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Coffee productive branch growth, development and nutrient accumulation from flowering to harvest under Colombian conditions

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ABSTRACT

In many Colombian regions, coffee vegetative and reproductive growth *Coffea arabica* L. occur simultaneously; hence, fertilization plans must address both needs at the same time. The objective of the present study was to evaluate coffee productive branch growth, development, and nutrient accumulation from flowering to harvest. During an event of high concentration of flowering, which occurred in a coffee crop, Castillo Rosario® variety, 35 plants were randomly selected, and two opposite plagiotropic branches of the same stem node in the production zone were marked on each plant. One of the branches was detached at full anthesis and the other at harvest. Growth variables and nutrient concentration were measured at each time. Between flowering and harvest, branch length increased by 22 cm, number of nodes by 6.2, total biomass by 33 g, and defoliation from 14.5% to 32.5%. During this period, the concentration of all nutrients in the branch decreased, and the concentrations of N, P, Mg, and B in the leaves were lower. Total nutrient export increased differentially: N 73%, P 76%, K 142%, Ca 40%, Mg 51%, Fe 112%, Mn 87%, Zn 41%, Cu 156%, and B 36%. At anthesis, the highest proportion of nutrients was found in the leaves (57.35%-86.19%), followed by the branch (11.37%-37.41%) and flowers (1.58%-7.38%); at harvest, fruits contained the highest proportion of N, P and K, and leaves the highest export of Ca, Mg, Fe, Mn, Zn and B. These results corroborate the importance of branches and leaves in supporting nutrient demand by fruits and vegetative growth.

Key words: *Coffea arabica* L; nutrient concentration; defoliation; nutrient partitioning; Colombian coffee zone.

1 INTRODUCTION

For perennial species such as coffee, vegetative and reproductive stages are complex to define because after the first flowering occurs, there will be an overlapping of both stages, which means that the vegetative organs grow, such as leaves, branches, stem, and roots, will take place simultaneously with reproductive grow during the rest of plant life (Arcila, 2007; Cannell, 1985).

Coffee growth and fructification follow a single annual cycle in "non-equatorial regions", such as southern India, Ethiopia, Hawaii, Central America, south-central Brazil, and Zimbabwe.

In contrast, in tropical areas, such as Colombia, where two dry and wet seasons take place, two fast growth periods of sprout, flowering, and fructification occur, thanks to the influence of the intertropical converge zone (Cannell, 1985). In Colombia, a wide range of coffee harvest distribution occurs in different country regions due to water and energy availability (Jaramillo, 2018).

Coffee flowering, as a starting point of the reproductive stage, is considered a complex physiological process that is closely related to climate conditions (rain, temperature, and light), mainly dry periods between two and four months (Almeida et al., 2021; Garcia et al., 2022; Tavares et al., 2018). Additionally, biochemical, physiological, and morphological events involved in flowering depend on the genetic factors, carbon-nitrogen ratio, and crop load interactions (López et al., 2021).

In some Colombian regions, where ten or more flowering events occur between November and April, the principal harvest takes place in the second semester of the year. Among these events, one or two of greater magnitude stand out, as long as periods with low rainfall occur, followed by high rainfall, which is responsible for breaking the flower dormancy (Jaramillo, 2018). Under the conditions described, the main harvest represents 75% of the annual production, while the remaining 25% corresponds to the "mitaca" (secondary harvest) of the first semester. In response to this environmental supply, the coffee tree constantly forms new branches and reproductive structures that account for the harvests of each semester and, at the same time, determine the growth rate of the different organs; likewise, vegetative growth occurs in the reproductive branches during the development of the fruits as a consequence of climatic stimulus (Arcila, 2007).

In regions where concentrated flowering occurs, such as Brazil, fruit development and fast vegetative growth tend to occur at different moments, which suggests incompatibility or competence among both processes (Barros et al., 1999; Damatta et al., 2007). This unsynchronized, governed by climatic factors, allows the development of an adequate foliar area to support fruit expansion; this also sustains why a vigorous flowering is not accompanied by a concomitant balance in leaf area formation (DaMatta et al., 2007).

It is been proven that coffee varieties exhibit different nutritional needs; it is also known that the total nutrient extraction by plants does not vary by production (Corrêa et al., 1986). This is because, in years of lower harvest, branch growth replaces the fruit as a sinking ground for carbohydrates and nutrients (Barbosa et al., 2021; Malavolta et al., 2002).

Despite the similarity in the total nutrient quantity that plantations with different production levels can extract, the amount of removed elements of the soil by a harvest increases with the increase of production. Therefore, it is recommended that nutrient doses be adjusted according to the expected production, both for *C. arabica* (Quaggio et al., 2022) and *C. robusta* (Cararo et al., 2022). For Colombian conditions, it is suggested that nutrient doses be adjusted based on plant density per hectare and the level of shading, variables that affect productivity (Sadeghian, 2008).

An essential part of the nutrients accumulated in the fruits come from closer leaves, and a certain amount comes from the reserves located in other plant parts (Valarini et al., 2005; Toro-Herrera et al., 2023). In this sense, the leaves that fall during harvest maturation are related to foliar exhaustion caused by high nutrient mobilization through the fruits. For this reason, a more remarkable fall in leaves occurs during the high-production years, decreasing the harvest for the next cycle (Chaves; Sarruge, 1984). Regarding fruit development as sink organs, the filling stage will not be synchronized when these are the product of several flowering events. Therefore, this may indicate a lower depletion of coffee plant reserves (Cannell, 1985).

In some research conducted with two coffee cultivars (Catuaí Amarelo and Mundo Novo), Malavolta et al. (2002) found that the flowers constitute a substantial nutrient sink, especially Mg, being the cultivar response variable. Based on the obtained results, the authors suggest starting fertilization before flowering. Ramírez et al. (2002) measured the productive coffee branch growth of the Caturra variety and nutrient accumulation in fruits under Costa Rica conditions. The authors based on the accumulation nutrient curve to generate fertilization recommendations.

Nutrient accumulation is related to the compound amount increase that does not directly promote growth and can explain the short-term changes in their storage; however, on longer time scales, the photosynthesis and nutrient absorption capacities are adjusted to plant demand (Lambers; Oliveira, 2019). *C. arabica* young sprouts and nonproductive exhibit high foliar concentrations of N and soluble sugar, while mature sprouts present lower N and starch accumulation in inferior organs (Cambou et al., 2021). Sadeghian (2022) reports a similar tendency for foliar N, P, K and Mg.

Several studies have been conducted to understand coffee nutrient accumulation in fruits from the anthesis to harvest (Moraes; Catani, 1964; Cannell, 1985; Salazar et al., 1994; Ramírez et al., 2002; Laviola et al., 2008; Sadeghian et al., 2012; Sadeghian et al., 2013; Sadeghian; Salamanca, 2015). However, little information about what happens with the leaves and branches supporting the harvest is available. This study aimed to evaluate growth, development, and nutrient accumulation in productive coffee branches from flowering to harvest during a high-flowering concentration event.

2 MATERIAL AND METHODS

The field phase of this study was carried out at the Experimental Station La Catalina, located in the municipality of Pereira (Risaralda department, Colombia), with geographic coordinates 4° 44' 52.08'' North latitude; 75° 44' 17.52'' West longitude, at 1318 m.a.s.l. The climatic conditions during the evaluation period were: 2019 mm/year of cumulative precipitation, a daily average temperature of 22 °C, and a relative humidity of 78.1%. In this locality, the bimodal distribution of rainfall (drier periods in January-February and July-August) contributes to the annual coffee production regularly distributed in two periods: the first semester 25%, and the second 75%.

The measurements of the plant variables, dry matter determinations, and nutrient analysis were carried out in the laboratories of the Soil Discipline of the National Coffee Research Center, Cenicafé, located in the Manizales municipality (Caldas department).

A coffee plantation *Coffea arabica* L., Castillo Rosario® variety, established with topped seedling (two stems per plant) at a distance of 1.0 m between plants and 2.0 m between rows (5,000 plants ha^{-1}), was selected. Soil analysis, performed at the beginning of the research, yielded the following information: pH in water 5.1, organic matter 10.1%, P 12 mg kg^{-1}, S 19.8 mg kg^{-1}, K 0.40 $cmol_c$ kg^{-1}, Ca 4.1 $cmol_c$ kg^{-1}, Mg 0.82 $cmol_c$ kg^{-1}, Al 0.5 $cmol_c$ kg^{-1}, CEC 26 $cmol_c$ kg^{-1}, Fe 233 mg kg^{-1}, Mn 45.0 mg kg^{-1}, Zn 9.0 mg kg^{-1}, Cu 3.3 mg kg^{-1}, B 0.45 mg kg^{-1}, clay 24%, silt 37% and sand 39%. Based on these results, the following fertilization plan was defined, according to the recommendations of Sadeghian (2008): N 280 kg ha^{-1} $year^{-1}$ (determined based on soil organic matter content), P_2O_5 40 kg ha^{-1} $year^{-1}$ and K_2O 260 kg ha^{-1} $year^{-1}$, quantities that are distributed in two half-yearly applications at the beginning of the rainy seasons.

Two evaluations were carried out, the first in March, at full anthesis of one of the largest magnitude events of the year (the most abundant flowering event, but not the only one, generated by a severe water deficit two months earlier). The second evaluation, in November, was carried out on the peak harvest day, approximately eight months later.

In general, it is recommended that this type of research should be conducted over two or more harvests. However, the

flowering periods in the following year were scattered, making it impossible to repeat the evaluations.

At the time of the first evaluation, the crop was 21 months old and had its first low-magnitude harvest the year before, 196 kg ha^{-1} of dry parchment coffee. The yield obtained from the plot during the evaluation year was 4100 kg ha^{-1} of dry parchment coffee, which is considered high for a 3-year-old plantation in Colombia.

In the first evaluation, 35 trees were randomly selected from the entire lot. On each one, two plagiotropic branches were identified from the same stem node in the production area. At the flowering (anthesis), one of the two branches was detached, and the following variables were measured: branch length (BL), leaves number (LN), nodes number (NN), flowers number (FN), and nodes number with flowers (NNF) present per branch. At harvest, the second branch was detached, and its BL, LN, NN, fruit number (FRN), nodes number with fruits (NNFR), and leaves number in nodes with fruits (LNNFR) were quantified.

The 35 collected branches were randomly grouped into seven sets of five, thus forming seven replicates, as suggested by Malavolta et al. (2002), a procedure that reduced the number of analyzed samples (from 210 to 42).

Subsequently, the branches, leaves, flowers (first evaluation) and branches, leaves, and fruits (second evaluation) of each group were separated and dried in an oven for 72 h at 60°C to determine dry matter and concentration of nutrients (nitrogen-N, phosphorus-P, potassium-K, calcium-Ca, magnesium-Mg, iron-Fe, manganese-Mn, zinc-Zn, copper-Cu, and boron-B) in each organ

Based on dry matter values and nutrient concentration, accumulation in the branch for each evaluation time was calculated, according to equations 1 and 2 for macro and micronutrients, respectively:

$$\text{Export of macronutrient by organ (mg/branch)} = [\text{DM, g}] \times [\text{NC, \% x } 10^{-1}] \quad (1)$$

$$\text{Export of micronutrient by organ (µg/branch)} = [\text{DM, g}] \times [\text{NC, mg kg}^{-1}] \quad (2)$$

Being, DM dry matter and NC nutrient content.

Only those that had reached maturity (unripe and red) were considered for the compositional analysis of the fruits, representing approximately 80% of the total amount. It is assumed that green fruits (20%) would reach maturity in the following 15 to 20 days.

After verifying the assumptions of normality and homogeneity of variances, an average comparison test (paired t-test) ($p < 0.05$) was performed for the variables that were evaluated in the two seasons: BL, LN, NN, branch dry matter (BDM), leaves (LDM), flowers (FLDM) and fruits (FRDM) and total dry matter (TDM), concentration and export of nutrients in branches, leaves, flowers, and fruits. The TDM was calculated from BDM, LDM, FDM (at flowering), and FRDM (at harvest).

3 RESULTS

3.1 Growth variables

The paired t-test suggested higher mean values ($p < 0.05$) for BL, NN, BDM and TDM in the harvest compared to flowering (Table 1). Between flowering and harvest, the length of the branch increased by 22 cm and the node number by 6.2. During this period, on average, 0.78 nodes of 3.55 cm were formed each month. Since two leaves would be expected to be found at each node, it is concluded that on the peak day of flowering, on average, 3.89 leaves were missing from the branch, equivalent to a 14.53% defoliation at anthesis. The number of leaves present during harvest and flowering was statistically the same. Given the number of nodes on the branch at harvest, the number of leaves present, and the number of missing leaves, a total defoliation of 32.53% is estimated, of which 9.92% occurred at anthesis and 22.62% between this time and harvest. Additionally, the low number of leaves at nodes with fruit suggests that most defoliation occurred in the production area.

In the first evaluation, the node number with flowers per branch was slightly lower than the node number with fruits, registered in the second evaluation. A similar tendency was found in the flower number per branch with concern fruit number. This result reveals that the flowering event happened in a concentrated way, without this being the only evaluation period.

The growth of branches between flowering and harvest reflected a significant increase in its dry matter, which was not observed for leaves due to defoliation. The flower biomass per branch was very low; in addition, a part of this can be shed after fecundation. Considering the fruit's dry matter per branch and the number of these, a weight of 0.41 g per fruit is estimated. The total biomass per branch, including the other organs, increased by 33 g concerning the first evaluation, a value equivalent to an increase of 155%. In both assessments, the dry matter of leaves mean was equal (0.6 g); therefore, fruit growth did not affect this variable. Considering this quantity and the number of missing leaves, the lost biomass due to the defoliation of each branch during the evaluation period can be estimated at 5.8 g, a value that raises the total biomass to 60 g.

In the flowering, the higher biomass was represented by leaves, while in harvest, the predominance was given by the fruits (Figure 1).

Table 1: Mean values and standard error (S.E.) of coffee organ dry matter and growth variables evaluated in plagiotropic branches of the coffee production zone during flowering and harvest.

	First evaluation ----- (Flowering) -----		Second evaluation ----- (Harvest) -----	
	Mean	S.E.	Mean	S.E.
Branch length, cm	53.67 B	2.62	75.89 A	3.84
Node number per branch	13.39 B	0.53	19.61 A	0.76
Leaves number per branch	22.89 A	1.19	26.46 A	1.45
Node number with flowers per branch	8.58	0.46	—	—
Flower number per branch	53.58	1.53	—	—
Fruit number per branch	—	—	67.81	9.57
Nodes number with fruits per branch	—	—	9.31	0.58
Leaves number in nodes with fruits	—	—	7.49	0.79
Branch dry matter, g	6.46 B	0.58	10.19 A	1.08
Leaves dry matter, g	13.57 A	1.24	15.82 A	1.73
Flower dry matter, g	1.21	0.05	—	—
Fruit dry matter, g	—	—	28.21	4.75
Total dry matter, g	21.23 B	1.77	54.23 A	6.19

Means followed by different letters indicate statistical differences between evaluations, according to the t-test at 5% probability. Variables evaluated in a single period do not have the average comparison test.

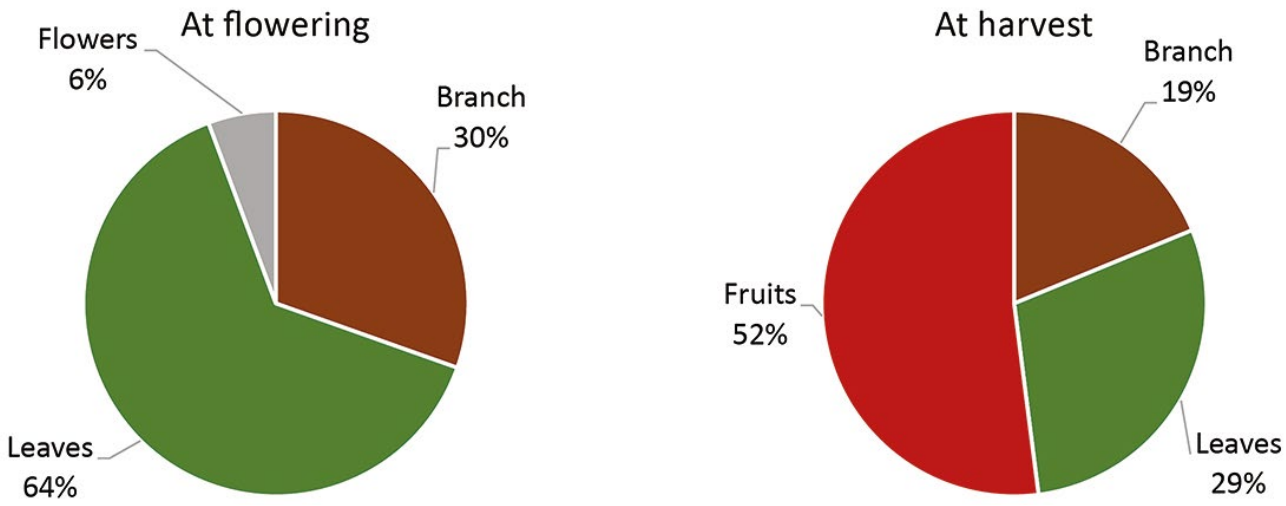

Figure 1: Partitioning of the dry mass of coffee organs biomass during flowering and harvest.

3.2 Nutrient concentration

The concentration of all branch nutrients was significantly lower during harvest than flowering (Figure 2). Three cases were detected for leaves: N, P, Mg, and B concentrations were lower at harvest; Fe, Mn, Zn, and Cu had an opposite tendency, and K and Ca did not register changes.

The following sequences of nutrient concentrations were present in the two evaluation periods:

Branch: N>K>Ca>P>Mg>Mn>Fe>Zn>Cu>B
Leaves: N>K>Ca>Mg>P>Mn>Fe>B>Zn>Cu
Flowers: N>K>Ca>P>Mg>Fe>Mn>Cu>B>Zn
Fruits: K>N>Ca>P>Mg>Fe>Mn>B>Cu>Zn

With few exceptions, the highest concentrations of N, Ca, Fe, Mn, and B were detected in leaves. The highest P, Cu, and Zn concentrations correspond to branch, and the lowest K concentrations were recorded in branch.

3.3 Nutrient export

The export of Mg, Fe, Mn, and B in the branch were lower in the evaluation carried out during the harvest. Although a similar tendency was detected for some other nutrients, the

effect was not statistically significant (Figure 3). As for the leaves, increases were detected in the micronutrients Fe, Mn, Zn, and Cu. With few exceptions, for all organs, the order of nutrient export evaluated in the two evaluation periods was the same as for the concentration.

Regarding total accumulation (the total nutrient export in branch, leaves, and flowers/fruits), significant increases were recorded for all the analyzed elements except Ca and B. The order recorded was the following:

Flowering: N>K>Ca>Mg>P>Mn>Fe>B>Zn>Cu
Harvest: K>N>Ca>P>Mg>Mn>Fe>B>Cu>Zn

The percentage increase in total nutrient quantity since flowering to harvest was the following: N 73%, P 76%, K 142%, Ca 40%, Mg, 51%, Fe 112%, Mn 87%, Zn 41%, Cu 156%, and B 36%. Table 2 presents the percentage distribution of nutrient export of organs evaluated during flowering and harvest. At flowering, a higher proportion of all nutrients, except Zn and Cu, were found in leaves (between 57.35% and 86.19%), followed by the branch (between 11.37% and 37.41%) and flowers (between 1.58% and 7.38%). Regarding Zn and Cu, a higher export was found in the branch. During harvest, fruits contained a higher proportion of N, P, and K, and leaves contained higher Ca, Mg, Fe, Mn, Zn, and B.

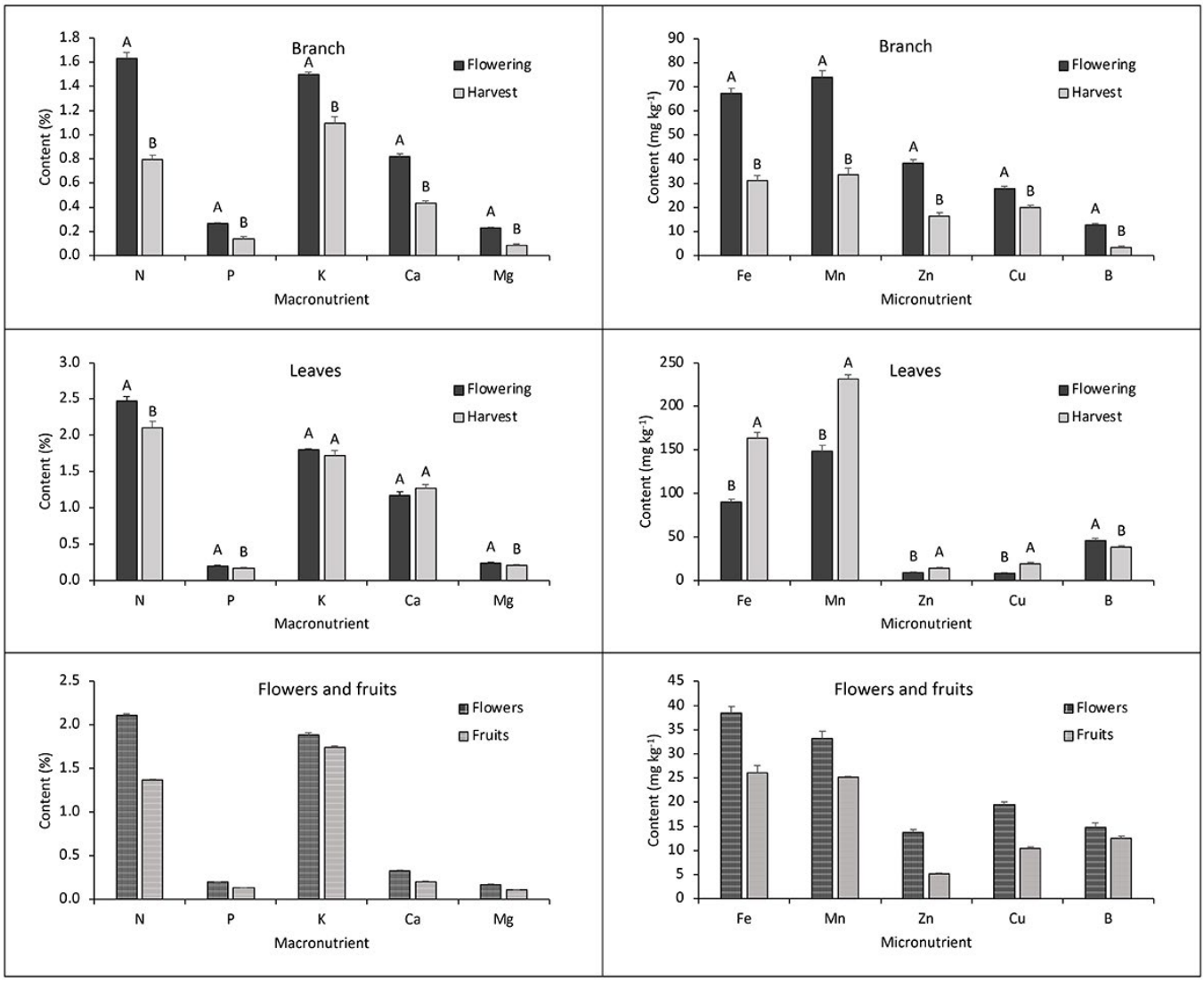

Figure 2: Mean values of nutrient concentration in the branches of the coffee production zone during flowering and harvest. Means followed by different letters indicate statistical differences between evaluations, according to the t-test at 5% probability. Variables evaluated in a single period do not have the average comparison test.

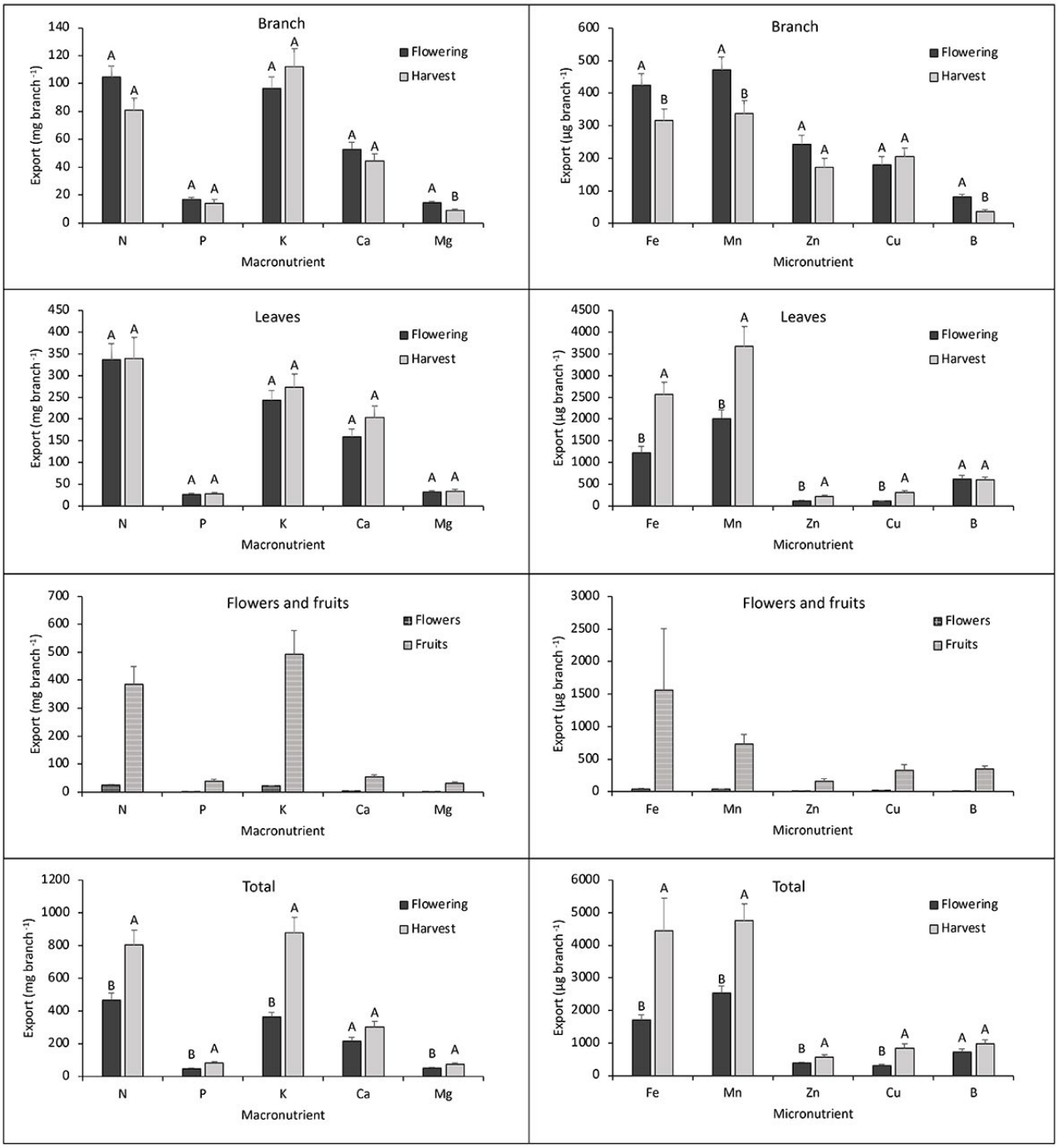

Figure 3: Mean values of nutrient export in branches in the coffee production zone during flowering and harvest. Means followed by different letters indicate statistical differences between evaluations, according to the t-test at 5% probability. Variables evaluated in a single period do not have the average comparison test.

4 DISCUSSION

4.1 Growth variables

At the harvest moment, branch length was higher than the one reported by Unigarro et al. (2021) for Castillo® Variety under Colombia conditions (between 48.8 and 58.0 cm) and the one mentioned by Carvalho et al. (2022) for the Catuaí cultivar in Brazil (between 46.2 and 48.9 cm); differences that would be both related with the variety and climate conditions.

Plagiotropic branch growth during the fruit formation period (22.0 cm long and 6.2 nodes) confirms the superposition of vegetative and reproductive growth, evidenced by Arcila (2007), Bote and Jan (2016), Cannell (1985) and Ramírez et al. (2002).

Table 2: Percentage representation of nutrients in the branches of the coffee production area during flowering and harvest.

Nutrient	First evaluation (At flowering)			Second evaluation (At harvest)		
	Flowers	Leaves	Branch	Fruits	Leaves	Branch
N	5.45	72.13	22.41	47.86	42.09	10.05
P	5.25	57.35	37.41	48.17	33.96	17.87
K	6.27	67.17	26.56	56.15	31.09	12.77
Ca	1.82	73.68	24.51	18.00	67.24	14.77
Mg	4.28	65.62	30.10	42.60	45.26	12.14
Fe	2.73	72.28	24.99	19.85	71.36	8.79
Mn	1.58	79.73	18.69	14.95	77.90	7.15
Zn	4.38	31.64	63.98	26.10	42.00	31.90
Cu	7.38	35.49	57.13	36.47	38.03	25.49
B	2.43	86.19	11.37	35.36	61.00	3.64

Concerning node number per branch in the flowering and fruit maturation phases, the obtained values were lower than those reported for low-growing varieties in Brazil (between 24.0 and 33.3). These plants were established in free sun exposure and with wide planting distances of 2.5 m between furrows, which favors a more significant extension of the branches towards the street (Ricci et al., 2011).

In the Colombian central coffee zone, coffee plants generate approximately one node each month (Arcila, 2007), a growth that results in a larger than the registered between anthesis and harvest (0.78 nodes per month). Based on this result, it can be assumed that the relatively high-fruit load decreased the branch vegetative growth by 20%, a smaller impact than that reported by Bote and Jan (2016) and DaMatta et al. (2007). The effect on the growth rate of plagiotropic branches due to the fruit-bearing capacity has also been reported for *Coffea canephora* (Corve et al., 2016; Partelli et al., 2013). The relatively normal growth of the branch during the fruiting period shows that, overall, there were no limitations to the plant's growth and development, particularly regarding nutrients.

As far as nutrients are concerned, the plant reserves, both those contained in the organs closest to the fruits (Valarini et al., 2005) and those accumulated in other parts of the plant (Toro-Herrera et al., 2023), were sufficient to support vegetative growth in the productive branches during fruit development, and thus avoid intense competition. The above would be related to the amount of reserves accumulated in the plant, possibly due to low production in the previous year and many unproductive branches (without fruits) from which the required carbohydrates were exported (Cannell, 1985).

In Castillo® variety coffee plants, the dry matter accumulation from the vegetative organs of the shoot system during the four years following planting represents 73% of the total biomass (35 t ha^{-1}), while the fruits constitute 27% (Sadeghian, 2022). The marked difference between the dry matter represented by vegetative and reproductive structures at the plant level in the productive cycle can be associated with the time it takes for the plant to begin the reproductive stage (18 to 24 months) and the continuous harvest patterns identified for the central coffee zone of Colombia, characterized by the permanent development of flowers and fruits throughout the year (Unigarro et al., 2023). The findings at the branch level indicate that the previous tendency can be changed when it comes to a high harvest, in which case, the highest proportion of the dry matter corresponded to the fruits (52%) rather than the leaves and the branch (48%).

Regarding defoliation, leaves fall during fruit formation processes; it has been related principally to the massive nutrient mobilization to sink organs, a phenomenon that reduces its concentration in foliar tissue. For this reason, on many occasions, during years of high production, higher defoliation occurs, result that can diminished this way the following cycle harvest (Chaves; Sarruge, 1984; Arcila, 2007), a phenomenon known as bienniality.

4.2 Nutrient concentration

For most cultivated species, nutrient concentration follows a similar sequence to the one found in this study (Kirkby, 2023), with some variations that can be attributed to climate, soil, and crops (Havlin et al., 2017). The information published by Ramírez et al. (2002), Malavolta et al. (2002), and Sánchez et al. (2018) indicates a similar tendency for different *C. arabica* varieties under conditions in Costa Rica, Brazil, and Colombia. Generally, a lower nutrient concentration is highlighted in the branches concerning flowers, leaves, and fruits.

The concentrations of all flower nutrients were lower than those reported by Ramírez et al. (2002) and Malavolta et al. (2002) for Caturra in Costa Rica and Catuaí and Mundo

Novo in Brazil varieties. Furthermore, Malavolta et al. (2002) state that the flower Mg concentration is five times higher than that of leaves and branches, a result that was not found in this study.

Nutrient concentration reduction in branches and leaves occurs between flowering and harvest, which can be related to photoassimilate mobilization toward fruits due to their high demand. Despite the knowledge of this phenomenon for different *C. arabica* varieties, only some of the research developed around nutrient accumulation in the fruits have found conclusive evidence to justify the nutrient re-mobilization from the leaves. In this regard, Bote and Jan (2016), Chaves and Sarruge (1984), Lima Filho and Malavolta (2003), Sadeghian et al. (2012) and Valarini et al. (2005), report a reduction in N and/or K concentration as a result of the flux of these nutrients from the source (leaf) to the sink (fruit). For Ca, Mg, and S (Chaves; Sarruge, 1984; Laviola et al., 2007; Sadeghian et al., 2013) and micronutrients (Sadeghian et al. 2015), the studies did not detect changes, resulting that has been mainly attributed to the mobility of these elements in the plant, with Mg being the exception.

For Sadeghian and Salamanca (2015), the little or no reduction in nutrient concentration reported for leaves during the fruit formation stage is because the required elements by fruits come from to a greater extent from the leaves than in the production area (Valarini et al., 2005). In contrast, in the studies in question, the evaluation was carried out on the leaves closest to the apex of the branch, that is, the third or fourth pair. This justification makes more sense for two- or three-year-old plants (first and second harvest), where new nodes grow in the productive branches after flowering (Sadeghian; Salamanca, 2015), as occurred in this study.

For K and N, it would be expected a reduction in their foliar concentration due to the high demand of fruits (Sadeghian et al., 2012; Melke; Ittana, 2015), especially for pulp formation (Sadeghian et al., 2006). Laviola et al. (2008) also found no decreases in K leaves concentration, while Chaves and Sarruge (1984) did. The increase in Mn, Fe, Cu, and Zn concentration, both in branch and leaves, can originate in the reduced mobility of these micronutrients. Additionally, Fe-increased foliar may be associated with the increase in PSII photosystems number due to self-shading generated by the branches of the upper third of the plant (Buchanan et al., 2000).

Nutrient foliar concentration, both in flowering and production, was in the adequate ranges for the coffee crop under Colombian conditions (Sadeghian, 2020), being partially low N level. This suggests that the nutritional state of plants was optimum and, in a good way, supported the branch's growth during the evaluation period.

The diminished nutrients in branches were clear evidence that this organ is an essential source of photoassimilates for fruits, a fact that, on occasion, does not receive enough attention due to its lower effect in comparison with leaves. Although there is no available information on branches of coffee adequate nutrient levels, it can be assumed that these were not low because, otherwise, there would be branch growth limitations and node new formations.

Nutrient concentration changes in a predictable manner with plant development. In woody plants, the C:N ratio of the whole plant increases with age and as a consequence of the increase in the ratio of woody mass and leaves and roots mass, active physiological. On the other hand, nutrients associated with metabolism, particularly N, P, and K, have higher concentrations when a leaf or other organ is first produced. Subsequently, the concentrations decrease due to leaf expansion and senescence (Lambers and Oliveira, 2019; Sadeghian, 2022). In coffee leaves and branches, the decrease in N, P, and K concentrations is related to the demand for these nutrients for fruit development, even more so when there is an overlap of phenological stages, with nodes in the branches that differentiate buds for the formation of leaves, flowers, and fruits at different stages of development.

Fruits are sink organs with high photoassimilate capacity for importing. They are characterized by their high competency concerning other functional sink organs, such as leaves in expansion and vegetative branches in growth (Toro-Herrera et al., 2023). Recent studies show that carbon reserves (structural and non-structural carbohydrates) are also remobilized from the branches to provide assimilates in years of greater production in *C. arabica* trees (Cambou et al., 2021).

4.3 Nutrient export

Despite branch growth (measured as length, number of nodes, and dry matter), the nutrient export did not increase in this organ between flowering and harvest; in fact, it decreased significantly for Mg, Fe, Mn, and B. This added to the reduction in nutrient concentrations, confirms the role of the branch as a sink during fruit growth.

On some occasions, nutrient concentration decreases due to plant growth, a phenomenon known as the dilution effect (Taiz, 2017). However, in these cases, nutrient export increases. The results of this study indicate that, despite branch growth, nutrient export did not increase or even decrease, a finding that reveals mobilization toward other sink organs, particularly fruits.

In the event of high production, it would have been expected that apical drying of the branches (dieback) would have been observed due to the inability of the leaves to support the carbohydrate demand (Carvalho et al., 1993). This symptomatology was not observed and, as already discussed, was related to the sufficiency of the reserves contained in the plant, especially when the obtained production was relatively high, or at least not low, for three years old plants.

The reasons for the lack of detection of increases in nutrient export in leaves during fruit formation include defoliation and the reduction in the concentration of some elements (N, P, Mg, and B). The main cause of these two processes is the mobilization of nutrients towards the fruits (Chaves; Sarruge, 1984; Arcila, 2007; Valarini et al., 2005).

The total biomass increased and the nutrient amount accumulated in productive branches, recorded between flowering and harvest, is mainly due to the fruits; hence, their recognition as the preferential sink organs for nutrient partitioning (Carvalho et al., 1993; Lima Filho; Malavolta, 2003; Rena; Maestri, 1985). Despite the importance of fruits as sinks for photoassimilates, the most significant proportion of the Ca, Fe, Mn, Zn, and B export was located in the leaves before the fruits (Table 2), a response that can be related to their low mobility via phloem (Taiz et al., 2017). Of the above elements, Ca and Mn were the ones least translocated to the fruits, remaining mainly in the leaves.

The nutrient accumulation sequence in flowering and harvest differs little and largely coincides with those mentioned above. According to Sadeghian (2022) reports for Colombia, during all stages of coffee cultivation (seedling, growing, and production), the plants extract a more significant amount of N and K than the other nutrients, in second place is Ca and, subsequently, P, Mg, and S, followed by the micronutrients Fe, Mn, Zn, Cu, and B. For fruits of the Castillo® variety, the following order of appearance is specified: K> N> Ca> P> Mg> S> Mn> Fe> B> Cu> Zn (Sadeghian et al., 2012; Sadeghian et al., 2013; Sadeghian; Salamanca, 2015). This sequence agrees with what was found in this work as well as other reports for *C. arabica* (Chaves; Sarruge, 1984; Laviola et al., 2009; Ramírez et al., 2002; Valarini; Bataglia, 2005) and *C. canephora* (Corve et al., 2018a; Corve et al., 2018b; Dubberstein et al., 2016; Torres et al., 2022).

5 CONCLUSIONS

Nutrient export in coffee fruits did not hinder branch growth. During anthesis, leaves had the most biomass, followed by branches and flowers, while at harvest, fruits dominated. Total branch biomass increased by 155% between anthesis and harvest, with increased defoliation and reduced nutrient concentration in branches and leaves due to photosynthate mobilization. The percentage increase in the total amount of nutrients exported from flowering to harvest showed the highest values for K, Cu, and Fe, and the lowest values for B, Ca, and Zn.

6 AUTHORS' CONTRIBUTIONS

Conceptual Idea: Sadeghian, S.; Methodology design: Sadeghian, S.; Data collection: Sadeghian, S.; Díaz, V.C.; Data analysis and interpretation: Sadeghian, S.; Díaz, V.C.; Rendón, J.R.; Writing and editing: Sadeghian, S.; Díaz, V.C.; Rendón, J.R.

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