MORPHOPHYSIOLOGICAL CHARACTERISTICS OF (*Coffea arabica* L.) IN DIFFERENT ARRANGEMENTS: LESSONS FROM A 3D VIRTUAL PLANT APPROACH

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ABSTRACT: 3D vegetative structural and functional models are useful in simulations of ecophysiological and biophysical processes. The main objective of this study was to model a 3D *Coffea arabica* L. structure. The specific aim was to use 3D mock-ups for analysis of vertical leaf and berry distribution and light interception in coffee crops cultivated in different planting densities and arrangements. The mock-ups were built after abstraction and codification by VPlants, based on morphological measurements (orthotropic shoot height and its number of internodes; positions of second to fourth branching order plagiotropics; internode number on first to fourth branching order plagiotropics number of leaf pairs), and several hypotheses. Mock-ups were visualized in PlantGLViewer, while Silhouette to Total Area Ratio (STAR), leaf area (LA) and berry distribution were processed in VegeSTAR. Planting arrangements influenced STAR when the plants were grown in a low density (6,000 plants ha^{-1}). Plant density had a significant effect on the number of berries in square arrangements. The higher layers were occupied by first order foliage and few berries, allowing more light to pass to the lower canopy layers. Berries were abundant in the first and second order plagiotropic branches, in the highest and middle layers. Light distribution was more uniform than leaf area distribution, indicative of a disperse foliage and efficient space occupation. STAR correlated strongly with berry number, especially in the upper, less shaded canopy layers, where flower induction was the most intense.

Index terms: Leaf area, plagiotropic branches, plant architecture, STAR, VPlants.

CARACTERÍSTICAS MORFOFISIOLÓGICAS DE (*Coffea arabica* L.) EM DIFERENTES ARRANJOS: LIÇÕES DE ABORDAGEM DE PLANTAS VIRTUAIS TRIDIMENSIONAIS

RESUMO: *Os modelos vegetativos estruturais e funcionais em 3D mostram-se úteis na simulação de processos ecofisiológicos e biofísicos. O objetivo principal deste estudo foi modelar a estrutura 3D de C*offea arabica L.. *Os objetivos específicos foram analisar as distribuições verticais de folhas e frutos e a interceptação de radiação de cafeeiros cultivados em diferentes arranjos e densidades. As reconstruções 3D (maquetes) foram obtidas após a abstração e codificação em VPlants, baseadas nas medições morfológicas (altura do tronco ortotrópico; número de entrenós do tronco; posição e comprimento de ramos primários plagiotrópicos; posições de ramos de segunda a quarta ordem; número de entrenós nos ramos plagiotrópicos primários a quaternários; número de pares de folhas) e diversas hipóteses. As maquetes foram visualizadas no PlantGLViewer, enquanto a Razão da Área Total da Silhueta (STAR), área foliar (LA) e a distribuição dos frutos foram processados no VegeSTAR. O arranjo de plantas afetou STAR quando cultivadas em baixa densidade. A densidade influenciou significativamente o número de frutos no arranjo quadrangular. O espaço das camadas superiores foi ocupado por folhagem da primeira ordem e por poucos frutos, permitindo maior transmissão de radiação para as camadas inferiores. Os frutos foram localizados em abundância nos plagiotrópicos de primeira e segunda ordem, nas camadas superiores e medianas. A distribuição de luz foi mais uniforme do que a da LA, o que indica uma folhagem dispersa com ocupação eficiente do espaço. Houve alta correlação entre número de frutos e STAR, especialmente em camadas superiores, menos sombreadas, onde a indução floral foi mais intensa.*

Palavras chave: Área foliar, ramos plagiotrópicos, arquitetura vegetal, STAR, VPlants.

1 INTRODUCTION

Godin (2000, p. 414) defined plant architecture as “any individual description based on decomposition of the plant into components, specifying their biological type and/or their shape, and/or their location/ orientation in space and/or the way these components are physically related to one another”. Plant architecture expresses the equilibrium between endogenous growth processes and exogenous constraints exerted by the environment. In this sense, the aim of any architectural analysis “is to identify these endogenous processes and to separate them from the plasticity of their expression resulting from external influences by means of observation and sometimes experimentation” (BARTHÉLÉMY &

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CARAGLIO, 2007, p. 376). To define and assess 3D plant architecture various computational formalisms and platforms, such as L-systems (PRUSINKIEWICZ & LINDENMAYER, 1996) and VPlants (GODIN et al., 1999), have been developed.

The architecture of *Coffea arabica* L. is described by Roux's model (HALLÉ et al., 1978), which defines branching pattern, branch longevity and inflorescence positions. One of the model's specificities is the existence of branch dimorphism. The main shoot is orthotropic, erect and radial, presenting opposite leaves and constituted by internodes of relatively regular length. Each pair of opposite leaves on the orthotropic shoot is cross-positioned to a lower pair, resulting in an opposite, crossed or decussate phyllotaxy. The lateral branches are plagiotropic. They are attached to the orthotropic shoot at average angles of 42° to 44º (OROSCO, 1977) and evolve to a nearly horizontal position with age and the extra weight caused by an increase in length, leaf number, branching process and production. The plagiotropic branches of *C. arabica* follow the orthogonal - decussate pattern of leaf initiation, but both internode torsion and petiole angle reorient the leaves, resulting in a dorsiventral shoot (DENGLER, 1999). The first order branches have a great longevity and bear second to fourth order plagiotropic branches.

Currently, 3D architectural analysis of the genus *Coffea* is based only on the modeling of the growth and mortality of robusta coffee (*Coffea canephora* Pierre ex A. Froehner) orthotropic and plagiotropic meristems by random processes (REFFYE, 1981) and on the probability of distribution of secondary plagiotropic branches (REFFYE, 1982). The productive ideotype of robusta coffee plagiotropic branches has been studied recently (CILAS et al., 2006).

3D functional models uncoupled with 3D models of the vegetative structure of isolated trees (SINOQUET et al., 2007) or plant canopies (SINOQUET et al., 2000) were named functional-structural plant models (FSPM) by Sievänen et al. (2000). FSPM are helpful in the modeling of various biophysical and ecophysiological variables, such as light interception, transpiration and photosynthesis (SINOQUET et al., 2001), carbon allocation (GÉNARD et al., 2008) or leaf temperature (SARDEAU et al., 2007).

Expensive equipment and long-term experiments are necessary to measure light interception by plants and canopies. This is why many laboratories choose other sophisticated tools, such as mathematical models of light interception (ZANETTI et al., 1999). Light interception can be estimated, for example, as directional light interception on the canopy (WILLAUME et al., 2004) by solving the radiative transfer equation and using the discrete ordinates method in 3D space (SINOQUET et al., 2001). The light interception pattern of crops, measured or estimated during a certain time interval, correlates strongly with their final yield.

The main aim of this work was to model a *C. arabica* structure in 3D using the VPlants methodology. The specific aim was to use 3D mock-ups to assess the vertical leaf and berry distribution and light interception of coffee plants cultivated in different planting densities and arrangements.

2 MATERIAL AND METHODS

The experiment was set up at the Instituto Agronômico do Paraná (IAPAR)[1], Londrina, Brazil (23°18'S and 51°17'W), in 2007 with 14-year-old *C. arabica* trees (cv. IAPAR 59). The seedlings were planted in 1995 and pruned close to the ground in 2000. Six treatments were defined according to plantation density: 14,000 plants ha^{-1} in square (0.84 x 0.84 m) and rectangular (2.00 x 0.35 m) arrangements; 10,000 plants ha^{-1} in square (1.00 x 1.00 m) and rectangular (3.00 x 0.33 m) arrangements and 6,000 plants ha^{-1} in square (1.29 x 1.29 m) and rectangular (3.00 x 0.55 m) arrangements.

The morphological characteristics sampled were: height of the orthotropic shoot, diameter of the crown, number of internodes on the orthotropic shoot, position and length of first order plagiotropic branches position of secondary, tertiary and quaternary plagiotropic branches, number of berries for each internode, number of green internodes and number of leaf pairs. Two to five plants were measured and reconstructed in 3D for each treatment.

The mock-ups of coffee plants were built in VPlants (new version of AMAPmod) on the platform OpenALEA - http://www-sop.inria.fr/virtualplants/

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wiki/doku.php?id=software (PRADAL et al., 2008). The plants were measured and abstracted mathematically by codification in Multiscale Trees Graphs (MTG's). The MTG's were decomposed in three scales - plants, shoot/branches and internodes. Basic virtual colors were attributed to each branching order.

The mock-ups were visualized in the PlantGLViewer (VPlants visualization module) and saved as "vgx" files, which allows them to be imported by the VegeSTAR software. The vgx files were manipulated and different false colors (Red Green Blue) were attributed to each of the 10 cm and 40 cm-thick horizontal layers in the vertical profile, in order to geometrically recognize the position of the foliage in the plant canopy and its origin per branching order.

VegeSTAR (http://www2.clermont.inra.fr/piaf/fr/telechargement/telecharger.php) is a software that simulates light interception (ADAM et al., 2006), computing STAR (Silhouette to Total Area Ratio) based on an analysis of 3D synthetic plant images. The virtual scenes for the coffee plants in this experiment were created on July 26th, 2007. Outputs showed the leaf area (LA) and STAR, which were calculated for each layer and branching order, computed in a particular day. A scheme of the methodology applied in this work is presented in Figure 1.

STAR, leaf area and fruit distribution, analyzed in small samples and in a non-normality distribution, were compared by the non-parametric Kruskal-Wallis test. The Pearson test was applied to correlate leaf and berry distribution. To test the accuracy of the geometrical reconstruction, bias and root mean square error (RMSE) were calculated to compare the measured diameter of cofee trees to the most distant X and Y values obtained from mock-ups. The data were analyzed by R software (version 2.11.1.).

3 RESULTS AND DISCUSSION

C. arabica leaves were modeled in 3D by 121 polygons (Figure 2A). Shoot and branches were dressed using VPlants SMB library cylinders (Figure 2B). An ovoid with a petiole was used as a geometrical dressing for the berries (Figure 2C). All the elements were adjusted to a basic 1 cm length/diameter size in an effort to reconstruct more realistic shapes and sizes using the morphological attributes.

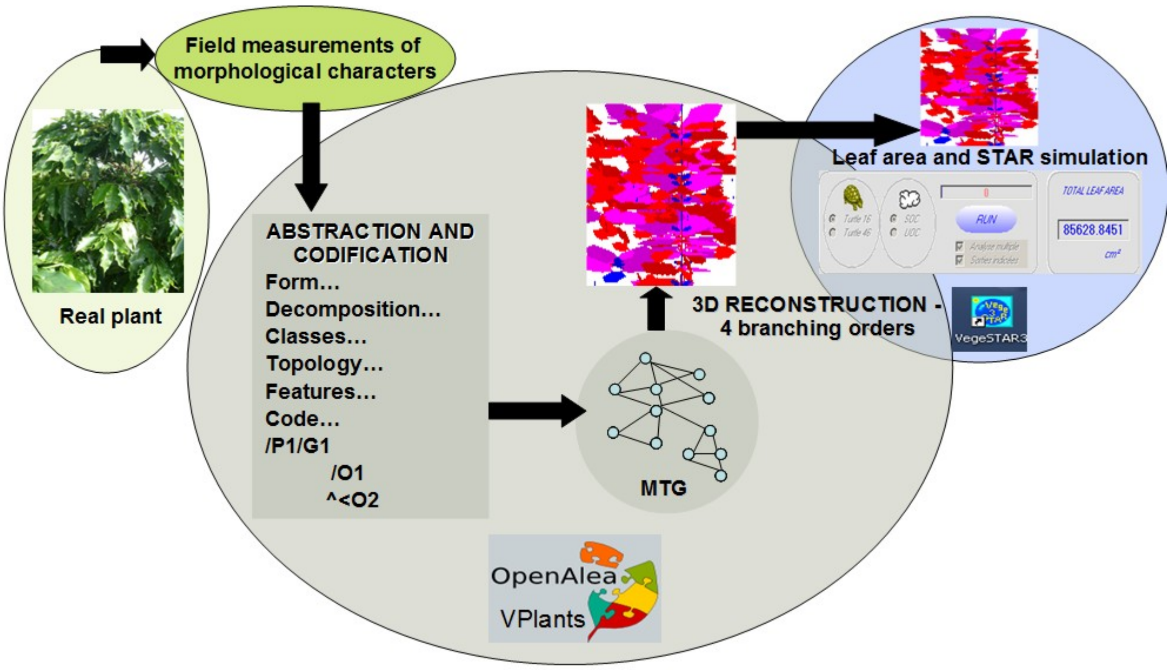
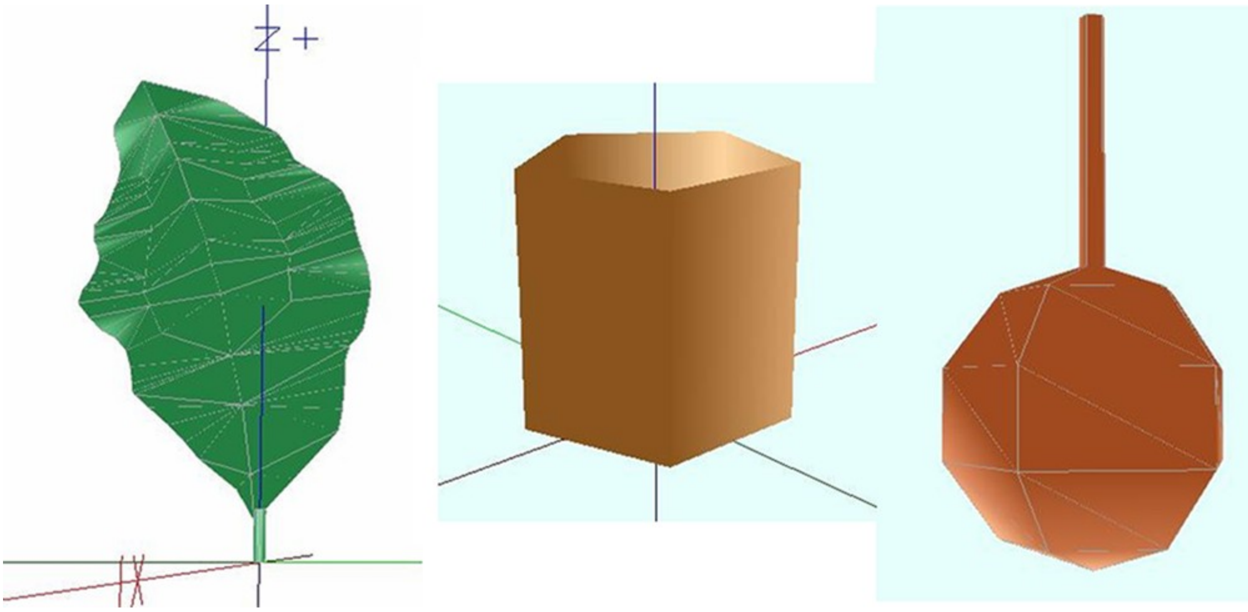


Figure 1 – Structure of the VPlants and VegeSTAR methodologies used to analyze the coffee trees.



(A) (B) (C)

Figure 2 – (A) Coffee leaf constructed in the GEOM library; (B) Cylinders for orthotropic shoot and plagiotropic branches in the SMB library; (C) Coffee berry constructed in the VPlants GEOM library.

Modeling always assumes a certain degree of simplification of reality which, in turn, depends on the actual understanding of the modeled objects and of the modeling tools (ZEIGLER, 2000). In light of the lack of data on the metamer scale, it was assumed that:

1) The length of all the internodes on the orthotropic shoot was the same and was determined based on the total length of the shoot and the number of internodes. A length of 0.2 cm was attributed only to the last internode emitted.

2) A reconstruction of first to fourth-order plagiotropic branch internodes was derived from the ancestral internode's length multiplied by the constant 0.7. The assumed gradual reduction in internode length of plagiotropic branches with increased branching order did not include the last three internodes, to which constant values of 0.7 cm, 0.5 cm and 0.2 cm were attributed.

3) Phyllotaxy is always 90°. The geometrical reconstruction of internode torsion was simulated by the insertion of some "false branches" (of infinitely short internodes – 0.001 cm) in the MTG's. Figure 3A illustrates the spiral change of crossed primary plagiotropic branches due to the insertion of the "false branches".

4) The inclination of primary plagiotropic branches was defined in ten levels (relative to the height of the orthotropic shoot), from 80° (primary branches close to the soil) to 35° (primary branches at the top of the plant).

5) The plagiotropic branches had a more natural shape following a Bézier curve or a polynomial curve, expressed as barycentric combinations of some representative points called control points. Ten control points were used to model the coffee branches and their shapes are illustrated in the lowest plagiotropic branches in Figure 3B.

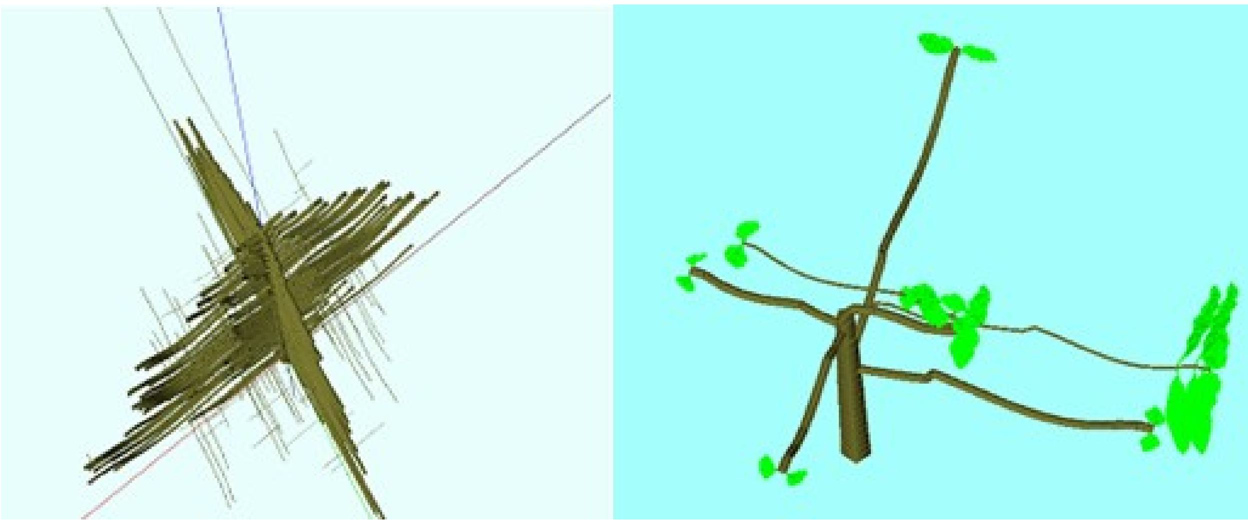
6) Leaves always appeared and were kept in pairs (the exact individual leaf position was not registered during the measurements, only leaf number). It was assumed that leaves were left only on the last green nodes of each branch. Their individual surface was assumed as a constant value (87.75 cm^2). Lower leaf surface was attributed to the last leaf pair on the orthotropic shoot (4.5 cm^2) and the three most recently emitted pairs on the plagiotropic branches (60, 15 and 4.5 cm^2). Figure

3B illustrates the reconstruction of the lowest plagiotropic branches with leaves and Figure 4 shows the reconstructions of the foliage of individual plants.

The spatial representation of plants can be detailed on different scales of precision, that vary from the description of each organ (leaf, metamer…) to global dressing of branching systems, or to entire plant scale (GODIN & SINOQUET, 2005). The coffee mock-ups were adequately reconstructed when built on a metamer scale and based on various assumptions (Figures 3 and 4), in spite of the relatively limited amount of information available on the vegetative entities.

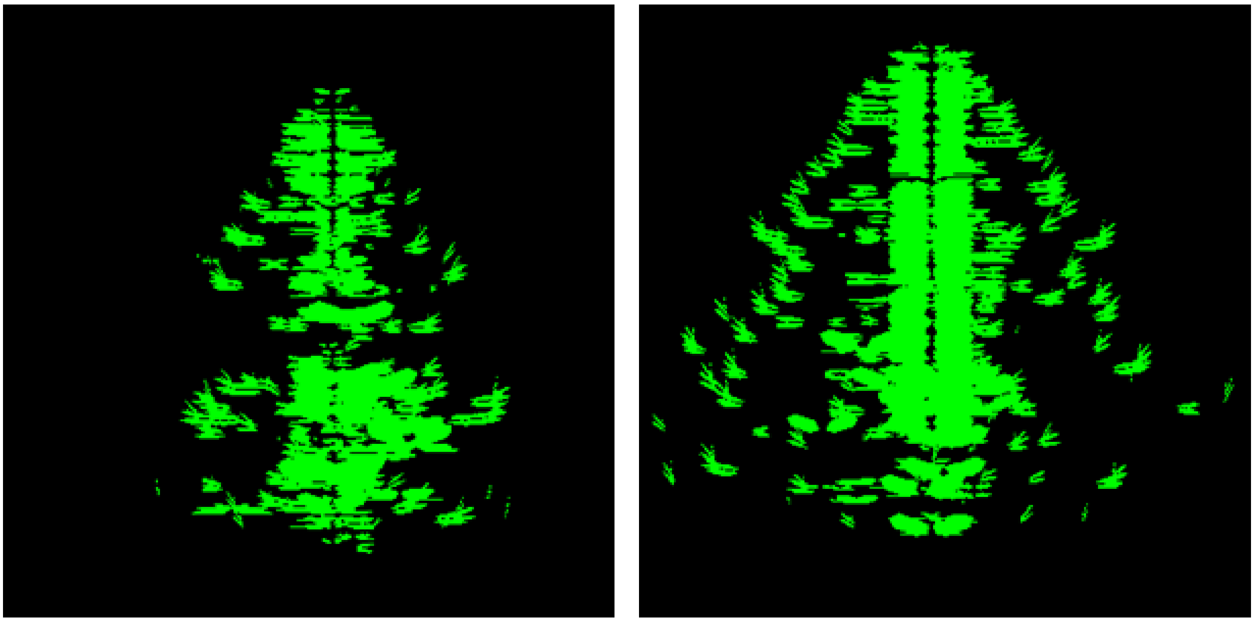
To test the accuracy of 3D geometrical reconstructions, the measured and the estimated diameters of coffee tree crowns were compared (Figure 5). The average crown projection was 0.1825 m larger than the measured projections (bias value). The dispersion of estimations was expressed through an RMSE value of 0.2252. Three reasons could explain such overestimations. First, Roux's model defines two metamer types, orthotropic and plagiotropic (HALLÉ et al., 1978). In simplified field data acquisition in this experiment, a constant internode length was assumed and adapted to plagiotropic branches by applying a coefficient of correction (0.7) in relation to the ancestral branching order. Second, with the insertion of primary plagiotropic branches at 80-35° angles from the lower to the higher layers and the Bézier curve's relatively low sensibility, the mock-ups obtained more open plant shapes than the real ones. Third, in seven-year-old plants some growth marks are less visible (such as cicatrisation, which indicates node position). In this sense, the metamer number per orthotropic shoot could be underestimated during the field measurements and evaluated with more precision in younger plagiotropic branches, leading to a general overestimation of the plant diameter.

The leaf/berry distribution in 10 cm layers in vertical profiles and leaf/berry origins in plagiotropic branching order (first to fourth) are shown in Figures 6 and 7, respectively. In general, a strong dependency of leaf/berry distribution on branching order was observed. The LA and berry numbers varied considerably due to the small number of mock-ups assessed (n=2-5) and the single evaluation in time (stage of coffee fruit ripening on July 26th, 2007).



(A) (B)

Figure 3 – Reconstruction of (A) a coffee plant branching "skeleton" applying the Beziér curve and inclinations between 80 – 35° from the lower to the higher layers and (B) the lower part of a coffee plant with leaves on only the last green internodes.



(A) (B)

Figure 4 – Mock-ups of the reconstructed foliage of coffee plants cultivated in a density of 10,000 plants ha^{-1} and visualized in VegeSTAR. **(**A) Square and (B) rectangular arrangements.

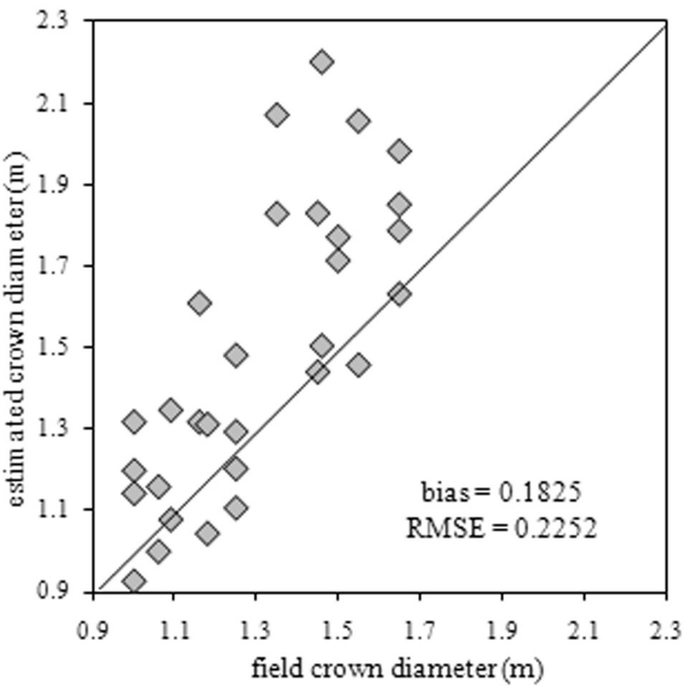


Figure 5 – Comparison of measured and estimated crown diameters. The bias, root mean square error (RMSE) values and 1:1 line are indicated.

The foliage originating in the first-order plagiotropic branches predominates only in the highest layers, located mostly between 150 cm and 170 cm in the canopy, and when the trees were cultivated in higher densities – 14,000 and 10,000 plants ha^{-1} (Figures 6A-D). The foliage originating in the second-order plagiotropic branches was the most abundant and the most important in the constution of seven-year-old coffee trees. The LA originating in third and fourth-order plagiotropic branches appeared only in the mid and the lowest trees layers (below 70-80 cm). The foliage originating in the fourth-order plagiotropic branches was significant only in the lowest planting density (Figures 6E-F) and in a rectangular arrangement (Figures 6B, 6D and 6F).

Berries appeared abundantly on the first and second-order plagiotropic branches in the highest (Figures 7A-D, Figure 8B) and middle (Figures 7E-F, Figure 8B) layers of the vertical canopy profile. The most regular berry distribution in the vertical canopy profile was observed in the lowest planting density (6,000 plants ha^{-1}) (Figures 7E-F).

P-values of LA, STAR and berry distribution dependant on planting density, arrangement, position in the canopy profile and branching order are shown in Table 1. Branching order, especially in the upper plant layers, had the highest impact on LA, STAR and berry distribution (Table 1A-F, Figure 8). Berry number increased significantly with canopy height and decreased gradually as branching order increased (Figure 8B, Table 1).

The STAR, LA and berry distributions were also dependant on foliage and berry positions in the plant canopy (Table 1A-F, Figures 6-8). The highest layers were characterized by leaves formed in the first-order plagiotropic branches (Figure 8A) and a low berry production (Figure 8B). Due to the low LA and poor branching process in the highest layers, light was transmitted to the lower layers, which affected berry production. Berry production was significantly affected by plant density in the square arrangement (Table 1A-B). In this arrangement berry distribution was most abundant when coffee plants were cultivated in a 6,000 plants ha^{-1} density (Figure 7E). Previous studies indicate that the square arrangement provides higher grain yield in comparison to the rectangular (ANDROCIOLI-FILHO et al., 2002).

STAR distribution was significantly influenced by planting arrangement in a lower density crop (Table 1F). Light interception (STAR) was generally higher in the leaves on the first and second-order plagiotropic branches (Table 1A-C, Figure 8A). Although the foliage on the third and fourth-order branches was important in plant light interception, here interception was significantly lower than among the foliage on the first and second-order plagiotropic branches (Table 1, Figure 8A). The light interception by the foliage on the lowest canopy layer was significant, contributing to a more uniform light interception along a vertical plant profile (Figure 8A). Thus, the disperse foliage leaf area and more uniform STAR distribution indicate an efficient space occupation.

The plants cultivated in high densities presented a lower yield than those in the low density treatments (Figure 7, Table 1). As the mock-ups of cv. IAPAR-59 were built for coffee trees seven years after pruning, the results indicate that, to enhance their yield, plants cultivated in higher densities should be pruned more frequently. The necessity of frequent pruning was also observed in other coffee cultivars, such as “Mundo Novo” and “Caturra”, which have a high yield when cultivated in high densities and whose berry production decreased drastically seven years after pruning (TOLEDO & BARROS, 1999).

High correlations between LA and berry production were established, especially in higher planting densities and in first-order branching, but the correlation coefficient values were always low (Table 2). STAR correlated strongly with the number of berries, especially in a 6,000 plants ha^{-1} density in square rather than in rectangular arrangements, in first-order branching and in the upper rather than in the lower canopy layers. The correlations between berry distribution and position on first-order branches and the upper canopy layers are biologically related to floral induction photomorphogenetic reactions, which occur with higher red: far red ratios, corresponding to a less shaded environment (COCKBURN et al., 1996). In some species, the LA and light environment are consistent with flower (CUNNINGHAM, 1997) and fruit production (FUKUDA et al., 1992).

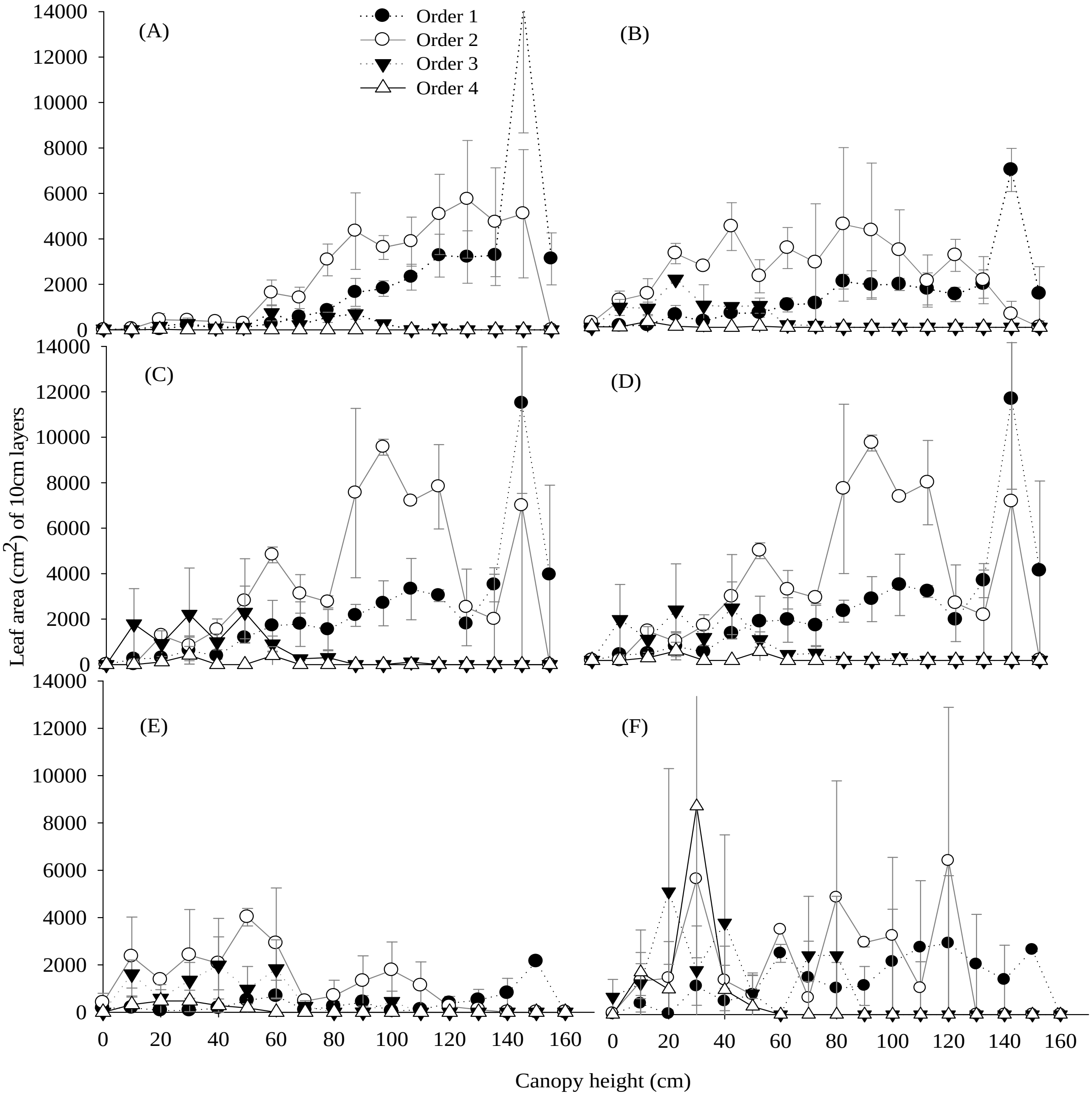


Figure 6 – Leaf area estimated in 10 cm layers calculated from mock-ups in VegeSTAR, built for coffee trees cultivated in the following treatments: (A) 14,000 plants ha^{-1} in square and **(**B) rectangular arrangements**;** (C) 10,000 plants ha^{-1} in square and (D) rectangular arrangements**;** (E) 6,000 plants ha^{-1} in square and (F) rectangular arrangements. Leaf area was identified per branching order (first to fourth).

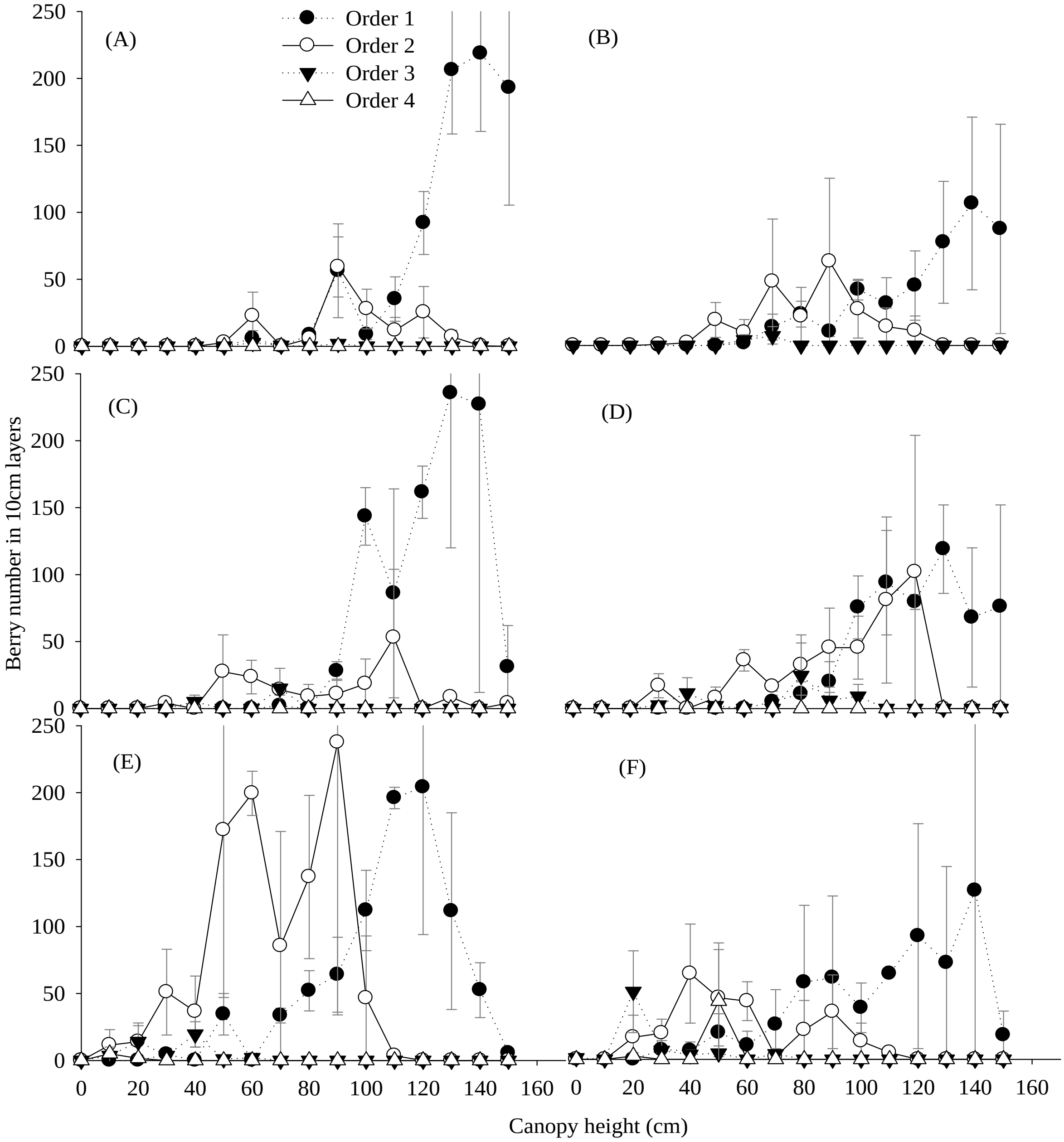


Figure 7 – Number of berries estimated in 10 cm layers calculated from mock-ups in VegeSTAR, built for coffee trees cultivated in the following treatments: (A) 14,000 plants ha^{-1} in square and **(**B) rectangular arrangements**;** (C) 10,000 plants ha^{-1} in square and (D) rectangular arrangements**;** (E) 6,000 plants ha^{-1} in square and (F) rectangular arrangements. Berry number was identified per branching order (first to fourth).

Table 1 – Kruskal-Wallis non parametric analysis for vertical distribution of berries, leaf area (LA) and STAR in layers of 40cm, differing four branching orders of adult coffee plants cultivated in different densities (14,000, 10,000 and 6,000 plants ha^{-1}), and arrangements (square and rectangular).

	Factors	D.F.	p-values BERRIES	p-values LA	p-values STAR
A/ General analysis	Density	2	0.0076	0.2924	0.8843
	Arrangement	1	0.6035	0.0619	0.3782
	Position by layers (1-4)	3	0.0006	0.4315	0.0002
	Branching order (1-4)	3	<0.0001	<0.0001	<0.0001
B/ Square arrangement	Density	2	0.04712	0.7345	0.3532
	Position by layers (1-4)	3	0.0063	0.1534	0.0296
	Branching order (1-4)	3	<0.0001	<0.0001	<0.0001
C/ Rectangular arrangement	Density	2	0.1535	0.4209	0.0792
	Position by layers (1-4)	3	0.0696	0.3529	0.0027
	Branching order (1-4)	3	<0.0001	<0.0001	<0.0001
D/ Density 14,000	Arrangement	1	0.7736	0.432	0.3785
	Position by layers (1-4)	3	0.0001	0.3164	0.1002
	Branching order (1-4)	3	<0.0001	<0.0001	<0.0001
E/ Density 10,000	Arrangement	1	0.649	0.2974	0.6059
	Position by layers (1-4)	3	0.081	0.6344	0.0659
	Branching order (1-4)	3	<0.0001	<0.0001	<0.0001
F/ Density 6,000	Arrangement	1	0.645	0.1032	0.0155
	Position by layers (1-4)	3	0.0766	0.0254	0.06737
	Branching order (1-4)	3	<0.0001	0.004	0.0001

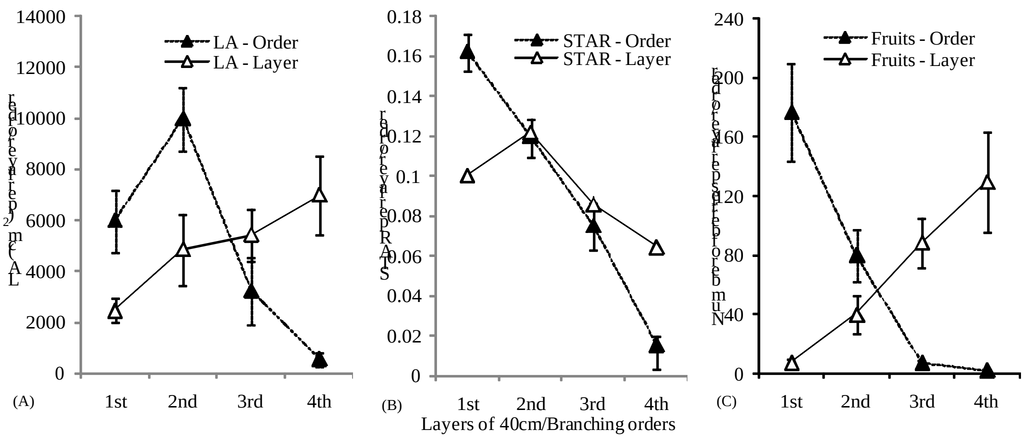


Figure 8 – Mean values and standard error of (A) leaf area, (B) STAR and (C) number of berries in function of branching order (first to fourth) and position in 40 cm layers (first to fourth) along the vertical profile of the coffee trees.

Table 2 – P-values and Pearson's coefficients calculated for correlations between berry and leaf area (LA) or STAR vertical distributions by layers of 40cm, differing four branching orders of adult coffee plants cultivated in different densities (14,000, 10,000 and 6,000 plants ha^{-1}), and arrangements (square and rectangular).

Factors	D.F.	Distributions of berries and LA		Distributions of berries and STAR	
		Coefficient of correlation	p-values	Coefficient of correlation	p-values
General analysis	254	0.2806	<0.0001	0.4167	<0.0001
Density					
Density 14,000	126	0.4087	<0.0001	0.2938	0.0008
Density 10,000	62	0.4250	0.0005	0.4934	<0.0001
Density 6,000	62	-0.0143	0.9106	0.6335	<0.0001
Arrangement					
Square	142	0.3111	0.0001	0.4902	<0.0001
Rectangular	110	0.2987	0.001	0.2219	0.01867
Position by layers					
Layer 1 (0-40cm)	62	0.3376	0.0063	-0.0455	0.7210
Layer 2 (41-80cm)	62	0.1315	0.3000	0.2432	0.0528
Layer 3 (81-120cm)	62	0.3308	0.0075	0.6251	<0.0001
Layer 4 (121-160cm)	62	0.2879	0.0210	0.7228	<0.0001
Branching order					
Order 1	62	0.3494	0.0046	0.4093	0.0008
Order 2	62	0.2000	0.1131	0.2831	0.0234
Order 3	62	0.343	0.1204	0.1137	0.3711
Order 4	62	0.1662	0.1892	0.2248	0.0741

4 CONCLUSIONS

3D structural modeling of *C. arabica* plants was satisfactory in the geometrical reconstructions. However, for more accurate architectural analysis, precise information on a metamer scale (i.e. length of each internode on the orthotropic shoot and plagiotropic branches, the exact size and position of the leaves, the angles of insertion of the leaves and branches) is recommended.

Light interception was more uniform than leaf area distribution in the vertical profile, which indicates disperse foliage with efficient space occupation.

Berry production was significantly affected by plant density in the square arrangement, indicating that the planting density management is efficient only in this arrangement.

Correlations between the distributions of vegetative and reproductive entities in coffee plants were established and the shape variations were detected. STAR correlated strongly with the number of berries, especially when positioned on the upper, less shaded canopy layers where flower induction was most intense.

5 ACKNOWLEDGMENTS

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