

Fruit load and branch ring-barking affect carbon allocation and photosynthesis of leaf and fruit of *Coffea arabica* in the field

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Summary Increasing fruit load (from no berries present to 25, 50 and 100% of the initial fruit load) significantly decreased branch growth on 5-year-old coffee (*Coffea arabica* L.) trees of the dwarf cultivar ‘Costa Rica 95’, during their third production cycle. Ring-barking the branches further reduced their growth. Berry dry mass at harvest was significantly reduced by increasing fruit load. Dry matter allocation to berries was four times that allocated to branch growth during the cycle. Branch dieback and berry drop were significantly higher at greater fruit loads. This illustrates the importance of berry sink strength and indicates that there is competition for carbohydrates between berries and shoots and also among berries. Leaf net photosynthesis (P_n) increased with increasing fruit load. Furthermore, leaves of non-isolated branches bearing full fruit load achieved three times higher P_n than leaves of isolated (ring-barked) branches without berries, indicating strong relief of leaf P_n inhibition by carbohydrate demand from berries and other parts of the coffee tree when excess photoassimilates could be exported. Leaf P_n was significantly higher in the morning than later during the day. This reduction in leaf P_n is generally attributed to stomatal closure in response to high irradiance, temperature and vapor pressure deficit in the middle of the day; however, it could also be a feedback effect of reserves accumulating during the morning when climatic conditions for leaf P_n were optimal, because increased leaf mass ratio was observed in leaves of ring-barked branches with low or no fruit loads. Rates of CO_2 emission by berries decreased and calculated photosynthetic rates of berries increased with increasing photosynthetic photon flux (PPF) especially at low PPFs (0 to $100 \mu\text{mol m}^{-2} \text{s}^{-1}$). The photosynthetic contribution of berries at the bean-filling stage was estimated to be about 30% of their daily respiration costs and 12% of their total carbon requirements at PPF values commonly experienced in the field (200 to $500 \mu\text{mol m}^{-2} \text{s}^{-1}$).

Keywords: *Arabica coffee, berry drop, berry mass, berry photosynthesis, branch dieback, carbohydrate demand, fruit:leaf ratio, leaf photosynthesis.*

Introduction

In fruit trees such as apple (Palmer 1992), peach (Génard et al. 1998) and coffee (Kumar and Tieszen 1976, Cannell 1985), fruit load has a large effect on dry matter production and partitioning. High fruit load decreases shoot growth and results in strong alternate bearing and production patterns in coffee. Furthermore, branch dieback is often observed at high fruit load as a result of the high carbon demand of coffee berries, which represents up to 60% of carbohydrate production over the annual cycle (Cannell 1971a). At high fruit loads, there is competition for carbohydrates among berries that strongly affects coffee bean size, biochemical composition and beverage quality (Vaast et al. 2005). Cannell (1971b) demonstrated that the presence of coffee berries increased total branch dry matter gain and speculated that berries stimulated leaf net photosynthesis (P_n). As documented in orange (Moreshet and Green 1980), avocado (Blanke 1992) and peach (Pavel and DeJong 1993a), there is evidence that green fruits are photosynthetically active and can contribute to their own carbohydrate requirements for growth and maintenance. Cannell (1971b) indirectly demonstrated that immature, green coffee berries could contribute to their own carbohydrate needs. However, there are no published data on coffee berry CO_2 exchange rates and the contribution of berry photosynthesis to the carbohydrate requirements of the developing fruit.

Leaf P_n increases in response to increasing fruit load when carbohydrate accumulation in the fruit is high in peach (DeJong 1986) and apple (Palmer 1997), and maximum leaf P_n of

peach is strongly related to leaf:fruit ratio and fruit carbohydrate demand (Ben Mimoun et al. 1996). However, several authors have observed feedback inhibition of leaf P_n in response to the accumulation of leaf reserves (Guinn and Mauney 1980, Foyer 1998).

Cannell (1971b) documented that large, long-distance carbohydrate transfers occur in coffee trees. The rest of the tree generally buffers the fruit load effect on fruit-bearing branch development by acting either as a source or a sink (Ben Mimoun et al. 1998). To study the effect of assimilate partitioning between the tree and individual branches, carbohydrate transfer can be altered by branch ring-barking (Dann et al. 1984). In response to this treatment, branches usually support increased fruit growth with reduced vegetative growth as shown in peach (Dann et al. 1984) and apple (Schechter et al. 1994). Branch ring-barking can also alter leaf characteristics by increasing leaf mass ratio and decreasing leaf P_n (Schechter et al. 1994).

In view of the strong sink strength of coffee berries, especially during bean-filling (Vaast et al. 2002), information is needed to evaluate the effect of foliar carbohydrate accumulation on coffee leaf P_n . The main objective of this research, therefore, was to gain deeper insight into carbohydrate production and allocation in coffee with respect to source–sink relationships, and to evaluate branch dependence on other tree parts. Effects of fruit load (100, 50, 25 and 0% of initial load) and branch ring-barking on branch vegetative and reproductive growth, as well as on leaf and berry photosynthesis, were evaluated in field-grown coffee trees. We also evaluated the effect of increasing PPF on berry CO_2 exchange rates and the photosynthetic contribution of berries to their carbohydrate requirements at the bean-filling stage.

Materials and methods

The study was carried out from April to November 2002 on Arabica (*Coffea arabica* L.) trees of the dwarf cultivar ‘Costa Rica 95’ in an experimental plot at the research station of the Coffee Institute of Costa Rica (ICAFE) in Barva de Heredia, Costa Rica. The station is located at 1180 m elevation on Andosol soil, and has a mean annual temperature of 22 °C and a mean annual rainfall of 2200 mm. ‘Costa Rica 95’ is a dwarf cultivar with a maximum height not exceeding 2.5 m after four to five years of growth.

The plot was established in June 1997 without shade. Plant spacing was 2 m between rows and 1 m within rows. Plants received 1000 kg ha⁻¹ of N,P,K,Mg,B (18:3:10:8:0.5) fertilizer annually, as two applications in May and August, along with 250 kg ha⁻¹ of N in November and two foliar applications per year of copper hydroxide (1.5 kg ha⁻¹) to prevent berry diseases (berry brown eye spot, *Cercospora coffeicola* Berk. & Cooke).

A group of 24 trees was selected within the plot in adjacent planting rows. After flowering in early April 2002, four fruit loads (full fruit load = 100; half of the initial fruit load = 50; a quarter of the initial fruit load = 25; and no fruit load = 0) were imposed on two pairs of branches in the middle part of the can-

opy at branch Position 15 from the tree top. The rest of the tree was maintained unchanged at its initial full load. One branch of each pair was carefully ring-barked at the base of the branch by entirely eliminating the bark over a length of 4 cm. The exposed tissues were protected with pruning seal to avoid drying and prevent fungal diseases.

In May, July and September 2002, nondestructive measurements of branch length, foliar area and berry number were made to follow branch development over time. In late November 2002 during the coffee harvest, branches were removed and characterized. The numbers of leaves and berries were recorded per branch. Leaf area was measured with an LI-1800 area meter (Li-Cor, Lincoln, NE) and leaf area of individual branches was calculated. Twig, leaf and berry dry matter were recorded. Leaf mass ratio (leaf dry matter per unit leaf area) for each branch was calculated.

Gas exchange was measured in late August to mid-September 2002 in the middle of the rainy season, during the bean-filling stage with a differential $\text{CO}_2/\text{H}_2\text{O}$ infrared gas analyzer Lcpro (ADC BioScientific, Hoddesdon, U.K.) connected either to a broadleaf chamber for leaf measurements or to a conifer chamber for berry measurements, both with automatic control of temperature and photosynthetic photon flux (PPF). Net CO_2 exchange of berries was measured directly on attached green berries by inserting the conifer chamber around a fruiting node. Leaf P_n data were collected from an exposed, fully developed leaf from the third pair of leaves at the apex of the branch. For leaves and berries, CO_2 exchange was measured at saturating PPF (900 $\mu\text{mol m}^{-2} \text{s}^{-1}$), a constant chamber temperature of 27 °C and ambient humidity ranging from 65 to 80% of relative humidity (RH). For leaves and berries, P_n was measured in early morning (0700–0900 h), at midday (1100–1300 h) and late in the afternoon (1500–1700 h). Two series of measurements were made for leaf and berry P_n at an interval of one week. Additional measurements were made exclusively in the morning (0700–1000 h) to study the effects of PPF (from 0 to 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$) on berry CO_2 exchange rates. These measurements were performed starting from ambient PPF, and increasing the PPF to high values, returning to the ambient PPF and then decreasing the PPF to darkness. Net CO_2 exchange rates were converted from $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (as directly given by the ADC-Lcpro) to $\text{nmol CO}_2 \text{ g}^{-1} \text{ berry dry mass s}^{-1}$ after collecting the coffee berries following CO_2 exchange measurements and determining their dry mass. Fruit photosynthetic rates were calculated as the difference between the rates of CO_2 evolution in the light and dark as proposed by Pavel and DeJong (1993a). The volume of berries, which was determined by immersing them in a graduated cylinder containing water, was used to estimate the total area of berries per branch.

To assess light availability around coffee leaves and fruits at different positions in the coffee canopy, PPF was measured around solar noon with a quantum sensor of the ADC-Lcpro in four strata regularly distributed (upper branch in Position 8 from tree top; middle-upper branch in Position 15; middle-lower branch in Position 22; lower branch in Position 29) in the canopy of coffee trees.

To determine if ring-barking affected branch transpiration, sap flow of four branches was monitored with SGA flow sensors (Dynamax, Houston, TX) connected to a CR10X data logger (Campbell Scientific, Logan, UT) that read sap flow rates every minute, and averaged and registered values every 15 min. For each branch, mean daily sap flow per unit leaf area ($\text{ml m}^{-2} \text{day}^{-1}$) was calculated over a period of six continuous days before and after branch ring-barking.

Statistical analyses were performed with Statistica V5, edition 1997 and means were compared with the Newman and Keuls test.

Results

Branch characteristics and final berry mass

Branch ring-barking did not significantly affect sap flow rates or daily transpiration of branches (Figure 1). No significant effects of branch ring-barking and fruit load on branch growth were observed at 3 and 5 months into the production cycle, except for a significant effect on branch leaf area after 5 months (Table 1). On the other hand, branch growth and leaf area were significantly affected by fruit load and ring-barking at harvest. Strong competition for carbohydrates was evident only during the last 3 months of bean-filling and resulted in a significant reduction in branch development. During this period, branches with high fruit loads had smaller increases in shoot elongation (Table 2), higher rates of leaf senescence and developed fewer new nodes with smaller leaves than branches with low fruit loads (data not shown). Dieback of branches was also evident during this period with significantly higher mortality for branches bearing high fruit loads. Branch mortality for branches with 0, 25, 50 and 100% fruit loads was 7, 11, 14 and 20%, respectively.

Comparison of the final total mass of branches with full fruit load versus that of branches bearing no berries clearly revealed the influence of berries on dry matter accumulation and hence carbohydrate demand (Table 2). Branches bearing a high fruit load were almost twice as heavy as branches bearing no berries. In the 100% fruit load treatment, dry matter accumulation

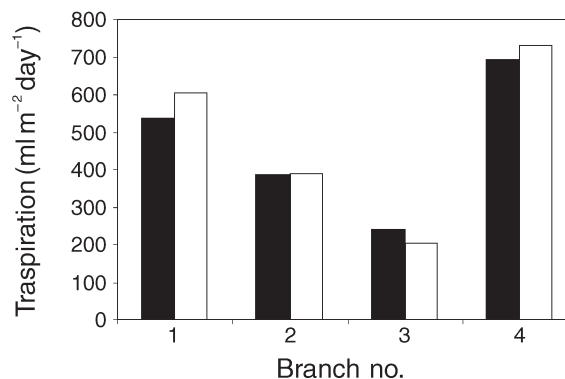


Figure 1. Mean daily transpiration per unit foliar area ($\text{ml m}^{-2} \text{day}^{-1}$) of coffee branches before (filled columns) and after (empty columns) branch ring-barking.

by berries represented more than 76% (33 out of 43 g) of the total branch mass. Furthermore, vegetative branch mass gain during the production cycle was only 8 g, when its initial mass was subtracted and shoot elongation, new leaf formation and leaf fall during the whole production cycle was taken into account. Therefore, dry matter allocation to berries accounted for more than four times that allocated to branch development during the production cycle.

On ring-barked branches, fruit load significantly affected final individual coffee berry mass, indicating that there was competition for carbohydrates not only between berries and shoot but also among berries (Table 2). On ring-barked branches, individual berry fresh mass increased substantially from 0.97 g at 100% load to 1.52 g at the 25% load (Table 2). Smaller and nonsignificant differences were observed on non-isolated branches (i.e., not ring-barked), with a mean berry fresh mass of 1.02 g at 100% fruit load compared with a mean berry fresh mass of 1.10 g at the 25% fruit load.

In concordance with the reduction in berry mass as a result of competition among berries, berry drop was more pronounced on branches with high fruit loads during the last period of bean-filling (Table 2). Consequently, the lowest fruit load, initially set at 25% of the full fruit load after flowering, was close

Table 1. Effects of fruit load and branch ring-barking on branch leaf area, increase in branch length and percentage of berry drop after 3 and 5 months of flowering and fruit thinning. Abbreviations: RB = ring-barked; and NRB = non-ring-barked.

Treatment	Branch leaf area (cm^2)		Increase branch length (mm)		Berry drop (%)	
	3 months	5 months	3 months	5 months	3 months	5 months
<i>Ring-barking</i>						
RB	467 a ¹	482 a	30 a	53 a	13 a	21 a
NRB	502 a	723 b	35 a	66 a	15 a	16 a
<i>Fruit load</i>						
100	483 a ¹	554 a	45 a	63 a	21 a	29 a
50 ²	490 a	557 a	34 a	65 a	24 a	29 a
25	446 a	658 a	23 a	56 a	11 a	12 a
0	520 a	642 a	27 a	55 a	–	–

¹ Means ($n = 5$) within a column followed by different letters differ according to the Newman and Keuls test, $P = 0.05$.

² Means of four replicates for the treatment with 50% of the initial fruit load.

Table 2. Effects of fruit load and bark-ring on branch leaf area, increase in branch length (over the last 3 months), final berry load, leaf area per berry, total branch dry mass, individual berry dry mass, leaf mass ratio, percentage of berry drop (over the whole production cycle) of branches at harvest. Abbreviations: RB = ring-barked; and NRB = non-ring-barked.

Fruit load (%)	Branch leaf area (cm ²)		Increase in branch length (mm)		Final load (berries per branch)		Leaf area per berry (cm ² berry ⁻¹)		Total branch mass (g)		Individual berry mass (g)		Leaf mass ratio (mg cm ⁻²)		% Berry drop	
	RB	NRB	RB	NRB	RB	NRB	RB	NRB	RB	NRB	RB	NRB	RB	NRB	RB	NRB
100	279 a ¹	275 a	2 a	49 b	27 bc	33 c	10 a	8 a	36 bc	43 c	0.97 a	1.02 a	12.6 b	10.7 a	74 c	57 b
50 ²	281 a	383 b	43 b	146 c	20 b	23 b	14 b	17 b	30 b	35 bc	1.20 a	1.03 a	13.1 b	12.5 b	54 b	41 b
25	324 b	543 c	69 b	215 d	16 a	17 a	20 b	32 c	28 b	31 b	1.52 b	1.10 a	13.9 b	12.6 b	38 b	12 a
0	554 c	625 c	219 d	216 d	—	—	—	—	20 a	26 b	—	—	15.5 c	12.8 b	—	—

¹ Means ($n = 5$) within a column followed by different letters differ significantly according to the Newman and Keuls test, $P = 0.05$.

² Means of four replicates for the treatment with 50% of the initial fruit load.

Table 3. Effects of fruit load and branch ring-barking on net assimilation ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) of coffee leaves at a photosynthetic photon flux of $900 \mu\text{mol m}^{-2} \text{ s}^{-1}$. Abbreviations: RB = ring-barked; and NRB = non-ring-barked.

Ring-barking treatment	Fruit load (%)			
	100	50 ²	25	0
RB	4.43 b ¹	3.68 c	3.07 c	1.70 d
NRB	5.25 a	4.97 ab	4.24 b	4.05 b

¹ Means ($n = 15$) followed by different letters differ significantly according to the Newman and Keuls test, $P = 0.05$.

² Means of 12 replicates for the treatment with 50% of the initial fruit load.

to 63% of the highest fruit load treatment in terms of total berry dry mass at harvest on ring-barked branches. Likewise, the intermediate fruit load, initially set at 50%, was close to 74% of the highest fruit load treatment at harvest.

Leaf mass ratio was significantly affected by ring-barking. Leaves of ring-barked branches were heavier than leaves of non-ring-barked branches. Furthermore, there was a trend of increasing leaf mass ratio with decreasing fruit load (Table 2).

Leaf photosynthesis

Branch ring-barking significantly decreased leaf P_n from 4.63 to $3.22 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Increasing fruit load resulted in significantly higher leaf P_n with a more pronounced effect on ring-barked branches (Table 3). Leaves of the ring-barked branches bearing full fruit load achieved a P_n 2.6 times higher than that of ring-barked branches without berries, with values of 4.43 and $1.70 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively. In contrast, leaves of non-isolated branches bearing full fruit load achieved a P_n only 30% higher than that of non-isolated branches without berries with values of 5.25 and $4.05 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively. For the ring-barked branches, there was a curvilinear trend of decreasing leaf P_n with decreasing number of berries per unit leaf area and a particularly sharp decrease in leaf P_n below five berries per dm^2 leaf area, equivalent to

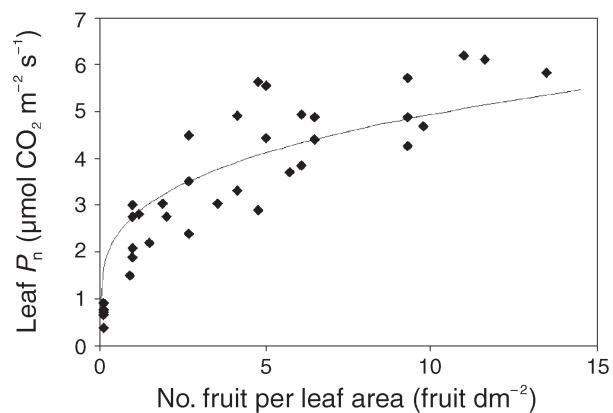


Figure 2. Effect of fruit load on net leaf assimilation rate (P_n ; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for ring-barked branches (data of three daily periods pooled, $y = 0.55 + 2.2x^{0.3}$ with $r^2 = 0.83$ where y = mean leaf assimilation rate and x = berry number per dm^2 of leaf area).

20 cm² of leaf area per berry (Figure 2).

Leaf P_n was significantly higher in the morning than at mid-day or in the afternoon with mean values of 4.59, 3.72 and 3.63 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively. However, the period of the day \times fruit load interaction was insignificant.

Berry photosynthesis

Assuming that half of the berry area was exposed to solar radiation, berry photosynthetic area accounted for about 20% of the total tree photosynthetic area at the highest fruit load. Berry CO_2 exchange rates per unit dry mass decreased sharply with increasing PPF in the low range (0 to 100 $\mu\text{mol m}^{-2} \text{ s}^{-1}$), more gradually in the middle range (100 to 500 $\mu\text{mol m}^{-2} \text{ s}^{-1}$) and very little thereafter (Figure 3). Similarly, calculated berry photosynthetic rates per unit dry mass increased sharply with increasing PPF in the low PPF range to become nearly saturated at PPFs above 500 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ (Figure 4). Dark respiration rates per unit dry mass decreased with increasing berry dry mass. At the time of these measurements (2/3 into the growing season), berries with the lowest dry mass (0.12 g) exhibited a dark respiration rate of 15.6 $\text{nmol CO}_2 \text{ g}_{\text{DM}}^{-1} \text{ s}^{-1}$ whereas the dark respiration rate of berries with the highest dry mass (0.22 g) was 6.5 $\text{nmol CO}_2 \text{ g}_{\text{DM}}^{-1} \text{ s}^{-1}$. The CO_2 exchange rates per unit dry mass also decreased with increasing berry dry mass in response to PPF (data not shown). Consequently, this resulted in decreasing calculated berry photosynthetic rates per unit dry mass in response to PPF as berry mass increased (Figure 5). Berries with low dry mass were far more responsive to increasing PPF than berries with higher dry mass and achieved photosynthetic rates almost three times higher than berries with the highest dry mass, with values of 13.2 and 4.6 $\text{nmol CO}_2 \text{ g}_{\text{DM}}^{-1} \text{ s}^{-1}$ at a PPF of 465 $\mu\text{mol m}^{-2} \text{ s}^{-1}$, respectively.

Ring-barking had a significant effect on berry CO_2 exchange rates (Figure 3) and calculated berry photosynthetic rates (Figure 4). Contrary to leaf P_n , the period of the day had

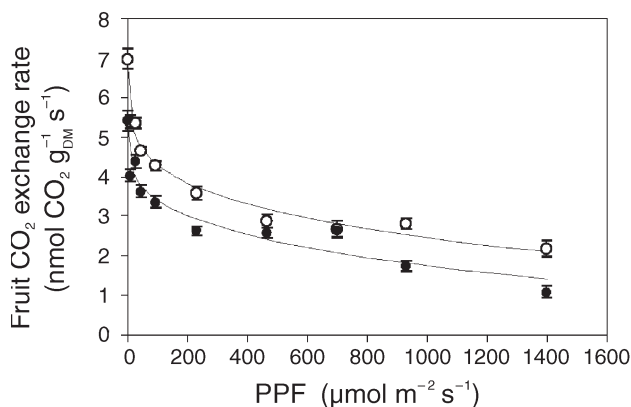


Figure 3. Effect of photosynthetic photon flux (PPF) ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) on berry CO_2 exchange rates per unit dry mass ($\text{nmol CO}_2 \text{ g}_{\text{DM}}^{-1} \text{ s}^{-1}$) of attached green coffee berries on ring-barked (●) and non-ring-barked (○) branches (mean \pm SE of 15 measurements; $y = 5.36 - 0.57x^{0.19}$ with $r^2 = 0.94$ for ring-barked and $y = 7.01 - 0.97x^{0.22}$ with $r^2 = 0.98$ for non-ring-barked, where y = mean fruit CO_2 exchange rate and x = PPF).

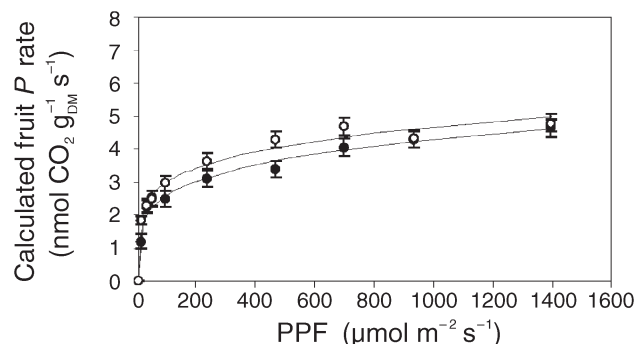


Figure 4. Effect of photosynthetic photon flux (PPF) ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) on calculated berry photosynthetic rates per unit dry mass (P ; $\text{nmol CO}_2 \text{ g}_{\text{DM}}^{-1} \text{ s}^{-1}$) of attached green coffee berries on ring-barked (●) and non-ring-barked (○) branches (mean \pm SE of 15 measurements; $y = 0.97x^{0.22}$ with $R^2 = 0.99$ for ring-barked and $y = 1.25x^{0.19}$ with $R^2 = 0.98$ for non ring-barked, where y = mean calculated fruit P rate and x = PPF).

no significant effect on berry CO_2 exchange rates (data not shown). Berry photosynthesis could contribute up to 60% of instantaneous berry respiration costs, quantified as dark respiration, during the midday period (0800 to 1600 h) when PPF was in the high range of 400–800 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ (Figure 6). With berry PPF exposures around 200 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ during 4 h per day (early morning and late afternoon) and 500 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ during the midday hours (8 h), photosynthetic contribution of berries was estimated to be about 30% of the daily berry respiration costs and 12% of the total daily berry carbon requirements at the bean-filling stage.

Discussion

Our results illustrate the competition for carbohydrates between vegetative and reproductive plant components on one of the dwarf compact coffee cultivars planted predominantly in Central America and Mexico during the last 25 years (Samper

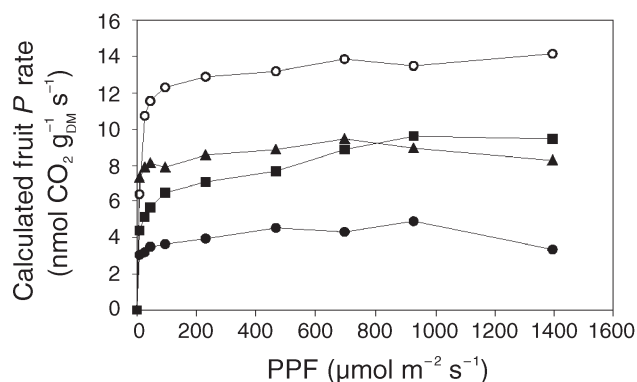


Figure 5. Effect of photosynthetic photon flux (PPF) ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) on calculated berry photosynthetic rates per unit dry mass (P ; $\text{nmol CO}_2 \text{ g}_{\text{DM}}^{-1} \text{ s}^{-1}$) of attached green coffee berries as affected by their mean dry mass (low dry mass = 0.120 g (○), medium-low dry mass = 0.176 g (▲), medium-high dry mass = 0.194 g (■) and high dry mass = 0.222 g (●)).

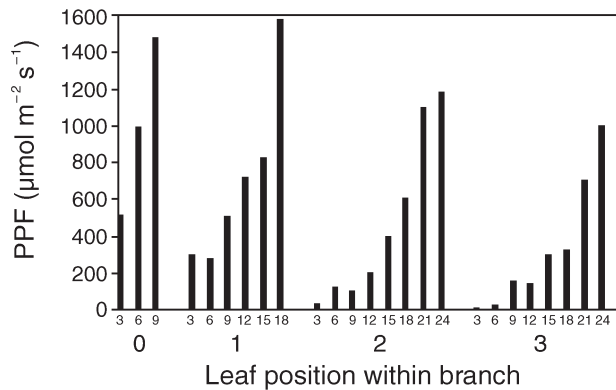


Figure 6. Light distribution (PPF; $\mu\text{mol m}^{-2} \text{s}^{-1}$) around midday at the leaf and fruit levels in four strata regularly distributed in the canopy of coffee trees (0: upper branch in Position 8 from top; 1: middle-upper branch in Position 15; 2: middle-lower branch in Position 22; 3: lower branch in Position 29).

1999, Soto-Pinto et al. 2000). With dry matter allocation to berries being more than four times that allocated to branch growth over the annual production cycle, these results confirm the strong sink strength of coffee berries already observed for traditional, less productive cultivars in East Africa (Cannell 1971a, 1971b, Kumar and Tieszen 1976). Our data highlight that shoot growth and berry drop were mainly affected during the last third of the production cycle, which corresponds to the time of bean-filling (Cannell 1985). We observed reduced shoot growth and high branch dieback in response to high fruit load (Table 2). Wormer and Ebagole (1966) and Cannell (1985) associated these phenomena with the high carbohydrate demand of berries and the depletion of reserves, notably starch, in coffee storage organs (branch, stem and thick roots). Because carbohydrates were preferentially allocated to berries, to the detriment of young apical vegetative branch parts that determine the production level in the following year, our results provide a clear explanation of the strong bi-annual production pattern that has been observed in this highly productive cultivar (Vaast et al. 2005). The data also indicate that there was competition for carbohydrates among berries at high fruit loads resulting in reduced individual berry mass and hence bean size—the most important criterion on which coffee quality and price are assessed. The highest individual berry mass was produced on ring-barked branches with 25% of the initial fruit load that had an initial minimum of 15 cm^2 leaf area per berry and one of 20 cm^2 per berry at the bean-filling stage. These results are in agreement with previous studies demonstrating that no further increase in berry mass was obtained by decreasing fruit load to 12.5% of the initial fruit load and that a minimum of 15 cm^2 as initial leaf area per berry was necessary to produce coffee beans of maximum size on this dwarf cultivar (Vaast et al. 2002).

Ring-barking did not affect branch transpiration (Figure 4), but prevented the export of carbohydrates from source leaves as indicated by the higher leaf mass ratio of ring-barked branches compared with their non-ring-barked counterparts (Table 2). Similar results have been reported for apple (Schechter

et al. 1994). Leaves of ring-barked branches bearing the full fruit load achieved a P_n 2.6 times higher than that of ring-barked branches without berries, whereas leaf P_n of non-isolated branches bearing the full fruit load was only 30% higher than that of non-isolated branches without berries. This demonstrates that there is a strong relief of leaf P_n inhibition by the carbohydrate demand from berries and other parts of the coffee tree when excess product of assimilation is exported from the source leaves. Thus, the data indicate that the presence of coffee berries, especially on ring-barked branches, alleviates the inhibition of leaf photosynthesis caused by the buildup of reserves as demonstrated for other fruit trees such as apple (Palmer et al. 1997) and peach (DeJong 1986, Ben Mimoun et al. 1996). Our leaf P_n values are much lower than the maximum values of $14 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ registered for sun-grown coffee leaves at saturating PPF under optimal field conditions (Kumar and Tieszen 1980) or controlled conditions (Yamaguchi and Friend 1979). Nevertheless, our P_n values are similar to values reported for coffee growing under field conditions (Cannell 1985, Gutierrez et al. 1994). Leaf P_n decreased during the day, starting around solar noon. This decrease is usually attributed to partial or total stomata closure caused by high leaf-to-air vapor pressure deficit, leaf temperature (Gutierrez et al. 1994), high irradiance and possibly photoinhibition (Ramalho et al. 1999, 2000). Nonetheless, a feedback effect on leaf P_n of reserves that accumulated in the morning could also contribute to the midday depression of coffee leaf P_n because there is a strong and significant relationship between leaf reserves and leaf P_n (Nicolás Franck, personal communication). A feedback effect is also consistent with the higher leaf mass ratio observed in our ring-barked branches without berries or with low fruit loads, which suggests a build-up of carbohydrate reserves in the leaves. Higher carbohydrate reserves (mostly starch and soluble sugars) in leaves with low fruit loads, especially on ring-barked branches, have been reported by Cannell (1971a). Several authors have reported a feedback inhibition of leaf P_n through the accumulation of reserves in leaves (Guinn and Mauney 1980, Foyer 1998). This mechanism of leaf P_n regulation has been studied in other perennial fruit trees. For example, DeJong (1986) in peach and Palmer (1997) in apple found that leaf P_n increased in response to increasing fruit load when accumulation of carbohydrates in the fruit was high. Ben Mimoun et al. (1996) reported that maximum leaf P_n in peach was strongly related to leaf:fruit ratio and to the carbohydrate demand of fruit. The importance of this feedback effect in coffee is currently under investigation on plants with a wide range of fruit loads and fruit:leaf ratios as investigated in apple by Palmer et al. (1997).

Although preliminary, our results show that CO_2 exchange rates of berries decreased and calculated berry photosynthetic rates increased with increasing PPF as reported for orange (Moreshet and Green 1980) and peach (Pavel and DeJong 1993a). Calculated berry photosynthetic rates increased sharply in the PPF range between 0 and $200 \mu\text{mol m}^{-2} \text{ s}^{-1}$, and were nearly saturated at PPFs above $500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in a manner similar to shade-acclimated coffee leaves (Kumar and Tieszen 1980). This suggests that assimilation by berries could sub-

stantially contribute to their instantaneous respiration costs at PPFs commonly experienced by berries in the field (Figure 6). However, our data do not support the speculation of Kumar and Tieszen (1976) that green coffee berries could provide 100% of their maintenance requirements and up to 30% of the growth requirements through their own photosynthetic activity. Because berries are commonly exposed to high PPF for more than 8 h per day (Figure 6), we estimated that they could produce about 30% of their daily respiration costs and contribute around 12% to their total carbon requirements at the bean-filling stage. This coffee berry photosynthetic contribution is in the same order of magnitude as that reported for peach and cited for cherries and blueberries by Pavel and DeJong (1993b). Therefore, we conclude that coffee berry photosynthesis is important, especially in view of the large berry sink strength and the finding that the berry photosynthetic area represents up to 20% of the total tree photosynthetic area at the highest fruit load.

At bean-filling, dark respiration rates and CO₂ exchange rates per unit dry mass were higher for berries with lower dry mass. Consequently, this resulted in higher calculated berry photosynthetic rates per unit dry mass for less mature berries (Figure 5). As proposed by Pavel and DeJong (1993a) for peach, these higher dark respiration rates of smaller berries may be related to high metabolic activities in less mature berries that are still in the phase of intense dry matter accumulation. Therefore, the finding that ring-barking had a significant negative effect on berry CO₂ exchange rates (Figure 3) and calculated berry photosynthetic rates (Figure 4) may be related to the higher berry dry mass on ring-barked branches than on non-isolated branches (Table 2). It appears that calculated coffee berry photosynthetic rates are likely to vary over the growing season as reported for avocado (Blanke 1992) and peach (Pavel and DeJong 1993a). Clearly, more data are needed over the entire production cycle to provide a better estimate of the photosynthetic contribution of developing coffee berries to their carbohydrate demand.

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