

SOURCE-SINK MANIPULATIONS IN *Coffea arabica* L. AND ITS EFFECT ON GROWTH OF SHOOTS AND ROOT SYSTEM

Manipulação da relação fonte-dreno em *Coffea arabica* L. e seu efeito no crescimento da parte aérea e do sistema radicular

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ABSTRACT

This paper investigated changes in growth and carbohydrate content of shoots and root systems in response to source-sink manipulation in field-grown coffee trees. The source-sink manipulations were carried out using manual de-fruiting. Two plots of trees were established: in one group, the fruit was left on the tree, while in the second group all fruits were removed manually. Similar results were obtained for coffee trees with and without fruit in terms of height, stem and skirt diameter and branch lengths. A biochemical evaluation of the roots showed that no differences were found between the levels of carbohydrates. In the leaves, levels of soluble sugars and reducing sugars were higher in plants with fruit. The starch concentration in leaves and roots did not vary between the plots. Root length density did not vary between plants with and without fruit in the 0 - 0.4 m soil layer. However, plants without fruit had a higher root length density than plants with a full fruit load. These results contrast with results published by others on source-sink relationships of coffee plants. The joint data analysis shows that young trees, with a moderate fruit load, and with good nutritional and health status, produce carbohydrates in sufficient quantities to maintain vegetative and reproductive growth, without harming root system growth.

Index terms: Carbohydrates, source-sink, coffee tree, root system.

RESUMO

Foram investigadas as alterações no crescimento e nos teores de carboidratos da parte aérea e sistema radicular em resposta à manipulação fonte-dreno em cafeeiros cultivados em condições de campo. Essas manipulações foram realizadas mediante desfrutificação manual. Dois grupos de plantas foram estabelecidos: em um grupo, a produção de frutos foi mantida, enquanto no segundo grupo, todos os frutos foram retirados manualmente. Cafeeiros, com e sem frutos apresentaram resultados semelhantes em termos de altura, diâmetro do caule e saia e comprimentos de ramos. Nas avaliações bioquímicas nas raízes não foram verificadas diferenças entre os níveis de carboidratos. Nas folhas, os teores de açúcares solúveis e açúcares redutores foram maiores nas plantas com frutos. As concentrações de amido nas raízes e folhas não variaram entre os tratamentos. A densidade de comprimento de raízes na camada de solo de 0-0,4 m não se diferenciou entre plantas com e sem frutos. Entretanto, as plantas sem frutos apresentaram maior densidade de comprimento radicular que aquelas plantas com carga completa. Esses resultados contrastam com os resultados publicados por outros autores considerando-se as relações fonte-dreno do cafeeiro. A análise conjunta dos dados mostra que os cafeeiros jovens, com carga moderada e com bom estado nutricional produzem carboidratos em quantidades suficientes para manter o crescimento vegetativo e reprodutivo, sem prejudicar o crescimento do sistema radicular.

Termos para indexação: Carboidratos, fonte-dreno, cafeeiro, sistema radicular.

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INTRODUCTION

The growth and development of plants involves a complex relationship between shoots and the root system. The assimilated compounds produced by the leaves during the process of photosynthesis are translocated throughout the plant to satisfy demand for the carbon and energy that will be responsible for the formation of new tissues (TAIZ; ZEIGER, 2006). According to their ability to export and

import photoassimilates, plant organs can be classified as source and sink, respectively (WUBS et al., 2009).

With coffee plants, the interdependencies between source-sink organs (leaves, fruits) and sink-sink (fruit branches) are well established. Cannel (1976) studied the partitioning of assimilates between leaves and fruits, and concluded that a leaf area of 20 cm² is required to fulfill the requirements of each coffee fruit growth. Thus, it is easy

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to conclude that to support high production, coffee plants must have an appropriate level of foliage that enables them to fix a sufficient quantity of carbon to meet the high demand for assimilates from the fruit (ALVES, 2008). For woody plants, a leaf area index of around eight generally meets this need (KINNEY et al., 1997).

Regarding fruit branches, the vast majority of research with coffee plants has been conducted by manipulating the source-sink relationship, by means of controlled unfructification or phenological studies to determine changes in the growth of the shoot. In these cases, it was shown that shoot growth is lower in plants with full fruit load compared to those with reduced fruit load (AMARAL et al., 2006). Several studies show that during phases of rapid fruit growth and accumulation of dry matter in the seed, there is a restriction on branch growth and in the number of internodes, proportional to the number of fruits (PEZZOPANE et al., 2008). Therefore, there is a competitive relationship between these two organs of coffee plants, and the fruit, when at peak growth or in high numbers, are preferential sinks.

Although the leaf/fruit and fruit/branch relationships are already conclusive for coffee plants, it is rare to encounter both research involving assimilate partitioning (considering only the root system as sink) and research on the relationship between fruit and root as two competitive, strong sinks. Despite this consideration, there are some studies that show, albeit indirectly, competition between shoot and root systems. It is common to observe, in some fields of Southwest Bahia, trees with a height of four meters and a shallow root system, not exceeding 60 to 80 cm deep. This high shoot height to root depth ratio has been attributed to the high temperatures that occur during most of the year, constant irrigation and high fertilization in trees grown in sandy soils (GUERRA et al., 2007). These conditions favor an almost continuous growth of stem, branches and leaves at the expense of the root system. On the other hand, in the Zona da Mata and Southern Minas Gerais, Brazil, where distinct hot and rainy and cold and dry seasons exist, there is coordination between the growth of shoot and root systems that favors the growth of both parts (RENA; MAESTRI, 1986).

Developing fruit and roots compete with each other for assimilates produced in leaves (MARCELIS et al., 2006). This observation led some authors to conclude that the competition between reproductive and vegetative growth should be largely involved in the biennial production of coffee plants (RENA; MAESTRI, 1986; CARVALHO et al., 1993; LAVIOLA et al., 2007). In fact, there are some studies which, although based on circumstantial evidence, report

intense death rates of young roots after harvest in years of high production, attributed to the competition for carbohydrates between fruit and root system (RENA; CARVALHO, 2003).

Considering that a well-developed root system depends on the maintenance of an active leaf area (CANNEL, 1976) and that the strength of the leaves as a source of assimilates to the roots depends on the amount of fruit, a reduction in the number of fruit (for a constant leaf area) could benefit root growth. This study aimed to evaluate the growth of shoots and the root system, compared to the availability of carbohydrates in leaves and roots, in response to fruit load manipulation.

MATERIAL AND METHODS

The experiment was conducted at the Procafé Experimental Farm in Varginha, Minas Gerais, Brazil. *Coffea arabica* L. cv. Catucaí-Açú, around four years old, were grown in full sun, spaced at 3.5 x 0.75 m in a red latosol soil (cerrado phase) at an altitude of 950 meters. In November, we selected a group of plants that had its fruit load maintained in the “pinhead” productive stage and in a second group we removed all fruit, thus establishing two experimental plots (plants with and without fruit). The plots were arranged in a randomized block design with four replications, and were composed of six plants. The two edge plants served as borders and the four plants in the center were used for data collection. The same cultural practices were applied in both groups and followed recommended practices for coffee plants at that age (GUIMARÃES et al., 1999).

Ten months after establishing the plots, and soon after fruit harvest, plant growth data was collected. Plant height, diameter of the stem and skirt, number and length of branches and vegetative vigor were determined. The height was measured as the distance between the collar region and the apical meristem. The stem diameter was measured with a caliper, in the collar region. The length of the major branches was measured using the lower third in both directions, relative to the planting row. The number of new branches originating in the orthotropic stem was counted and the length of six branches in the upper third was measured, in both directions relative to the row. The vegetative vigor of the plants was evaluated by two well-trained individuals, using an arbitrary scale ranging from zero to 10, with the maximum value being assigned to the plot with the highest number of green and bright leaves, no sign of pests and diseases or mineral deficiency. At the same time, five leaves were collected from the third node of branches in the middle third of the trees. Immediately after collection, leaves were placed in liquid nitrogen and

stored at -20°C for subsequent analysis of total soluble sugars, reducing sugars and starch.

From two plants of the plot, root samples were collected from three depth increments (Figure 1). Roots were collected by extracting 400 cm^3 of soil with an auger. After removal, the samples were packed in plastic bags and stored in a freezer at -20°C until processing. Roots were washed on 50- and 100-mesh screens and stored in 10% methanol in the refrigerator. Roots were placed on glass plates ($30 \times 21 \times 0.2\text{ cm}$) and scanned, considering only roots less than 1.0 cm in diameter. The image analysis was performed using WinRizo software, which provided the length (cm) and root diameter (mm). With these results and using the software SURFER 32, we performed a mapping of the root system distribution in the soil profile and the preparation of isolines graphs, by determining the density of root length (DRL - $\text{mm}^3/100\text{cm}^3$). In the other two plants of the plot, roots samples were collected for the determination of carbohydrates. In this case, soil samples were stored in Styrofoam boxes containing ice, washed with water to separate the roots from the soil and stored in the refrigerator at 5°C until analysis.

For carbohydrates quantification, samples of 0.3 g of fresh matter were macerated in a mortar with 5 mL of potassium phosphate buffer 0.1 M, pH 7.0 and taken in to water-bath under agitation at 40°C for 30 minutes. The extracts were centrifuged at 11,000 g for 20 minutes, at 18°C . Then, the supernatants were collected and the pellets re-suspended in 5mL of the same buffer and centrifuged under the same conditions described previously. The

supernatants were collected and stored at -20°C for the quantification of reducing and total soluble sugars (YEMM; COCCKING, 1954; MILLER, 1959). The resulting pellets were re-suspended in 8mL of potassium acetate buffer 0.1 M, pH 4.8 and incubated in a water bath at 100°C for 5 minutes. Then, 2mL of amyloglucosidase enzyme, corresponding to a total of 12.6 units of enzyme, were added to each sample and incubated in a water-bath at 40°C . After two hours, the homogenates were subjected to centrifugation at 11,000 g for 20 minutes at 18°C . The supernatants volume was supplemented with 15mL distilled water and then frozen for later measurement of starch (YEMM; COCCKING, 1954).

Statistical analyses were performed using the STATISTICA software (ver. 5.0, Statsoft, Inc. Tulsa, OK, USA). The data were subjected to an analysis of variance and the means compared for significant differences by Tukey's test ($p < 0.01$).

RESULTS AND DISCUSSION

Ten months after the establishment began, similar results were obtained for coffee trees with and without fruit in terms of height, stem and skirt diameter, number and length of branches (Figure 2). However, the plant vigor was significantly higher in trees that had its fruit removed at the "pinhead" productive stage.

With regard to the biochemical evaluation of the roots, no differences were found between the levels of carbohydrates in the three depths (data not shown). Thus, the data refers to

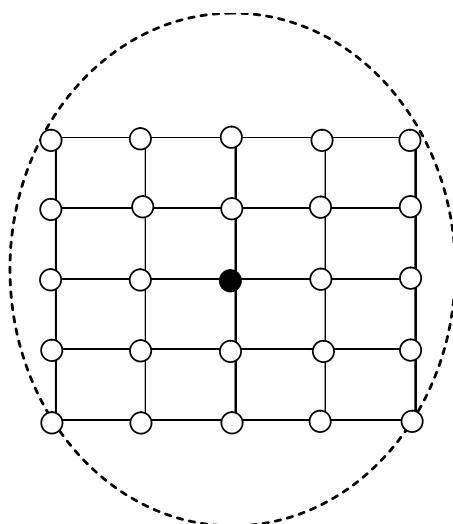


Figure 1 – Scheme of root sampling in 24 equidistant points (30 cm) at depths of 0-20, 20-40 and 40-60 cm. (O: sampling sites; the dotted line represent; — projection of canopy).

average values and shows a higher levels of soluble sugars and lower levels of reducing sugars in fruiting plants (Figure 3). In the leaves, the levels of soluble sugars and reducing sugars were higher in plants with fruit. The starch content in leaves and roots did not vary between the two groups.

For the root system there were no significant differences (in terms of root length density) in the 0-20 and 20-40 cm layers between plants that were being cultivated with and without fruit (Figure 4). However in the 40-60 cm layer, we found that plants without fruit had the highest root length densities. These plants concentrated 40% of their root length density in this latter layer while in the fruit loaded plants, this percentage dropped to 34%. The relative root length density distributions in the 0-20 and 20-40 cm layers were respectively: 32 and 28% for plants with no fruit and 37 and 29% for those loaded with fruit. In general, plants that had their fruits removed produced 31% more roots than those with fruit.

The spatial distribution of density of root length (DRL) was shown to be uneven in the three soil layers (Figure 5). For plants without fruit, in the 0-20 cm layer there was a concentration of roots in the direction of the planting row,

concentrated on the first 20 cm in parallel with the rows. In the 20-40 cm layer there was a lower concentration of roots, as shown in Figure 4, with no accumulation at specific points. Finally, at a depth of 40-60 cm there was a wider distribution of roots in the opposite direction of the slope of the terrain in relation to the planting row. For the fruit loaded plants, there was a more uniform horizontal distribution of roots in soil. Figure 4 also shows a reduction in root concentration at the 20-40 cm layer in relation to other depths. The comparison between the distribution of roots in the 40-60 cm layer between plants with and without fruit, shows, as presented in Figure 4, a greater presence of roots in plants without fruit.

In studying source-sink relationships, the development of both the vegetative and reproductive parts of the plant is subject to a functional interdependence between the two, where they both benefit from and compete with each other. This direct relationship between the two parts is more clearly understood when the leaf is called the source, because it produces and exports photoassimilates, while the fruit is called a sink, because it imports and consumes the photoassimilates (WUBS et al., 2009).

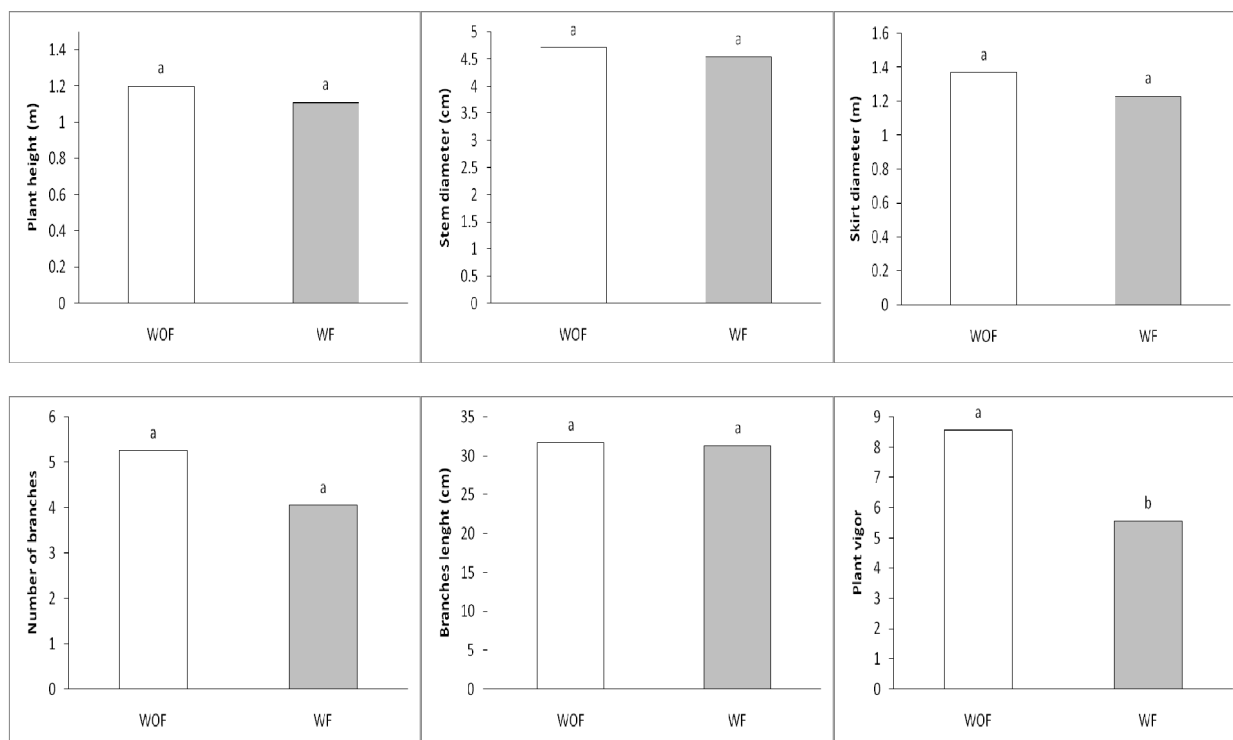


Figure 2 – Shoot growth of coffee trees, ten months after the manipulation of the source-sink ratio, via controlled fruit removal. WOF = plants without fruit, WF = plants with fruits. Columns pairs with matching letters did not differ according to a Tukey test ($P < 0.01$).

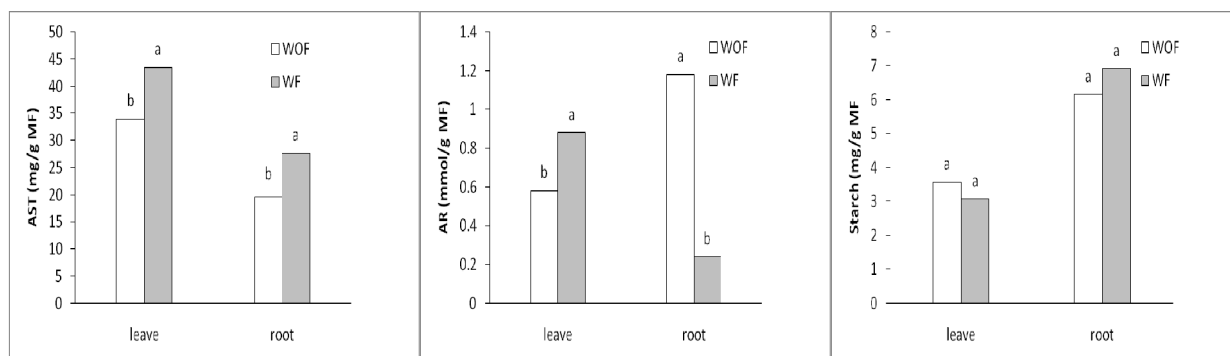


Figure 3 – Carbohydrate levels in leaves and roots of coffee trees, ten months after the manipulation of the source-sink ratio, via controlled fruit removal. WOF = plants without fruit, WF = plants with fruits. Columns pairs with matching letters did not differ according to a Tukey test ($P < 0.01$).

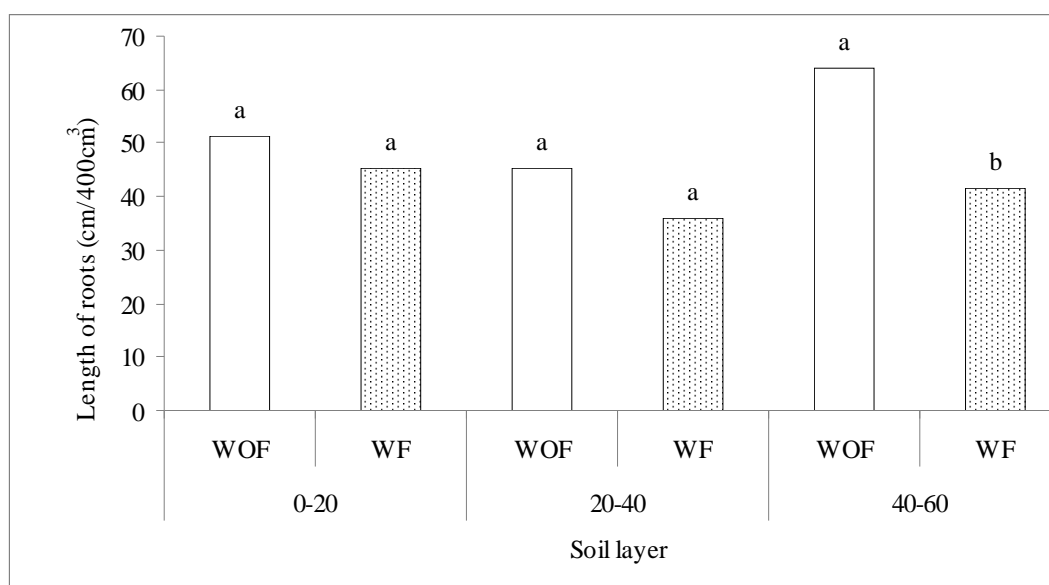


Figure 4 – Length of roots of coffee trees in three depths, ten months after the manipulation of the source-sink ratio, via controlled fruit removal. WOF = plants without fruit, WF = plants with fruits. Columns pairs with matching letters did not differ according to a Tukey test ($P < 0.01$).

In this study, it was considered that the competition between the reproductive (fruit) and vegetative sinks (stem and branches) was not fully established, as it was verified that the fruit load essentially did not alter the plant height, stem and skirt diameter and length of branches (Figure 2). Contrary to expectations, the presence of fruit did not inhibit vegetative growth. This fact can be traced to the low fruit load of this crop (400 g/plant) due to its young age, coupled with appropriate management and the absence of biotic and abiotic stresses during the years that preceded the measurements.

Many authors have reported strong competition between the two types of growth in coffee plants (CANNEL, 1971; AMARAL et al., 2006). Some have even pointed out that the biennial production of the crop is the most profound expression of this competitiveness (CANNEL, 1976; RENA; MAESTRI, 1986; LAVIOLA et al., 2007; CARVALHO et al., 2009). For them, if there is no significant increase in leaf area by the end of the rapid fruit growth stage, there may be a depletion of the plants during the period of greatest demand (grain filling) and, thus intensifying the biennial production phenomenon

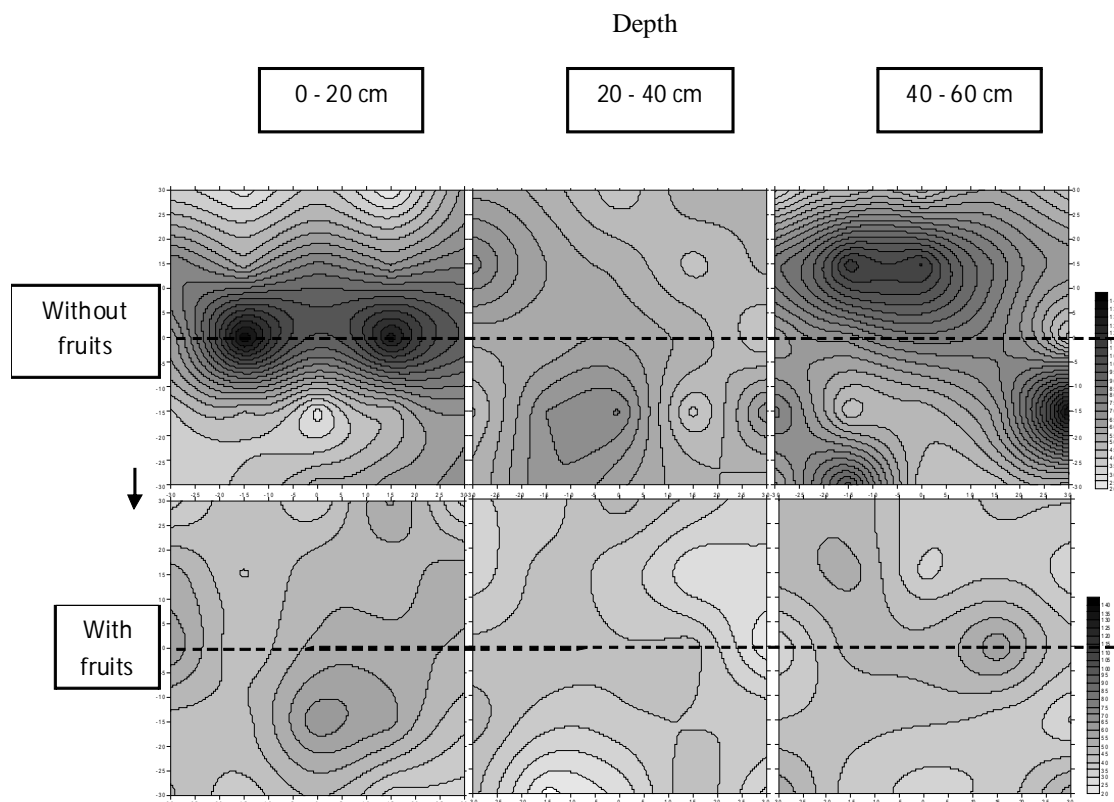


Figure 5 – Isolines graph of the root system of coffee trees ten months after the manipulation of source-sink ratio, via controlled fruit removal. The scale provides the density of root length ($DRL = \text{mm}^3/100\text{cm}^3$). The numbers on the abscissas and ordinates refer to the distance (cm) of the roots sampling points, considering the coordinates 0/0 as the central point of the root system.

The dotted line represents the planting line, and the arrow indicates the slope of 15% of the land.

(PEZZOPANE et al., 2008). Prior to the reproductive stage, proper cultural practices (such as control of pests, diseases and weeds; irrigation and balanced fertilization) provide a rapid increase in leaf area and improves the chances of a good grain formation (LIVRAMENTO et al., 2003). These authors argued that trees in these conditions synthesize sufficient amounts of carbohydrates to ensure high fruit loads, whilst at the same time maintaining its vegetative state. However, in crops with high yields that do not receive appropriate cultural practices, reserves are exhausted.

This study confirmed the observations made by Livramento et al. (2003), who found a positive relationship between carbohydrate content and fruit load. In general, trees with fruit had higher levels of soluble sugar and the same level of starch in leaves and roots, compared to those that had their fruit removed (Figure 3). The lowest level of reducing sugars (RS) in the roots of plants with fruit is probably due the mobilization of glucose to the synthesis of starch. This may explain the same level of starch in

plants with and without fruit. Alternatively we can not discard the hypothesis that the lowest level of RS is probably due to mobilization of glucose and fructose, derived from the conversion of sucrose to the root growth. This behavior, as previously mentioned, probably happened because of the excellent health and nutritional status of the trees and because of the low fruit production of the four year old trees. Several studies show that an increase in the source-sink ratio through the removal of fruit can cause a decrease in the net assimilation rate of carbon due to retro-inhibition derived from the accumulation of carbohydrates in leaves (STITT, 1991). This possibility does not apply in this case, since there was no accumulation of soluble carbohydrates in the leaves of the trees that had all fruits removed. On the other hand, higher levels of carbohydrates in leaves and roots of trees with fruit shows (indirectly) that they were operating at much higher rates of carbon assimilation than those without fruit. This observation is confirmed when one considers

that the size of the fruit and the weight of the seeds were not deficient. As the fruits and seed were well developed, and the plants did not have any dry branches, it is considered that the strength of these sinks had not been diminished. These results suggest that coffee plants adjust their photosynthetic capacity to the fruit load. Higher values of photosynthesis, to the extent that the fruit load increases, have been reported for coffee (FRANCK et al., 2006). This gain in photosynthesis was credited to the greater availability of internal CO₂ associated with higher stomatal conductance (DAMATTA et al., 2008; SILVA et al., 2010).

This work also discusses the source-sink relationship, considering the behavior of shoot and root system. In the topmost layer of soil ranging from 0-40 cm, the density of root length (DRL) of plants with and without fruit essentially did not change (Figure 4). However in the 40-60 cm layer there was greater DRL in plants that had their fruits removed. Overall, the fruit removal in these plants provided a 31% increase in DRL. This data, as well as data provided by Bragança et al. (2007) in "conilon" coffee, apparently reveal the establishment of competition between shoots and root system, where the presence of fruit, as an additional sink (of carbohydrates and nutrients) to the branches, imposes a major limitation to root growth. Our data shows that the presence of fruit on the plants limited the mobilization of assimilates to the root system since, in this organ, the levels of soluble sugars were lower than those plants without fruit (Figure 3).

As mentioned earlier the lowest level of RS in the roots of plants with fruit is probably due to mobilization of glucose and fructose, derived from the conversion of sucrose in root growth. It should be noted here that the plants with fruit were possibly operating with high rates of net carbon assimilation. This remark comes with the observation that there was a great mobilization of sucrose to the roots and yet its level in the leaves, here represented by AST, still remained high (34 mg g⁻¹ FM) in plants without fruit. Once in the roots, much of the sucrose may have remained as such and the rest may have been cleaved, generating glucose and fructose. Finally, these simple sugars may have been directed towards the growth of roots, and part (of the glucose) mobilized into starch. From the above it is concluded, similar to what was reported by Livramento et al. (2003), that the fruit did not behave as sinks strong enough to the point of exhausting the reserves of carbohydrates in different parts of the plants. The mobilization of sugars from the shoot stimulating the growth of roots was also observed in peach by Borba et al. (2005) and stimulation of photosynthesis by the fruit load on coffee trees by Cannel (1976) and Damatta et al. (2008).

Finally, we did observe that plants without fruit showed greater vegetative vigor than the fruit loaded plants (Figure 2). Thus it is possible to suggest that this vigor was due to other factors not related to carbohydrate reserves. In addition, these results suggest that the positive relationship between levels of fruit and carbohydrate content cannot be generalized, since it does not benefit all growth parameters. In fact, it reflects a particular condition in which the plants were still young, had low fruit load and were strong, due to proper management of the crop.

The greater amount of foliage on plants without fruit, here represented by the greatest vegetative vigor (Figure 2), may have been responsible for further developing root systems (Figure 4). These results reveal, for plants with high vegetative vigor, the existence of a compensatory growth between roots and shoots in order to benefit each other without leading to the depletion of its carbohydrate reserves. This compensatory distribution of the size of carbohydrates sinks (fruit and shoot) associated with the quality of sources (leaves), allows root system growth to benefit from changes in shoot growth. So it can be stated that the final root system conformation depends, among other factors, on physiology, plant health and crop management.

There are reports that show coffee fruit as carbohydrate-preferential sinks, limiting the growth of other organs, especially the roots (BRAGANÇA et al., 2007). In this case, the majority of the explanations refer to the accumulation of high proportions of the total assimilates in the fruit, limiting the mobilization of these metabolites to the roots with negative effects on their growth. In addition, previous studies show intense death of radical roots soon after harvest (RENA; MAESTRI, 1986). This death has been attributed to the competition for carbohydrates established between the shoot and root systems, especially in plants with high production. During the fruiting process, fruit filling occurs primarily through the use of photosynthates produced directly from current photosynthesis. As the photosynthesis of coffee trees compared to other C3 plants is low (CEULEMANS; SAUGIER, 1993) and insufficient to meet the demand for assimilates by the fruit, trees with large yields use carbohydrate reserves stored in different plant organs, including the root system. Such behavior was reported by Hidalgo (1993) in grapes and Borba et al. (2005) in peaches where it was observed that these reserves are used for processes that require energy, such as sprouting, growth of branches, flowering and fruiting. By acting as a source of photosynthates, the radical roots have their

carbohydrates stocks depleted and respiration paralyzed, resulting in death (BORBA et al., 2005). In our case, this sequence of events culminating in the death of radical roots was not observed, probably due to the high vigor of the crop throughout the growing season and high levels of carbohydrates in the roots of plants with fruit. Additionally, chemical and physical conditions and soil moisture are also determining factors (ALVES; LIVRAMENTO, 2003).

The spatial distribution of roots horizontally into three soil depths showed that the roots grew preferentially in a zone laterally located to the planting row, corresponding to the area of fertilizer deposition under the canopy of tree. It also revealed, as example of the quantitative data, a higher density of roots at 0-20, which decreased in the 20-40 and increased again in the 40-60 cm deep layer. A greater presence of the roots in the surface layers of the soil has been reported in several studies (HUXLEY et al., 1974) and is attributed to zone that has better chemical and physical characteristics. Studies made by Matiello et al. (2005) in coffee plantations in southern Minas Gerais, Brazil, show that a leaching of mobile nutrients occurs along the soil profile, accumulating in the deeper layers. According to these authors, the presence of nutrients at depth was responsible for the wider distribution of the root system in the deep soil. This fact helps to explain a greater concentration of roots in the layer of 40-60 compared to 20-40 cm.

The results of our paper clearly contrast with what has been published by some authors in the literature about source-sink relationships for coffee plants. The joint data analysis shows that young trees, with moderate fruit load, and with good nutritional and health status produce carbohydrates in quantities sufficient to maintain the vegetative and reproductive growth, without harming the growth of the root system.

CONCLUSION

In the most superficial layer of soil ranging from 0-40 cm, the density of root length (DRL) of plant with and without fruit essentially did not change. However in the layer of 40-60 cm, plants without fruit had higher DRL than plants with full fruit load. Our data show that the presence of fruit on the plants limited the mobilization of assimilates to the root system, since in this organ, the levels of soluble sugars was lower than those plants without fruit. The joint data analysis shows that young trees, with moderate fruit load, and with good nutritional and health status produce carbohydrates in quantities sufficient to maintain vegetative and reproductive growth, without harming root system growth.

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