ AIC
Complete model	26	0.83	0.83	1428	0
Typology + Diam (1)	17	0.80	0.80	1443	16
Counts (0-2) + Diam (1)	14	0.79	0.79	1444	16
Typology only	16	0.72	0.73	1500	56

n = 184. R^2 m = marginal coefficient of determination; R^2 c = conditional coefficient of determination. AIC, Akaike Information Criterion. Bold = chosen model.

estimated coefficients for the fixed effects, expressed as percentage changes on the response scale, are shown in Figure 5. They highlight the strong effect of architectural typology on pod production: relative to the reference typology (24+), trees of typology 1x produced on average about 37% fewer pods, whereas typologies 35-, 35+ and 4x were associated with increases of approximately 20%, 31% and 54% in annual pod production, respectively. The positive effect of tree vigor is also clear, with an average increase of about 16% in yearly pod production for each additional 1 cm in the mean diameter of 1st order branches.

3.4 Observations on the moderation effects of crown geometry

To support pruning guidelines, we tested whether crown geometry modulates production capacity for a given architectural structure. Figure 6 illustrates the additive effects of crown traits on pod production and their moderating effects on 1st-order branch diameter.



The projected crown surface had a significant positive additive effect on pod production ($p < 0.001$), but also a significant negative moderation effect ($p < 0.001$), which means that diameter gains taper as projected crown surface increases. These additive and moderation effects were consistent across all architectural types. However, GAM analyses indicated a strictly increasing, monotonic relationship between projected crown surface and pod production, with no detectable threshold or optimum value, as observed on Figure 6a.

Minimum foliage height also had a strong positive additive effect ($p < 0.001$), and a small but significant negative interaction with diameter ($p = 0.003$), which indicated that pod production increases accordingly with crown height, but the benefit of larger branches decreases slightly in trees with higher foliage. These effects were consistent across typologies, and the GAM analyses did not evidence any plateau or change in orientation in the effect of projected crown surface, as observed on Figure 6b.

Conversely, crown thickness showed no direct effect on yield, and GAM analyses revealed no non-linear effects, thresholds, or plateau, underlining no relationship between crown thickness and production. However, a significant negative moderation effect, consistent across architectural types, indicates that the positive effect of larger 1st-order branches diameters is weaker in trees with thicker crowns, as illustrated by Figure 6c.

The crown volume showed similar results as the projected crown surface, consistent with the redundancy of this trait, as volume was calculated as projected crown area x crown thickness. However, the trait showed lower effect on pod production than projected crown surface alone, which accounts for a low effect of crown thickness on the relationship. Moderation effect was similar to projected crown surface, and GAM analyses did not evidence any

threshold or optimum values. Figure 6d illustrates the modulating effect of crown volume, with lower estimations of pod production for trees with large crown when average diameter of 1st-order branches exceeds 12.5cm.

4 Discussion

4.1 System and genotype effects on the studied cacao features

Cropping systems significantly affected vegetative variables. Cacaos in monocultures were the most vigorous, particularly under conventional management (MC). This was evident for architectural traits of the leafless zone, where they exhibit larger branch diameters (from orders 0 to 4), higher branch numbers, and longer total branch lengths compared to those under dynamic agroforestry. These features were associated with higher woody biomass spread over a greater number of branches, which likely increased the potential number of positions available for flower cushions to develop, as well as the potential carbohydrate reserves (Tosto et al., 2022; Wibaux et al., 2025).

Similar differences in vegetative development were also observed in the projected crown surface and maximum volume of the leafy crown. These larger crowns likely reflect a greater photosynthetic capacity of cacao trees in monocultures, as well as the potential for increased consumption of nutrients and water (Thomas and Balasimha, 1992; Yapp and Hadley, 1994). Conversely, crown height and thickness appeared to be more

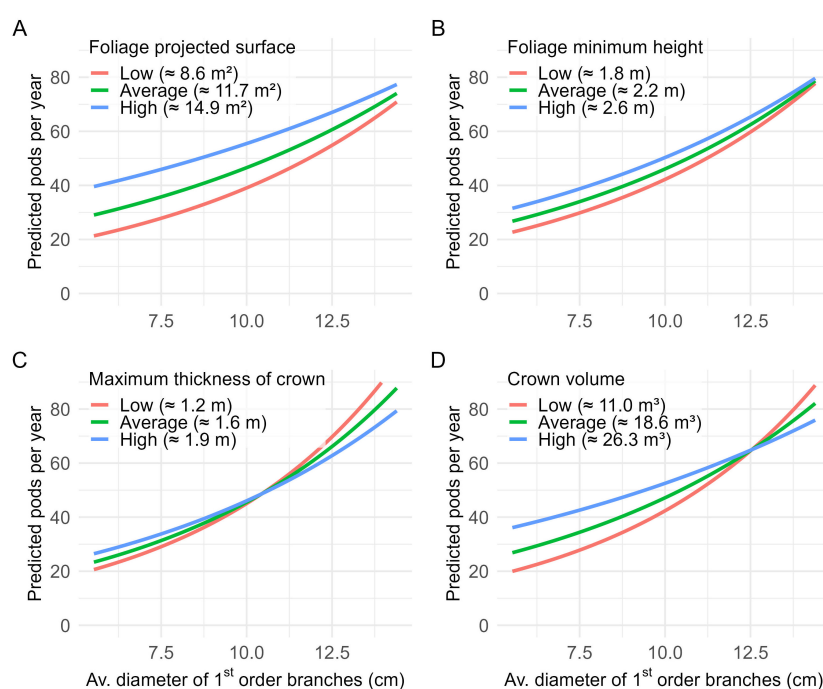


FIGURE 6

Average modulating effect of (A) foliage projected surface, (B) foliage minimum height, (C) maximum thickness of the crown, (D) crown volume on estimated yearly pod production, over average diameter of 1st order branches. Red, green and blue line represent low (Mean – SD), average (Mean) and high (Mean + SD) values of the crown-trait, to illustrate its modulating effect on the relationship.

responsive to pruning management, as suggested by the significant block effect, likely resulting from the allocation of the two pruning operators to different blocks.

In contrast, cacaos from conventional and organic agroforestry had intermediate values for all these architecture and crown geometry traits. In practical terms words, there was a gradient in the size of cacaos across the different cropping systems: MC=MO > AFC=AFO ≥ DAF. A similar gradient existed for fresh pod and bean production, and our findings suggest that cocoa bean production is closely tied to the trees' vegetative growth, which, in turn, highly depends on light availability and crop management (Saj et al., 2025; Tosto et al., 2022; Yapp and Hadley, 1994).

Genotype significantly affected both vegetative and generative variables. Specifically, the ICS 1 × IMC 67 genotype was clearly distinct from the other three studied genotypes, showing considerably lower architectural development and vigor in the leafless zone, as expressed by the low values in branch diameter, number, and length. This result highlighted a cumulative effect of the cropping system and genotype on tree biomass and, consequently, on production potential. However, while the cropping system exerted a strong influence on certain vegetative (e.g. lower-order branch diameters) and reproductive traits (flower-cushion density and pod or bean production), the genotype-dependent differences were broadly conserved across systems. This broadens our understanding of both additive and interactive effects of cropping systems and genotypes on cacao development and subsequent pod production potential. The case of ICS 1 is illustrative: although this genotype generally showed slightly higher vegetative and generative (flowering sites density) indicators than IIa 22 and IIa 58, its overall production was lower than that of IIa 22. This can be explained by its late entrance into production, which does not fully align with the climatic conditions of the region (Armengot et al., 2023). Meanwhile, although IIa 58 exhibited similar branch diameter and flowering site density but higher branch number and length than IIa 22, it still produced less than the latter.

All in all, these results underline that both factors, i.e. the cropping system and genotype, should be carefully considered in field tree management.

Our architectural models focused on pod production because this variable is directly linked to flowering and fruit-set processes and therefore provides a suitable indicator of production potential. Fresh bean production was also measured and analyzed throughout the study and showed broadly similar responses to genotype and cropping system.

4.2 Cacao architectural features and equilibrium between leafy and non-leafy wood

Beyond the effects of genotype and cropping system, several architecture and leafy crown traits were associated with substantial variations in pod production and fresh bean yield. Some of these variables were used to build a typology and derive various indicators - such as the ratio of leafy crown thickness to tree height and the mean production per meter of branch - to identify architectural traits favorable to pod production. Indeed, higher production was

associated with a greater number of branches in orders 1 and 2. These branches structure the core part of the tree, are likely to support the development of higher-order branches, leafy crown expansion, and consequently greater carbon fixation and space for flower cushion formation.

The strong effect of 1st-order branch diameter likely reflects not only architectural complexity but also the physiological capacity of the tree. These scaffold branches connect the reproductive woody framework to the leafy crown and their diameter is generally associated with greater conductive capacity for water, nutrients, and photoassimilates. Larger branches may also support greater carbohydrate reserves and a larger surface of ageing woody tissues bearing persistent flower cushions. In this context, 1st-order branch diameter can be viewed as an integrated indicator of the tree's ability to sustain flowering, fruit set, and pod development (Yapp and Hadley, 1994; Thomas and Balasimha, 1992; Pang and Lockwood, 2008; Wibaux et al., 2025).

The total branch length in type 3 and 4 trees was found to be on average about twice as long, or more, than that of type 1x trees. Number of 2nd-order branches also appeared particularly associated to production potential, especially when the number of 1st-order branches was less or equal to 2. While 1st-order branches established the range for overall tree development capacity from its "base", 2nd-order branches clearly contributed to both the total branch length and crown expansion of the tree, as shown by the average 30% loss in total branch length and 17% loss in crown projection surface when moving from type 24 to type 24- and from type 35+ to type 35-.

Our results also clearly showed that crown development had been effectively and consistently controlled by the pruning team. First, the projected crown surface indicated that only a few trees (<10%, mostly in monocultures) had a surface greater than 16 m² (data not shown), which underlines that light competition between neighboring cacaos was minimal in our planting system. Second, although the minimum and maximum foliage height as well as foliage thickness significantly varied among cropping systems and genotypes, the ratio between leafy crown thickness and total tree height remained on average the same (ca. 41%) across all types studied, underlining a stable balance between the leafy crown zone and the pod-productive zone below.

The analysis of crown geometry identified significant additive associations across all studied traits. Specifically, projected crown surface (PCS) demonstrates a distinct positive additive effect, though this is modulated by a negative interaction with 1st order branch diameter. Consequently, the positive association between branch diameter and pod production becomes weaker as PCS increases, yet without reaching a distinct threshold or optimum. Crown volume exerts a positive influence but proves largely redundant to PCS, displaying a similar pattern of moderation. Minimum foliage height shows a positive additive effect, whereas foliage thickness becomes negligible in GAMs once PCS is included. Crucially, these effects and their moderation of the diameter-yield relationship appear consistent across typologies. Therefore, our results suggest that management may benefit from maintaining or increasing PCS, noting that while the marginal benefit diminishes for large-diameter trees, it remains positive. Consequently,

strategies probably should focus on keeping foliage levels not too low, treating the leafy crown thickness as a secondary concern.

4.3 Implications for the cacao tree monitoring and management in the field

The effects of cropping systems and genotypes on cacao tree size, branching patterns, and architectural typology enabled us to identify the architectural configurations most strongly associated with pod production in our trial, addressing an important issue raised by [Tosto et al. \(2022\)](#). Based on the relationships identified between leafless-zone architecture, crown geometry, and bean production, we propose a framework for monitoring and managing cacao trees at different stages of cultivation that complements existing pruning guidelines.

It is important to note, however, that the typology and results presented here were developed under the specific conditions of a low-density clonal orchard comprising four cacao genotypes planted at a spacing of 4×4 m. Although such arrangements are common in Bolivia, cacao is grown elsewhere under contrasting planting densities, spatial configurations, genotypes, training systems, and management practices. Consequently, the recommendations proposed below should be interpreted in light of the specific characteristics of each orchard, particularly where intraspecific competition is greater because of reduced spacing or higher planting density. Further studies across a broader range of production conditions are needed to refine these recommendations. The architectural typology and modelling framework developed in this study provide a foundation that can be adapted and expanded for this purpose.

An additional consideration concerns the practical feasibility of the management interventions discussed below. Although this study focuses on the biological relationships between tree architecture and production potential, the adoption of practices such as supplementary grafting, coppicing, or regrafting will also depend on labor availability, implementation costs, and expected economic returns. This is particularly relevant given that the adoption of cacao pruning recommendations depends not only on their expected benefits but also on their compatibility with farmers' constraints and objectives ([Obeng Adomaa et al., 2022](#)). Likewise, rehabilitation interventions based on grafting or coppicing require additional labor and technical skills ([Effendy, 2015](#); [Yacomelo-Hernández et al., 2021](#)), but may represent viable alternatives to maintaining low-producing trees or undertaking complete orchard renewal ([Mbile et al., 2025](#)).

4.3.1 Initial and young stage: plot implementation, young grafts and formative pruning

Our results emphasize the probable advantage of having a mature tree with more than two 1st-order scaffold branches. Therefore, the primary objective at the plantation stage should be to ensure the use of scions capable of developing more than two of these scaffold branches. The target number of scaffold branches can vary between 3 and 5 depending on the spatial branching behavior of the genotype and the expected aerial development of the tree, in

response to planting arrangements. Trees with more than 5 scaffold branches are likely to cause intra-order competition, with more reciprocal overshadowing, and destabilize the structural part of the tree resulting in uneven diameter or length (personal observation). To get the targeted number of scaffold branches, one can use either (i) longer scions carrying at least 4 to 5 viable buds, or (ii) double graft the rootstock with at least two scions of the same genotype in opposite positions.

In the field, young graft development should be monitored to promote strong growth and regular spacing of the future scaffold branches (1st-order, originating from the scion's buds). Once the development of these primary branches is satisfactory (i.e. they have reached a diameter and height sufficient to support the next branch order) the first formative pruning can occur by removing the scaffold branch tips. Cutting the terminal bud removes apical dominance and allows the nearest axillary buds to resume growth ([Leyser, 2009](#)). If any 1st-order branch shows weakness or is too close to a neighbor, it should be removed. This initial pruning can also be used to balance the height and length of scaffold branches, as well as to remove any secondary branches sprouting from them. This will prevent overgrowth of the 1st-order branches, which can cause them to bend or collapse under their own weight. Afterward, the tree should be allowed to grow freely for a longer period while monitoring the development of second-order branches and the formation of the very first leafy crown. The second formative pruning should be performed only once this leafy crown is well-developed in terms of volume, which should also have allowed for diameter growth of the scaffold branches. This pruning targets the selection of 2nd order branches, aiming to retain at least two 2nd order branches per 1st order branch, or more to maintain sufficient leaf cover (e.g., avoiding gaps in the leafy crown). After this pruning, the basic tree structure is established, and subsequent pruning will primarily focus on controlling crown development in terms of surface area and height until the tree reaches its mature final height.

4.3.2 Production stage: tree maintenance pruning

At the production stage, the tree structure is well defined, and its management should primarily focus on three aspects: (i) maintaining the volume occupied by the leafy crown and its balance with the production zone on the leafless part of the tree; (ii) preserving the efficiency of carbon fixation; and (iii) maintaining the sanitary condition of the tree (not discussed here but important for witches broom in the SysCom Bolivia trial). These three aspects can be effectively managed through pruning.

While the total volume of the leafy crown depends greatly on planting density and neighboring trees ([Lachenaud and Montagnon, 2002](#); [Trebbissou et al., 2021](#)), our results emphasize that under certain conditions, the studied cacaos can produce more than 8 kg of fresh beans per year. This outcome is achieved through regular pruning of mature trees and maintaining a leafy crown height-to-total height ratio around 40%, regardless of architectural type. Therefore, our results support the use of this simple indicator as a practical proxy to assess the balance between the tree's carbon-fixing foliage and its pod production. However, further investigation is needed to determine which levels would indicate optimal

balance for pod production and/or sustainable use of the tree (i.e. which lifespan to expect with a given level of the indicator).

Preserving the efficiency of carbon fixation requires regularly renewing the leaf stock of the crown to maintain it functional and take into account cacao leaves lifespan, which depends on the cropping system, self-shading and genotype (Miyaji et al., 1997; Susanti et al., 2017; Zuidema et al., 2005). Additionally, renewal is necessary to keep the trees at a fixed height. Although we did not estimate the quantity, number, or fraction of leaves renewed per tree each year through pruning, Schneidewind et al. (2018) reported that for the Ila22 genotype, between 2.4 and 5.3 kg of branches were removed per tree during maintenance pruning in the same trial, depending on tree size. Although the date back to 2016, it still represents in 2024 15–30% of the branch biomass of the five orders under the leafy crown and most likely indicates a thorough effort of leaf removal. Hence, a particular attention should be paid to the last leafless branches (e.g. orders ≥ 5) during maintenance pruning to both keep enough branches to renew partially but regularly the leaf stock.

4.3.3 Assessing tree architecture to monitor tree and plot performance during mature stage

Our results are consistent with the practice adopted by some cacao technicians in Latin America of assessing productive potential through the count of “productive linear meters” of branches (U. Lopes, CEPLAC, Brazil, pers. comm.; R. Cerda, CATIE, Costa Rica, pers. comm.), an approach that is also being explored in the CATIE-KoLFACI project trials (Orozco-Aguilar et al., 2024). They even simplify this proxy by emphasizing that the branch count of the first two orders could be suitably used and complemented by measuring the diameters of the 1st order branches. Depending on the tree’s architectural model and the health and development of its branches, architectural reshaping of the leafless zone could be achieved through selective pruning or supplementary grafting.

For instance, if some trees exhibit a low count of 1st or 2nd order branches (e.g., types 1x or 24- in our typology), they could be strategically grafted to stabilize or increase their productive linear meters in the mid-term. Yet, we found no references on this specific topic while the potential adoption of this technique depends on balancing the time required for grafting, its success rate, and the potential gains in productivity.

The same applies to trees whose architecture cannot be restored or improved, as well as to trees with correct architecture but low yield. In these cases, complete coppicing and/or regrafting would be necessary, involving significantly more labor due to the need for comprehensive formative pruning. Coppicing has been demonstrated to sustain yields at the plot level in non-grafted cacao populations, probably thanks to the rejuvenation of the aerial part of the tree and the higher productive linear meters of coppiced trees (Mbile et al., 2025). On-field rehabilitation through grafting has also been shown to be successful, although outcomes vary depending on the graft type (on old trunk or on sucker) and genotype (Effendy, 2015; Ocampo-Ariza et al., 2025; Yacomelo-Hernández et al., 2021). While we demonstrated in our study that genotypes could exhibit

specific architectural characteristics, it is highly likely that a lateral graft on an old branch or trunk does not provide the same architectural basis as a graft directly on an old trunk.

Hence, our results suggest that monitoring tree architecture should be routinely adopted to assess the production potential of a plot and guide decision-making for renovation or rehabilitation at this scale (Somarriba et al., 2021).

5 Conclusion

Our study demonstrates that cacao pod production is closely linked with the tree’s vegetative structure, particularly the vigor and complexity of scaffold branches within the leafless zone. Although cropping systems and genotypes significantly influence overall tree development, with full-sun systems promoting a greater number of more vigorous branches, the positive association between architectural complexity, especially branch orders 1 and 2, and pod production was consistently observed across all contexts examined. The proposed architectural typology provides a simplified framework for assessing production potential in the field and offers a useful basis for further research and management applications. Our findings suggest that traditional pruning practices focused primarily on height restriction or canopy opening may inadvertently constrain yield potential by removing productive wood. However, further validation across a wider range of environments, management systems, and genetic backgrounds will be necessary to assess the wider applicability of this framework for cacao pruning and canopy management.

Data availability statement

The original contributions presented in the study are included in the article/[Supplementary Material](#), further inquiries can be directed to the corresponding author/s.

Author contributions

SS: Project administration, Validation, Data curation, Formal analysis, Methodology, Visualization, Funding acquisition, Investigation, Supervision, Writing – review & editing, Conceptualization, Writing – original draft. TW: Investigation, Writing – original draft, Writing – review & editing, Formal analysis, Data curation. SW: Writing – review & editing, Methodology, Data curation. LD: Methodology, Writing – review & editing. CC: Methodology, Writing – review & editing. RH: Writing – review & editing, Methodology. JR: Writing – review & editing, Funding acquisition, Project administration. P-EL: Writing – original draft, Investigation, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declared that generative AI was used in the creation of this manuscript. During the preparation of this work,

the author(s) used DeepLPro and Gemini 2.5 Pro (used via specific FiBL chatbot to ensure confidentiality) to correct the English grammar and language. Having used this tool/service, the author(s) reviewed and edited the content as necessary, taking full responsibility for the published article.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fagro.2026.1869482/full#supplementary-material>

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