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Influence of Temperature and Water on Coffee Culture

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ABSTRACT

Although originating in the understory of the Ethiopian tropical rainforest, coffee is nowadays cultivated under full sunlight in most of the producing countries. Such a transition from shade to light influenced growth and productivity stimulating several physiological studies about the effects of air temperature and water availability on coffee. In this review we summarize the main effects of water and air temperature on vegetative and reproductive growth of coffee plants, primarily focusing on Brazilian conditions. The use of modern technologies such as irrigation and increased plant density per area, as well as the influence of water management and controlled water deficits on flowering synchronization are also addressed.

Keywords: air temperature, growth, water management

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INTRODUCTION

Coffee (*Coffea arabica* L.) has the Ethiopian sub-forest as the its original habitat but nowadays it is cultivated under full sun (Söndahl *et al.* 1984; Carvalho *et al.* 1985). In Ethiopia coffee is wildly grown at 6º to 9ºN and 34º to 40ºE, where the temperature oscillates between 15 and 20°C and the annual rainfall is well distributed, varying from 1600 to 2000 mm, with a wet season lasting from three to four months. This change from mild temperature locations with low light intensity and good water availability to others with different and eventually opposite conditions caused a modification in the architecture of coffee. Coffee plants under high light intensity have more compact structures, smaller leaves, shorter internodes, higher number of branches, abundant flowering, a shallower root system, among other changes. This new developmental adaptation is exactly what turned full-sun-cultivated coffee into a more productive plant.

In Brazil, the world's largest coffee producer (Da Matta 2004a), total coffee yield was about 42,512 million of bags (60 kg) of green beans in 2006/2007, produced in an area of 2,152.397 ha (http://www.conab.gov.br/conabweb/index.php?PAG=132). Arabica coffee corresponds to approximately 77.1% of this production while *Coffea canephora* (Robusta coffee) accounts for the rest. Four Brazilian states (Minas Gerais, São Paulo, Paraná and Espírito Santo) account for 88.7% of the total Brazilian coffee production.

Coffee plantations in Brazil were initially concentrated in a few regions in the São Paulo, Paraná and Minas Gerais states. Although some of these regions were susceptible to frosts, soil fertility determined the crop limits. Nevertheless, factors such as input and workforce prices, soil depletion, attack of pests, especially nematodes, and disease together with the coffee price, have slowly displaced coffee production from appropriate climatic areas to areas previously considered marginal or inadequate for coffee plantation due to high temperatures and low water availability or inadequate distribution of rain during the year. This displacement was only possible after the selection of the best cultivars for these regions as well as the adaptation and development of new technologies, like irrigation, for instance. Nowadays most Brazilian coffee plantations are based on cultivars of the species *C. arabica* developed by the Instituto Agronômico de Campinas - IAC (see http://www.iac.sp.gov.br/Centros/centro_cafe/ACultivares.htm for a complete list of cultivars and their agronomical characteristics). Other cultivars developed by other research centers have their origin in the IAC material.

Together with irrigation, some other modern technologies, such as climate monitoring through satellites and interconnected climate stations, can give a precise definition of the areas with higher or lower risks regarding the temperature and water availability. Since these climate parameters are extremely important in the definition of the areas potentially suitable for cultivation, this review will be related to

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Invited Review

the influence of temperature and water availability for coffee plants.

Growth and development are affected by temperature and water

Temperature is one of the most critical environmental factors and exerts a great influence in all the physiological activities of plants, controlling the levels of the metabolic reactions within cells. All and any of the physiological functions and chemical reactions present a temperature optima and any higher or lower discrepancy might decrease their efficiency (Larcher 2000).

Plants have different degrees of tolerance to extreme temperatures, each one presenting defined limits for growth and reproduction. For instance, even if the seed of a plant germinates and develops at some temperatures, these same temperatures might not be appropriate for the reproductive phase. So, if the temperature is appropriate for only some phases of plant growth and development, the plant will not necessarily be successful in colonizing that environment. Thus, it is correct to assert that the environmental species distribution can be delimited through temperature oscillations (Schulze *et al*. 2005).

Water is equally important for plant growth and development. Besides being the cellular solvent, allowing chemical reactions to occur, it is water that promotes cellular volume growth, fulfilling the carbonic skeleton formed as a consequence of photosynthesis. Moreover, when water penetrates the plant, it takes with it the mineral nutrients and decreases foliar temperature, when evaporating through the stomata. To have a better idea about the water volume that a plant needs, we can cite that a maize plant weighing 800 g, in the panicle emission period, contains around 700 g of water and to be in such a situation, it must have absorbed 20 to 50 kg of water (Boyer 1995). The volume that passes through the plant, lost by transpiration, is exactly that which brings nutrients to the aerial part of the plant and which is associated with the carbon fixed during photosynthesis and will result in an increase in plant mass.

It is difficult to separate the influence that water stress and high temperatures have on plants, especially if field conditions are considered. Even in field experiments in which the effect of temperature is studied with good water supply, there is the possibility that high temperature and solar radiation triggers a temporary water stress in the hottest periods of the day (Da Matta 2003). Water has been considered the most limiting factor for plant growth, controlling its agricultural expansion, mainly in developing countries, where there is lack of financial investments limiting the use of irrigation, at least at current technological levels.

Coffee vegetative growth

Coffee vegetative growth is influenced by several environmental factors such as temperature, photoperiod, irradiance, water and nutrients supply and reproductive growth (Sylvain 1958). For local cultivars in Africa (Kumar 1979) and Brazil (Maestri and Barros 1977; Rena *et al*. 1994), once temperature is favorable, coffee growth exhibits periodicity strictly associated to rain distribution. In some cases, however, restart of active growth might precede the beginning of the rain period, as observed in the South regions of India (Mayne 1944) and in Santa Tecla, El Salvador (Reeves and Villanova 1948), despite major growth outbreaks occurring at the beginning of the rainy season. On the other hand, in some coffee regions where rain is regularly distributed and air temperature has little variation, such as in Costa Rica and Colombia, it is probable that growth seasonality is determined by small variations in sunlight intensity (Alvim 1964).

In Viçosa, state of Minas Gerais, Southeast Brazil, the active phase of coffee vegetative growth occurs from September to March, a period in which the temperatures are relatively high, the rain is abundant and the photoperiods are longer. The quiescent phase, though, follows dry and cold periods and declining photoperiods and is extended from March to September (Barros and Maestri 1974), with negligible growth rates from the end of May on (Mota *et al.* 1997). Nevertheless, drought does not seem to be the primary factor in the regulation of coffee growth rhythm in Viçosa, since irrigation during the dry and cold period does not alter growth rates (Mota *et al.* 1997). Barros and Maestri (1974) suggested that the decreases in the photoperiod that started in the beginning of March in Viçosa might be related to a reduction in growth. However, it is much more probable that the decrease in coffee growth is modulated by low temperatures, in particular, with the increase of days with temperatures lower than 16°C (Barros *et al.* 1997). Amaral (1991) observed highly significant correlations between coffee growth and the mean and minimum temperatures, since the lower growth rates coincided with the lower temperatures; in an opposite manner, the resumption of active growth in the beginning of September occurred concomitantly with an increase in the minimum temperatures. However, temporary growth, which decreased from January to February, seemed to be associated with high temperatures (Silva *et al.* 2004) and with high solar radiation. In fact, annual mean temperatures lower than 16°C and higher than 23°C seem to be inappropriate for Arabica coffee (*C. arabica*) growth, whose optimum temperature varies from 18 to 21°C (Alègre 1959).

Despite several studies having tried to correlate coffee growth periodicity with environmental factors, the relations found were, ordinarily, circumstantial. Control of the beginning, maintenance and the end of active and quiescent growth phases seem to be really complex and not very well understood (Barros *et al.* 1997). Nevertheless, according to the same authors there is a strict parallelism between reduction in stomatal conductance and decrease in growth rate of coffee plants at lower temperatures during the Brazilian winter. It is important to stress that in winter, a decrease of the photochemical efficiency of photosystem (PS) II is generally observed, evaluated through the variable and maximum fluorescence (F_v/F_m), being quantitatively reflected in photosynthesis and in the growth of several species (Ball *et al.* 1994). In many of them, the lower growth rates are related to a decrease in the balance of F_v/F_m obtained in the morning, which indicates chronic photoinhibition effects induced by low temperatures. In the coffee plant, the net photosynthetic rate and the photochemical efficiency are truly reduced during winter, for both *C. arabica* cv. 'Red Catuaí' and *C. canephora* cv. 'Kouillou', however no correlation to growth rate has yet been established (Da Matta *et al.* 1997). Da Matta *et al.* (1997) showed significantly reductions on net CO_2 assimilation (*A*) and photochemical efficiency of PS II (F_v/F_m) with values ranging from 2.8-4.9 $\mu mol\ m^{-2}\ s^{-1}$ (*A*) and 0.82-0.83 (F_v/F_m), in the summer, to 0.2-2.8 $\mu mol\ m^{-2}\ s^{-1}$ and 0.65-0.79, in the winter, for 'Red Catuaí' and 'Kouillou', respectively.

Silva *et al.* (2004) made seasonal evaluations of vegetative growth, leaf gas exchanges, carbon isotope discrimination (Δ) and carbohydrate status in de-fruited Arabica coffee trees grown in the field, from October 1998 through September 1999, in Viçosa (20°45′S, 42°15′W, 650 m a.s.l.), Southeastern Brazil, and established significant correlations among minimum air temperature with vegetative growth ($r = -0.67$, $P < 0.01$) and photosynthesis ($r = 0.83$ $P < 0.001$). These authors concluded that a decline in air temperature would be the factor responsible for the growth and decrease of photosynthesis in Arabica coffee, and that the depressions of photosynthesis and growth might have simply run in parallel, without any causal relationship. Changes in net CO_2 assimilation appeared to be due to stomatal limitations in the active growth season, with non-stomatal ones prevailing in the slow growth period. Leaf carbohydrates appeared to not contribute significantly to alterations in growth rates and photosynthesis.

In the nursery, under shade, coffee seedlings present a

Fig. 1 Arabica coffee (*Coffea arabica* L. cv. 'Obatã IAC 1669-20') showing leaf burning (brown leaves) in Campinas, São Paulo state, Brazil. Photo by Emerson Alves da Silva in May, 2001.

non-adapted photosynthetic apparatus to the continuous light intensity found in the field. Thus, prior to be taken to the field, they need to go through an adaptation period after which they can be kept under constant full sunlight. Excess light energy *per se* or associated with other environmental factors like water deficit and high temperature causes what is known as photoinhibition and plants must present mechanisms to dissipate this excess of energy or alternatively repair the potential photoinhibitory damage (Pearcy 1998). Demmig-Adams and Adams (1992) showed that down-regulation of PS II under high light conditions avoided excess excitation of the photosynthetic reaction centre and that the xanthophyll cycle located in the thylakoid membranes is involved in the dissipation of excess energy. Some studies have shown that coffee is able to respond to excess light (1,500 µmol m^{-2} s^{-1} during 6-8 hours) increasing the quantity of protective pigments in the leaves, such as the xanthophylls and that the response is related to nitrogen availability (Ramalho *et al.* 1997). Plants under full sunlight have less thylakoids per granum and less grana per chloroplast, an indication of the cellular adaptation to overcome excess light (Fahl *et al.* 1994). Besides radiant energy, the plant also receives thermal energy from the atmosphere and surrounding hot surfaces. In the case where air is hotter than the plant, the plant will receive this additional energy through convection and conductance. The heat absorbed by plants during the day usually exceeds the lost quantity, resulting in an internal elevation of tissue temperature, particularly of the tissues from the most external leaves, which receive direct sunlight. Leaf temperature around 40 and 50°C are not unusual in coffee (Maestri *et al.* 2001) even when the air temperature is not above 35°C.

High temperatures also cause chlorosis and burning (scald) in coffee leaves (Cannell 1985; Wrigley 1988). Excluding the effect of light, chlorosis caused by high temperatures in coffee leaves resembles that caused by iron deficiency (Franco 1970). The phenomenon is also a consequence of high temperature and/or water deficits (Da Matta and Rena 2001). In general, photo-oxidative damage causes leaf chlorosis that rapidly evolves into tissue necrosis (**Fig. 1**) leading to leaf abscission. It is believed that in this case, the loss of water by transpiration is faster than its reposition in the local cells. There is fading and the cells tend to die. In general, these symptoms are visualized on the leaves' extremities and this type of damage frequently appears in plants that are shaded and are rapidly exposed to full sunlight and, consequently, high temperatures. Thus, it is common to observe this problem in coffee seedlings not adequately adapted prior to be taken to the field (Franco 1970).

Low temperatures also affect the development of chlorosis in coffee leaves and, depending on the growth stage, the damage is irreversible when chloroplast destruction is observed. Nevertheless, there seems to be a strict relation between the carbohydrate content and the development of injuries (Franco 1970), which could be directly associated with the maintenance of leaf water potential and a lower freezing temperature. Some adaptations to tolerate light energy and excess temperature are leaf curvature and thickening, mainly due to the cuticle thickness. Compared to shaded coffee plants, those exposed to full sunlight have 11% thicker leaves (Fahl *et al.* 1994).

High temperatures might also cause injuries in the seedling due to the high temperature of the ground around the stem, which may be over 50°C. Depending on the period of exposure, the plant may even die (Franco 1970). Nevertheless, low temperatures cause frost. Coffee frosts in Brazil usually occur from June to August, the coldest period of the year. During this period the low-lying areas are most susceptible since cold air flows down the mountains and settles in the valleys where temperatures close to -2°C might kill the stem bark tissues, and when close to -5°C the plant may die (Franco 1970).

An adequate water supply is essential for seedlings transferred from the nurseries to the field, in order to give some time to for the root system to grow, increasing the capture area of water and nutrients. Most of the coffee plants' roots are placed in the first 50 to 60 cm aboveground. Low temperatures in the soil affect root absorption more than do high temperatures (Franco 1970; Alonso *et al.* 1997). However, excluding the superior upper portion of the soil (top 5 cm), the inferior layers are less affected by oscillations in air temperature. A good indication of this fact is that the growth rate of coffee roots is higher in cold seasons with a decreased growth of the canopy (Cannell 1972). Obviously, this increased growth would also be influenced by the reduced competition for photoassimilates between the canopy and roots, since photosynthesis tends to decrease at lower temperatures, i.e. in winter.

The problem in studying plants roots, especially from perennial plants, which penetrate deep into the soil, is to deal with a huge volume of soil and to recuperate roots of several diameters. Probably this is the main reason for so few reports on coffee roots. The first study with coffee roots was carried out in 1892, when it was determined that coffee plants from 10 to 40 year-old coffee plants produced from 20.1 to 47.8 kg of roots (Franco 1970). Other posterior ensuing publications reviewed in Rena and Da Matta (2002) have shown that in fact, most fine roots of coffee are restricted to the superficial layer of the soil and that this varies in function of plant age, implying that young plants have a root system concentrated more superficially in the soil, deepening as the plant ages, probably due to a greater influence of cultural traits and the environment, to the lower layers of the soil, varying from 50 to 60 cm. The taproot is deep, reaching up to 4 m.

Soil type largely influences root distribution. Heavier or more compacted soils tend to make root penetration more difficult and limit lateral root growth. However, very little is known regarding the influence of water in the root distribution. In a study carried out in Kenya, the effect of irrigation and mulching (soil coverage) using banana rejects on the distribution of Arabica coffee roots was evaluated for 20 years (Bull 1963). It was observed that irrigation diminishes the main root deep penetration (almost 0.5 m smaller, 20% of the maximum length observed) and also the development of primary (> 5 mm of diameter) and secondary roots in the lower layers. However, there was an increase in the lateral length of secondary roots. Mulching increased both depth and lateral growth, forming a net of thin roots close to the soil surface. The combination of both treatments provided better development of the roots, even when the main root growth decreased by 0.5 m.

Mulching, irrigation and plantation density were studied in coffee plantations of Zimbabwe by Cassidy and Kumar (1984). Mulching increased the distribution of roots at the soil surface, but had a lower effect at high plant densities (> 4.000 plants/ha), probably due to soil shading caused by the plants themselves. Curiously, the roots of plants placed at a denser spacing (4 to 6.000 plants/ha), when irrigated, deepened their root system (around 0.5 m). This could be explained by the decreased volume of lateral roots competing for the same soil space at high densities. The implications of this fact would be related not only to water availability but also to nutrients.

Roots' functional activity varies with water availability. Huxley *et al.* (1974) showed that mineral absorption, shown by the incorporation of radioactive phosphorus, and following a long period of drought, was higher in roots in the middle of the root system, while after irrigation, it increased in more superficial roots. As time passed, a more regular distribution of the absorption took place.

Several studies have offered evidence that genetic variability seems to exist in coffee with regards to drought tolerance (Josis *et al.* 1983; Meguro and Magalhães 1983; Renard and Karamaga 1984; Wrigley 1988). It is usual to find that, among the most tolerant plants, or those which maintain higher water potential, that several are dwarf varieties, such as 'Catuaí', 'Caturra', 'San Ramon', 'Mokka and 'Laurina'. There are no explanations for this coincidence, but in some publications it was observed that coffee plants were able to adjust osmotically, producing proline and glycinebetaine that in high concentrations might maintain the osmotic potential at levels favorable to the maintenance of the leaf water status (Venkataramanan and Ramaiah 1987; Meinzer *et al.* 1990; DaMatta *et al.* 1993; Maestri *et al.* 1995). However, DaMatta *et al.* (1993) believe that this adjustment is of limited value to maintain the plant water status.

Once the coffee plant is in the reproductive cycle, it begins to divide the carbon assimilated during photosynthesis between the vegetative growth and fruits. Coffee plants increase fruit production continuously up to the fifth or sixth production cycle, entering then in what is known as the biennial cycle. In some cases, excess fertilization might induce early entrance into the biennial cycle, even if the plant has not reached its maximum production. The alternation in production is explained by the reserve exhaustion from one year to another, i.e., in a high production year, a significant part of the photoassimilates is driven to fruit formation, with a consequent lower supply for vegetative growth, when less leaves and internodes are formed. Since production of the following production cycle takes place only in the growing branch, for over the next year there will be fewer nodes, flowers and, therefore, production. But, in this new year of low production, carbohydrates will be available for vegetative growth, since fruit competition will be reduced and in the following year, the production will be increased again. In coffee, starch is accumulated in the wood of young branches during vegetative growth. Once carbon is needed for fruit growth, it is has been observed that the wood starch is hydrolyzed probably to supply the carbon demand (Janardhan *et al.* 1971).

Thus, maintenance of branch growth is essential for coffee productivity. In addition, the opening of flowers is strictly related to the amount of leaves on the branches, probably due to the nutritional demand in the flowering season and in the initial stages of fruit establishment (Gopal *et al.* 1975; Magalhães and Angelocci 1976). In this sense, it is known that water stress may severely reduce the development of new branches as well as the growth of already existing ones, decreasing the number of internodes and the individual leaf area (Boyer 1969; Fisher and Browning 1979; Tesha and Kumar 1979). It is really interesting that branch growth seems to take place in an almost compensatory manner, i.e., plants submitted to moderate stress, when re-irrigated, seem to show higher vegetative growth than those constantly irrigated (Tesha and Kumar 1979; Drinnan and Menzel 1994). The exact reason is not known, but some authors suggest that it might be related to the lower resistance to water diffusion in the roots (Browning and Fisher 1975).

Since production and the biennial cycle are strictly related to the offer of photoassimilates, several authors have tried to select productive plants based on the photosynthetic rate. Despite some differences having been observed among species and varieties from the same species, in particular in *C. arabica*, it was not possible to establish a significant correlation between productivity and photosynthesis (Nunes *et al.* 1969; Söndahl *et al.* 1976). Photosynthesis in productive and less productive plants is similar, although less productive plants have a biennial cycle less pronounced than productive plants (Mazzafera *et al.* 1995).

Photosynthesis in coffee is well studied and several studies showed that above 30°C it starts to decrease significantly (Rena and Maestri 1984). Photosynthesis in coffee begins to saturate with radiation between 600 and 1000 μmol photons m^{-2} s^{-1}, a light intensity usually found in sunny days during the summer, between 9 and 10 am. Thus, considering that temperatures above 30°C are usual during the hottest months of the year and that this luminosity is easily reached in days of full sun, coffee production in tropical areas would theoretically be impractical. Production occurs because the plant canopy has to be considered as one whole object. Cannel (1985) suggested that an adult coffee plant could be divided into three photosynthetic layers, namely: a) an external one, which receives high luminosity and temperature, and as a consequence, presents inhibition of photosynthesis almost all day long; b) a second layer that receives indirect and diffuse light with lower temperature in which photosynthesis is satisfactory; c) an inner layer, which would has low rates of photosynthesis due to low light availability. In the second layer, besides diffuse light, rays of light which penetrate the canopy due to sun movement (sun flecks) would reach the leaves, permitting higher photosynthesis rates. Thus, correlating productivity to photosynthesis would only be possible if the entire plant was placed into a chamber and the CO_2 consumption was measured. Since the accumulation of dry mass basically represents a difference between carbon input in photosynthesis and its loss in respiration, monitoring dry mass variation would be as trustworthy as sampling the whole plant; however the material would be inconveniently destroyed.

The three-level structure in the coffee canopy occurs if it is considered that shaded leaves have higher net photosynthesis than leaves exposed to full sunlight (Cannell 1985). Several data showed that stomatal conductance is larger in shaded coffee leaves (Butler 1977; Fanjul *et al.* 1985; Gutiérrez *et al.* 1994). Field assays with the *C. arabica* varieties 'Bourbon' and 'Caturra' have shown that despite the stomata of plants growing at full sun remaining open at dawn, they close in the morning with an increase in temperature, irradiation and atmosphere air saturation deficit (Fanjul *et al.* 1985). According to Da Matta (2004b, and references there in), this stomatal behavior should be attributed to the sensitivity of the stomata to decreases in vapour pressure deficit (VPD) than to solar radiation. The relationship between stomatal conductance and VPD has been described either by a curvilinear and simple linear decay function for Arabica (Fanjul *et al.* 1985; Gutiérrez and Meinzer 1994; Gutiérrez *et al.* 1994; Kanechi *et al.* 2005) and Robusta (Pinheiro *et al*. 2005) coffees, respectively.

Plants exposed to full sunlight seem to close stomata with a lower air saturation deficit (Fanjul *et al.* 1985) than shaded plants (Hernandez *et al.* 1989), and photosynthesis is maintained for a longer period of time.

In the studies cited above, it was also evidenced that leaves at full sunlight with fast stomatal closure showed an increase in the leaf temperature, from 10 to 15°C above ambient temperature (Butler 1977; Kanechi *et al.* 1995). It is well known that high temperature affects the chemical reactions related to the incorporation of carbon in plants, since they are mediated by enzymes (Berry and Böjorkman 1980).

Low temperatures also affect photosynthesis. In assays in which the shoot of one year-old *C. arabica* seedlings were exposed to low temperatures only once, photosynthesis was considerably reduced, being more than 50% at 4°C (Bauer *et al.* 1985). At 0.5°C some injury occurred and the tissues stopped fixing CO_2. When the plants were repeatedly kept during nights at 4 and 6°C, photosynthesis was progressively reduced in the following days, and after 10 days it was 10% lower than the initial rates. Keeping the plants for 15 days at 12°C did not trigger tolerance to cold, implying that the plant avoided a reduction in photosynthetic activity. It was further observed that 25% of the photosynthetic reduction was due to stomatal closure and 75% to a decrease of carboxylation reactions of the photosynthesis (Bauer *et al.* 1985).

Temperatures lower than 12°C inhibit the accumulation of chlorophyll and other chloroplastidic pigments in Arabica coffee plants, resulting in a reduction of the photochemical reactions of photosynthesis and a consequent decrease in carbon assimilation (Oliveira 2000). Apparently, the decrease in carbohydrate reserves aggravates the problem.

Similar to that observed in Brazil for some Icatu lineages of *C. arabica*, which were more tolerant to cold in frost seasons (Fazuoli *et al.* 1995), experiments in Zimbabwe also showed evidence of the existence of genetic variability for this characteristic (Bauer *et al.* 1990). For Icatu cultivars, it was suggested that the accumulation of potassium in the leaves might explain the higher tolerance to cold, but no evidence stronger than foliar analyses have been shown so far.

Coffee reproductive phase

Fruit production is primarily dependent on the formation of floral buds and on the success of flowers blossom and their pollination (Bewley *et al.* 2000). In addition, it depends on the development of pollinated flowers and their retention on the plant throughout the growth and development of fruits. Higher number of buds theoretically means higher production. The control of floral bud number is genetically controlled and, consequently, is related with the success of plant breeding in economically explored plants. Photoperiod might alter the genetic expression and cause a decrease or increase in the number of buds per plant. Depending on the plant type, after flowering, adequate temperatures will be necessary for fruit growth.

The literature on the influence of environmental factors in flowering coffee plants is very controversial (Drinnan and Menzel 1995). Depending on the place of cultivation, the dominant factor influencing the vegetative and reproductive cycles of coffee plants is really variable (Gopal 1974). According to Camargo (1977), when Arabica coffee is cultivated in adequate climates with favorable thermal and water conditions, it is possible to admit photoperiod as a factor conditioning the flowering season. However, Cannel (1972) suggests that seasonal variations in the floral growth and development in coffee plants could be regulated by factors other than photoperiod, since both young and adult plants of several *C. arabica* cultivars have shown to be photoperiodically insensitive, maintaining their flowering capacity independent of day length, being more probable that the plants' responses were conditioned by fluctuations in air temperature and water supply.

For coffee, three flowering phases have been proposed (Majerovicz and Söndahl 2005): a) initiation and floral differentiation, b) dormancy and c) flowers opening (anthesis). Due to difficulties in determining exactly the beginning and the end of each one of these phases, initiation and differentiation are almost imperceptible processes. In these two processes, in which the transition from vegetative to floral bud takes place, the effect of temperature and water supply are almost unknown, as most of the work from the literature is based on gross visual observations, when the floral button is already differentiated. Therefore, there is a need for studies with advanced microscopic techniques as well as with biochemical (plant hormone levels and variations) and molecular (gene expression) tools to show the exact time coffee buds differentiate to flowers. The general concepts and the complexity of factors controlling plant flower formation can be found in Bewley *et al.* (2000) and Dornelas and Dornelas (2005).

Air temperature and flowering

Regarding the influence of the air temperature on coffee flowering, some studies show conflicting data. While Went (1957) showed that temperatures combined at 30°C day/23°C night induced more floral buds, Mes (1957) showed that buds were undifferentiated at 30°C day/17°C night and 30°C day/23°C night. Nevertheless, Mes (1957) determined that at 23°C day/17°C night bud formation increased. On the other hand, floral initiation was also very satisfactory in combinations of 23°C/20°C and 30°C/24°C, presenting faster bud development at higher temperatures or in these temperature combinations. Low temperatures (17°C day/12°C night; 20°C day/17°C night) inhibited floral initiation.

In Kenya, the rates of floral differentiation were high in cold months (Wormer and Gituanja 1970). In this sense, Browning (1973) suggested that a drop in air temperature followed by rain would play an important role in the dormancy break of floral buds in coffee plants. However, in this case, the available evidence is indirect, based on observations in which decreases in air temperature happen as a consequence of the rain, making it impossible to separate the effects from such environmental factors (Alvim 1985).

The data cited above presents a practical problem: all were obtained under controlled conditions. In field conditions, a study of the initial phases of coffee flowering is extremely difficult since the process is highly influenced by other factors, mainly photoperiod as the length of time plants are exposed to light determines the flowering process (Bewley *et al.* 2000). Moreover, the tools used for such observations were inadequate, i.e., many studies were based on visual observations instead of histological sections. Thus, it is not possible to conclude exactly if there is an annual cycle defining the periods of initiations and differentiation of floral buds in coffee.

In a histological study carried out in Campinas, State of São Paulo, Brazil, it was shown that under field conditions, most of the buds differentiated between January and February (Majerovicz and Söndahl 2005). In that study, carried out from 1980 to 1982, the daily mean temperature in January and February varied from 21 to 25°C. In the same municipality, the daily mean air temperature between 1956 and 1982 was close to 23°C.

Water and flowering

Conflicting data are also frequent when assessing the effect of water on the initiation and differentiation of coffee floral buds. In some cases, water stress may apparently promote these processes while in others, they are observed in more humid periods (Barros *et al.* 1978). Nevertheless, in the floral induction period, severe stress might certainly decrease the number of inflorescences (Drinnan and Menzel 1994). Therefore, we may conclude that there is not an apparent defined cycle for floral buds in coffee, initiation and differentiation being observed in different periods of the year, even in colder seasons. However, there seems to be synchronization, since there is a concentration of differentiation events during some periods of the year. Analyzing the conditions in Campinas, Brazil, it was observed that almost all buds had already started to differentiate by the beginning of March; however, there was induction up to the end of July (Majerovicz and Söndahl 2005). This is very important as from 4 to 5 floral buds per leaf axis, i.e. 80% of the flowers were related to the two older buds, i.e., those which had first differentiated.

After differentiation, the floral bud develops, growing continuously up to its entrance in the dormancy period, when it reaches from 4 to 8 mm and accumulates an external layer of wax. At this point, there is no accumulation of dry mass and the vascular connection between floral bud and the plant is done almost exclusively by the phloem. It is also in this stage that all the structures related with flower fertilization are formed, and the flower is now considered to be mature. The factors leading to bud dormancy in coffee are still unknown, and environmental conditions and biochemical factors involved in plant metabolism are considered as possible influences (Barros *et al.* 1978). It was suggested that this dormancy could be related to flower protection against a period of water stress since under field conditions, floral bud dormancy coincides with the dry season (Rena and Maestri 1984). The influence of low temperatures detected in this season on the flowering process was considered to be of minor importance (Barros *et al.* 1978) and according to the same authors the problem is to ascertain whether the bud growth arrestment is imposed by the environment or is at true dormancy due to intrinsic conditions.

Some authors suggested that independent of the reasons that lead to dormancy this process could offer some advantages, since it would permit the standardization of the development of differentiated buds in different periods (Cannell 1983). Nevertheless, one should still consider that dormancy may present genetic influence as is observed in hydroponic or constantly irrigated plants. Certainly, despite some controversy about this issue (Barros *et al.* 1978), the reason and mechanisms governing coffee dormancy are still unknown.

Coffee farmers and researchers know well that after the first occurrence of rain, coffee flowering takes place and that it might be influenced by temperature. At this stage, the flower undergoes rapid anatomical changes and if temperature does not decrease, flowering takes place between 8 to 10 days. If temperature falls, flower opening is delayed.

Even with the supposed protection offered by dormancy against the lack of water, periods of prolonged drought before flowering, still in dormancy, might lead to the formation of abnormal flowers (Huxley and Ismail 1969; Kumar 1979). Abnormal flowers may also be formed if high (Mes 1957) or low (Gouveia 1984) temperatures are imposed. Kumar (1979) suggested three types of abnormal flowers based on the premature exposure of the internal parts of the flower, which would cause a reduction in flower setting. The first and the worst case, which would cause up to 80% loss in production, the style and anthers would be exposed. In the second type, that would cause an intermediate loss, up to 40%, part of the style and the tip of the anther would be exposed. Finally, in the less problematic type that would not cause a loss, only the corolla tip would open. In the worst cases, the flowers are almost green, not presenting the white-cream color from normal development during anthesis. Since water deficit might be one of the factors causing the formation of abnormal flowers, irrigation might reduce the frequency at which they appear (Portères 1946).

Water seems to be the main environmental factor affecting flower opening and it seems that the development of water stress on leaves is necessary (Magalhães and Angelocci 1976; Cannell 1985; Crisosto *et al*. 1992; Drinnan and Menzel 1994). The water potential of the leaves needed to cause dormancy release seems to be around -1.0 MPa. The continuous water supply causes delayed flowering, making it disperse (higher number of small flowerings) and substandard when compared to stressed plants, or even preventing flowering from taking place. In field conditions, coffee plants continuously or regularly watered almost do not have flowers, or if they do, they have a reduced number of flowers (Portères 1946).

In coffee, prior to flowering, the xylem does not develop well and almost all the water flux to the bud coming from the leaves is done via the phloem. When the first rains start to fall, probably some alterations in the hormonal balance occur, leading to a fast development of the xylem, which permits water to enter the flower (Mes 1957; Drinnan and Menzel 1994). Studies with radioactive tracers (tritiated water and ^{45}Ca), however, showed that in constantly irrigated plants, xylem development could be slower, probably due to the smaller lumen of the vases, offering higher resistance to water flux to the floral bud (Astegiano *et al.* 1988).

Nevertheless, how is it possible to explain that hydroponic coffee plants not only flower but also do it in the same period that the flowers in the field? In fact, this happens, but at a low intensity (Mazzafera, unpublished data). Even in constantly irrigated or hydroponic plants (Franco 1970), an internal water stress may develop in the drier periods of the year due to low relative air humidity. Unfortunately, there are no cases in the literature in which hydroponic plants were kept under high air humidity to check this hypothesis.

Besides the possible stress imposed by low relative air humidity, it seems that there is some signal emission from the roots, which would also be sensitized by low soil humidity. Plants grown with the root system divided in two parts and in separate containers (one with good water supply and another one with low water supply) presented water potential in the leaves similar to plants with irrigation in both containers (Crisosto *et al.* 1992). Nonetheless, flower opening was observed in the plants in which one of the roots' sides had suffered water limitations.

After flower opening, the fruits start to develop, with an initial phase in which almost no growth is observed, the fruit being called a "pinhead". Then, there is a rapid expansion up to the maximum size, in which the formation of the endosperm occurs, its hardening and posterior maturation, when the fruit changes from green to red, or yellow, depending on the coffee variety. In the second phase, water is once again crucial, since initial growth is almost coincident with perisperm formation, which is an aqueous, translucent and firm tissue that occupies all the fruit interior (Mendes 1941). During perisperm formation the lack of water might lead to fruit fall. The exact function of the perisperm in coffee fruit is not known, but apparently it could be the supplier of water and nutrients to the endosperm (Geromel *et al.* 2005). Microscopic analyses have shown that this tissue is rich in xylem terminations, different from the endosperm, in which they are absent (Geromel *et al.* 2005). Moreover, the low variation of soluble sugar content in the perisperm, unlike what happens in the endosperm, would be indicative that this tissue works as a bridge between the leaves, nutrient suppliers, and the endosperm (Rogers *et al.* 1999; Geromel *et al.* 2005). In this sense, leaf production is extremely important for the coffee plant. Still, in the flowering stage, the degree of leaf production influences the success of flowering. Branches with flowers, but few leaves, result in a small number of fruits (Magalhães and Angelocci 1976; Gopal *et al.* 1975). The demand for organic nutrients in both stages would have to be supplied by the leaves.

Around 45 to 60 days after flowering, the first cell divisions, which will lead to endosperm formation (the economically interesting part of the fruit), takes place (Mendes 1941). During its formation, the fruit shows a small increase in size, but acquires dry mass, replacing the internal space previously occupied by the perisperm. The tissue known as silver skin in the ripe fruit is the residue from the perisperm. At the end of endosperm formation, it loses water and hardens.

A lack of water and high temperatures during fruit growth, i.e., during endosperm formation, might result in the formation of smaller seeds, reflecting directly in the coffee yield.

Data from Kenya showed that 50% of the annual variation in the size of bigger fruits was related to the number of rainy days between 10 to 17 weeks after flowering, a period in which the fruits are expanding their size (Cannell 1974). Irrigation and mulching would be two strategies with beneficial effects to guarantee bigger seeds.

Irrigation and flowering in coffee plants

Regarding the water aspect *per se*, flowering in coffee has been associated with cycles of water deficit in the plants, which would break dormancy of the totally differentiated floral buds, leading to anthesis in 8 to 12 days. In this model, it is probable that dry periods would be necessary for the uniformity in the maturation of the higher number of

Fig. 2 Fruit maturation of Arabica coffee plants (*Coffea arabica* L. cv. 'Obatã IAC 1669-20'). Plants subjected to treatments of non-irrigation (**A**), continuously irrigated (**B**) and withholding irrigation during 30 days in July (**C**) and 60 days in July and August (**D**) in Campinas, São Paulo State, Brazil. Treatment **D** shows good uniformity of fruit maturation with high number of fruits per branch. Photos by Emerson Alves da Silva in April, 2002.

buds, making it more sensitive to the factors that break dormancy (Alvim 1960; Drinnan and Menzel 1994). Magalhães and Angelocci (1976) suggested that the dormancy release by irrigation might be quantitatively related to the intensity of previous water deficit. According to these authors, a water potential threshold on coffee leaves of -1.2 MPa must be established to promote the flowering process in response to root irrigation. Crisosto *et al.* (1992) observed that flowering was stimulated by irrigation after a period of water deficit, if the water potential from the leaves decreased below -0.8 MPa. In a similar manner, Drinnan and Menzel (1994), aiming to synchronize flowering, observed that floral development was faster in coffee exposed to cycles of water deficit between -1.5 and -2.5 MPa, when compared to constantly irrigated plants (-0.5 MPa). It is important to emphasize that, in all cases, the response requires floral bud maturity for flowering (Mes 1957; Crisosto 1992).

According to this information, it is clear that periods of drought might contribute to a more abundant maturation of floral buds, favoring uniform flowering. However, most of the work from the literature was done under a controlled environment and, even when in field conditions, they aimed only to clarify the relation between water deficit intensity imposed on the plant and flowering uniformity. Thus, these studies do not determine the time interval needed to establish a water deficit able to break the dormancy of the floral buds and to stimulate flowering synchronization and fruit development; moreover, they do not quantify the reflexes on the final production of the coffee plants. Such information, still unavailable, would permit the development of practices that would help the farmer to plan and utilize irrigation efficiently, increasing coffee production and quality.

Although several studies about the effects of environmental factors on the development of flowers and fruits have already been done, few of them were dedicated to the identification, under field conditions, the period of time necessary to reach a water deficit sufficient to be efficient in promoting uniform coffee flowering, mainly considering different systems of cultivation, among which irrigation played an important role. Moreover, in the field, small restrictions faced by the root system and a more gradual development of water stress might lead to different responses from the plant.

Coffee irrigation in Brazil has been justified by the possibility of the culture expansion in areas previously limited due to water deficiency or irregular rain distribution, and in traditional regions by the offer of production warranty in low precipitation years or when short hot-dry periods occur in the critical phases of fruit development. However, regarding the importance of irrigation for coffee culture, its benefits on productivity and flowering control have not been adequately quantified. This is due, in part, to the fact that the need for irrigation and its function in the control of flowering period are very variable and dependent on rainfall distribution, drought severity and the type and depth of the soils.

According to Carr (2001), in Australia, aiming to synchronize coffee flowering, water deficit has been applied through irrigation suspension up to the point at which the plants present water potential on the leaves around -2.5 MPa, this condition being maintained for 2 to 3 weeks, then restarting irrigation to stimulate fast and uniform flowering. Nevertheless, according to that same author, no data about the period of time needed to reach such deficits or even quantifying the benefits for productivity and flowering uniformity derived from this technique was published, thus clear experimental evidence in which these recommendations would be based on are not available.

Silva (2004) worked with Arabica coffee cv. 'Obatã IAC 1669-20' under irrigated and non-irrigated conditions in three different macroclimatic regions of the State of São Paulo, Brazil, and showed that under field conditions that withholding irrigation for 60 days in the months of July and August favored leaf water to reach potentials ranging from -1.1 to -1.6 MPa. These potentials were more effective in flowering synchronization, allowing uniformity of fruit maturation (**Fig. 2**) and good fruit production. The higher number of flowerings episodes and the low uniformity in the production of the plants continuously irrigated (-0.5 MPa) confirm the need for a drought period for flowering synchronization. This author also observed that low water potentials (-2.5 to -2.8 MPa) of the non-irrigated plants significantly reduced the number of flowers when compared to the irrigated plants, reflected in the final production, indicating the need of irrigation to assure an appropriate floral initiation (Emerson Alves da Silva, unpublished data).

The practical implications of the above cited information are important mainly in regions where coffee has been irrigated, reflecting the need of water management, especially during the flowering period. In coffee areas with continuous irrigation, the better control of the water supply could lead to a higher concentration of opened flowers in the first flowerings. Thus, it would be possible to obtain uniform flower opening and, consequently, get fruits with more homogeneous maturation. Undoubtedly, this would bring some advantages to those places where mechanical harvest is done, not being necessary to harvest fruits still on the trees. This would also diminish the time needed for harvest, making the time available for the realization of different management techniques necessary for coffee production. Sparser flowering caused by excess of water tends to compromise the product quality, since the number of defects increases as the quantity of green fruits increase in each harvest.

Fig. 3 Closed spaced planting (0.80 × 0.50 m) of Arabica coffee (*Coffea arabica* L. cv. 'Obatã IAC 1669-20') in Mococa, São Paulo State, Brazil. Cv. 'Obatã' was developed by the Instituto Agronômico de Campinas (IAC) and is a semi-dwarf variety, displaying resistance to leaf rust (*Hemileya vastatrix*) and is indicated for close spaced plantings or in hedgerows. Photo by Emerson Alves da Silva in June, 2001.

Coffee physiology and close space planting

As a consequence of the considerations about photosynthesis in the different canopy levels, a question about closed spaced coffee planting (**Fig. 3**) arises. Considering that the positive balance of carbon between photosynthesis and respiration is what defines growth, an excessively closed spacing, which might cause intense shading of the coffee plants, would lead to low levels of photosynthesis and low yield. Then, to define the best spacing of planting, the main component is light penetration in the canopy. A close spacing or dense plantation will certainly require the elimination of some trees as they grow, in order to avoid excessive self-shading.

However, not only higher light intensity could explain or justify spacing. Considering that some regions have a higher mean maximum air temperature than others, self-shading would maintain leaf temperature at more desirable levels for photosynthesis to occur. On the other hand, an intense close spacing between plants associated with huge leaf growth would cause exaggerated self-shading.

In cold regions, the growth of coffee leaves is limited by temperature, independently if there is irrigation or not (Barros *et al.* 1997). The period for the leaf to reach its maximum size is almost doubled when compared to hotter seasons. Consequently, in a branch of coffee, the leaves produced in the cold periods are easily identified, as they are smaller.

Another really important aspect in the planting of close spaced coffee is the efficiency in the use of water. As cited above, the main root of close spaced coffee tends to deepen even when irrigated, and this would probably cause competition for nutrients (Cassidy and Kumar 1984). Nevertheless, in a study done in Kenya, with close spaced coffee from 5.000 to 20.000 plants/ha, there was no evidence that higher densities accentuated water stress more than lower densities (Fisher and Browning 1979). Similar conclusions were obtained by other authors (Kiara and Stolzy 1986), who observed that at high densities, there was self-protection among the plants, decreasing the evaporative demand, not affecting thus the water use per unit area. It would be extremely interesting if temperature and humidity data within the plantation were registered and available.

Therefore, the determination of the best planting density depends on several factors, which makes it reasonably complex. Even with the possibility to eliminate plants as shading increases, there will always be the economic aspect, implying that if planting and elimination of plants has a specific cost, would it be possible to start from a defined spacing that, at the same time would offer, at least, profit in productivity? Even if there is no answer to this question, there is enough information in the literature to make it possible to infer that it is possible to control the development of plants in dense plantations based on the knowledge available about coffee physiology. However, more detailed studies, such as temperature and radiation monitoring in the coffee area and in the plant canopy as well as monitoring of leaf water potential and soil humidity, would certainly give important information to understand the responses of coffee to new technological patterns of cultivation, mainly irrigation, in the regions where it is traditionally cultivated, but overall in the new regions with different water and thermal regimes.

FUTURE PERSPECTIVES

As well stated by Barros *et al.* (1999) and more recently by Da Matta and Ramalho (2006) gaps in our knowledge in the eco-physiology of coffee are numerous. To understand the control of vegetative and reproductive growth by the environment and how endogenous factors play a role in these processes is essential to grow coffee and increase the productivity. This becomes more important if we consider the different management systems of cultivation like irrigation and planting density and in the Brazilian case, the expansion of the coffee crop to regions before considered marginal or inapt for coffee cultivation due to excess of temperature, like the Brazilian savannah (Cerrado).

In addition to the air temperature and its effects on photosynthesis and vegetative growth, studies on the temperature influence on fruit maturation and ripening must be carried out, aiming to provide additional information on the coffee beans biochemical composition and coffee quality. The recent advances on molecular biology tools and the Brazilian EST-Coffee Genome project (Vieira *et al.* 2006) will be useful in these studies and helpful for the understanding of the temperature effects on coffee physiology.

The influence of distinct edapho-climatic conditions on water relations, growth and flowering of coffee are also important. The requirement of a period of water deficit to break bud dormancy and induce coffee flowering have been demonstrated, and irrigation management has been used to control flowering in coffee plantations. However, proper determination of the internal water status of the coffee plant is still a difficult task, mainly under field conditions and unusual for producers. The knowledge of this information would allow to model seasonal changes of coffee water status and water consumption in different regions and for different coffee cultivars, in such a way that controlling the relation between intensity/duration of water deficit might allow the control of breaking bud dormancy and consequently the synchronization of flowering. In this way, irrigation can be a useful technique.

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REFERENCES

Alonso A, Queiroz CS, Magalhães AC (1997) Chilling stress leads to increased cell membrane rigidity in roots of coffee (*Coffea arabica* L.). *Biochimica et Biophysica Acta* **1323**, 75-84

Astegiano ED, Maestri M, Estevão MM (1998). Water stress and dormancy release in flower buds of *Coffea arabica* L.: water movement into the buds. *Journal of Horticultural Science* **63**, 529-533.

Alvim P de T (1960) Moisture strees as a requirement for flowering of coffee. *Science* **132**, 354

Barros RS, Maestri M, Coons MP (1978) The physiology of flowering in coffee: a review. *Journal Coffee Research* **8**, 29-73

Barros RS, Mota JWS, Da Matta FM, Maestri M (1997) Decline of vegetative growth in *Coffea arabica* L. in elation to lea temperature, water potential and stomatal conductance. *Field Crop Research* **54**, 65-72

Bauer H, Comploj A, Bodner M (1990) Susceptibility to chilling of some central-African cultivars of *Coffea arabica*. *Field Crop Research* **24**, 119-129

Bauer H, Wierer R, Hatheway WH, Larcher W (1985) Photosynthesis of *Coffea arabica* after chilling. *Physiologia Plantarum* **64**, 449-454

Berry J, Böjrkman O (1980) Photosynthetic responses and adaptation to temperatures in higher plantas. *Annual Review of Plant Physiology* **31**, 491-543

Bewley D, Hempel FD, MacCormick S, Zambryski P (2000) Reproductive development. In: Buchanan BB, Gruissem W, Jones RL (Eds) *Biochemistry and Molecular Biology of Plants*, American Society of Plant Physiologists, Rockville, Maryland, pp 988-1043

Boyer JS (1969) Etude experimentale des effects due regime d´humidite du soil sur la croissance vegetative, la floraison et la fructification des caféiers Robusta. *Café Cacao Thé* **13** 187-200

Boyer JS (1995) *Measuring the Water Status of Plants and Soils*, Academic Press, Inc., London, 178 pp

Browning G, Fisher NM (1975) Shoot growth in *Coffea arabica* L. II. Growth flushing stimulated by irrigation. *Journal of Horticultural Science* **50**, 207-218

Bull RA (1963) Studies on the effect of yield and irrigation on root and stem development in *Coffea arabica* L. 1. Changes in the root systems induced by mulching and irrigation. *Turrialba* **13**, 96-115

Butler DR (1977) Coffee leaf temperatures in a tropical environment. *Acta Botanica Neerlandica* **26**, 129-140

Cannell MGR (1972) "Primary production, fruit production and assimilate partition in Arabica coffee: A review," Annual Report 1971-1972 Coffee Research Foundation, pp 6-24

Cannell MGR (1974) Factors affecting Arabica coffee bean size in Kenya. *Journal of Horticultural Science* **49**, 65-76

Cannell MGR (1983) Exploited plants: Coffee. *Biologist* **30**, 257-263

Cannell MGR (1985) Physiology of the coffee crop. In: Clifford MN, Wilson KC (Eds) *Coffee: Botany, Biochemistry and Production of Beans and Beverage*, Chapman and Hall, London, pp 108-134

Carr MKV (2001) The water relations and irrigation requeriments of coffee. *Ex-perimental Agriculture* **37**, 1-36

Carvalho A, Filho HPM, Fazuoli LC (1985) *Coloquio Internacional de Citogenética de Plantas*, Piracicaba, pp 215-234

Cassidy DSM, Kumar D (1984) Root distribution of *Coffea arabica* L. in Zimbabwe. 1. The effect of plant density, mulch and cova planting in Chipinge. *Zimbabwe Journal Agriculture Research* **22**, 119-132

Crisosto CH, Grantz DA, Meinzer FC (1992) Effects of water deficit on flower opening in coffee (*Coffea arabica* L.). *Tree Physiology* **10**, 127-139

Da Matta FM (2003) Drought as a multidimensional stress affecting photosynthesis in tropical tree crops. In: Hemantaranjan A (Ed) *Advances in Plant Physiology* (Vol 5), Scientific Publishers, Jodhpur, pp 227-265

Da Matta FM (2004a) Exploring drought tolerance in coffee: a physiological approach with some insights for plant breeding. *Brazilian Journal of Plant Physiology* **16**, 1-6

Da Matta, FM (2004b) Ecophysiological constraints on the production of shaded and unshaded coffee: a review. *Field Crops Research* **86**, 99-114

Da Matta FM, Rena AB (2001) Tolerância do café à seca. In: Zambolin L (Ed) *Tecnologias de Produção de Café com Qualidade*, Universidade Federal de Viçosa, Viçosa, pp 65-100

Da Matta FM, Maestri M, Barros RS, Regazzi AJ (1993) Water relations of coffee leaves (*Coffea arabica* and *C. canephora*) in response to drought. *Journal of Horticultural Science* **68**, 741-746

Da Matta FM, Maestri M, Mosquim PR, Barros RS (1997) Photosynthesis in coffee (*Coffea arabica* and *C. canephora*) as affected by winter and summer conditions. *Plant Science* **128**, 43-50

Demmig-Adams B, Adams, WW (1992) Photoprotection and other responses of plants to high light stress. *Annual Review of Plant Physiology and Plant Molecular Biology* **43**, 599-626

Drinnan, JE, Menzel CM (1994) Synchronization of anthesis and enhancement of vegetative growth in coffee (*Coffea arabica* L.) following water stress during floral initiation. *Journal of Horticultural Science* **69**, 841-849

Dornelas MC, Dornelas O (2005) From leaf to flower: revisiting Goethe's concepts on the "metamorphosis" of plants. *Brazilian Journal of Plant Physiology* **17**, 335-343

Dublin P (1957) Recherches sur la floraison et la fructification de caféier de la "Nana". *Agronomie Tropicale* **12**, 173-208

Fahl JI, Carelli MLC, Vega J, Magalhães AC (1994) Nitrogen and irradiance levels affecting net photosynthesis and growth of young coffee plants (*Coffea arabica* L.). *Journal of Horticultural Science* **69**, 161-196

Fanjul L, Arreola-Rodriguez R, Mendez-Castrejou MP (1985) Stomatal responses to environmental variables in shade and sun grown coffee plants in Mexico. *Experimental Agriculture* **21**, 249-258

Fazuoli LC, Camargo AP, Piccin C (1995) O café Icatu desenvolvido no IAC para resistência ao agente da ferrugem vem mostrando também em plantas adultas tolerância à geada. In: Proceedings of the 21º Congresso Brasileiro de Pesquisas Cafeeiras, IBC, Rio de Janeiro, pp 138-140

Fisher NM, Browning G (1979) Some effects of irrigation and plant density on the water relations of high density coffee (*Coffea arabica* L.) in Kenya. *Journal of Horticultural Science* **54**, 13-22

Franco CM (1970) Apontamentos de Fisiologia do Cafeeiro, Secretaria da Agricultura - CATI, Departamento de Orientação Técnica

Geromel C, Ferreira LP, Cavalari AA, Pereira LFP, Guerreiro SMC, Pot D, Leroy T, Vieira LGE, Mazzafera P, Marraccini P (2006) Biochemical and genomic analysis of sucrose metabolism during coffee (*Coffea arabica*) fruit development. *Journal of Experimental Botany* **57**, 3243-3258

Gopal NH, Raju KI, Venkataramanan D, Janardhan KV (1975) Physiological studies on flowering in coffee under South India conditions. III. flowering in relation to foliage and wood starch. *Turrialba* **25**, 239-242

Gutiérrez MV, Meinzer FC (1994) Energy balance and latent heat flux partitioning in coffee hedgerows at different stages of canopy development. *Agricultural Forest Meteorology* **68**, 173-186

Gutiérrez MV, Meinzer FC, Grantz DA (1994) Regulation of transpiration in coffee hedgerows: covariation of environmental variables and apparent responses of stomata to wind and humidity. *Plant, Cell and Environment* **17**, 1305-1313

Hernandez AP, Cook JH, El-Sharkawy MA (1989) The responses of leaf gas exchange and stomatal conductance to air humidity in shade-grown coffee, tea, and cacao plants as compared to sunflower. *Revista Brasileira de Fisiologia Vegetal* **1**, 155-161

Huxley PA, Ismail SAH (1969**)** Floral atrophy and fruit set in arabica coffee in Kenya. *Turrialba* **19**, 345-354

Huxley PA, Patel RZ, Kabaara AM, Mitchell HW (1974) Tracer studies with 32P on the distribution of functional roots of Arabica coffee in Kenya. *Annals of Applied Botany* **77**, 159-180

Janardhan KV, Gopal NH, Ramaiah PK (1971) Starch scoring by visual observation in fresh wood of coffee plants. *Indian Coffee* **35**, 219-221

Josis P, Ndayishimiye V, Renard C (1983) Etude des relations hydriques chez *Coffea arabica* L. II. Evaluation de la resistance a la secheresse de divers cultivars a Gisha (Burundi). *Café Cacao Thé* **27**, 275-282

Kanechi M, Uchida N, Yasuda T, Yamaguchi T (1995) Water stress effects on leaf transpiration and photosynthesis of *Coffea arabica* L. under different irradiance conditions. In: Proceedings of the 16th International Scientific Colloquium on Coffee, Kyoto. Association Scientifique Internationale du Café, Paris, pp 520-527

Kiara JM, Stolzy LH (1986) The effects of tree density and irrigation on coffee growth and production in Kenya. *Applied Agriculture Research* **1**, 26-31

Krause GH (1994) Photoinhibition induced by low temperatures. In: Baker NR, Bowyer JR (Eds) *Photoinhibition of Photosynthesis – from Molecular Mechanisms to the Field*, Bios Scientific Publishers, Oxford, pp 331-348

Kumar D (1979) Some aspects of the physiology of *Coffea arabica*. A review. *Kenya Coffee* **44**, 9-47

Larcher W (2000) *Ecofisiologia Vegetal*, Editora Rima, São Carlos, 531 pp

Maestri M, Da Matta, FM, Regazzi AJ, Barros RS (1995) Accumulation of proline and quaternary ammonium compounds in mature leaves of water stressed coffee plants (*Coffea arabica* and *C. canephora*). *Journal of Horticultural Science* **70**, 229-233

Maestri M, Barros RS, Rena AB (2001) Coffee. In: Last FT (Ed) *Tree Crop Ecosystem*, Elsevier Publishers, Amsterdam, pp 339-360

Magalhães AC, Angelocci LR (1976) Sudden alterations in water balance associated with flower bud opening in coffee plants. *Journal of Horticultural Science* **51**, 419-423

Majerowicz N, Söndahl MR (2005) Induction and differentiation of reproductive buds in *Coffea arabica* L. *Brazilian Journal of Plant Physiology* **17**, 247-254

Mazzafera P, Guerreiro-Filho O, Magalhães AC (1995) Investigations on coffee productivity. *Journal of Coffee Research* **25**, 7-18

Meguro N, Magalhães AC (1983) Water stress affecting nitrate reduction and leaf diffusive resistance in *Coffea arabica* L. cultivars. *Journal of Horticultural Science* **58**, 147-152

Meinzer FC, Grantz DA, Goldstein G, Saliendra NZ (1990) Water relations and maintenance of gas exchange in coffee cultivars grown in a drying soil. *Plant Physiology* **94**, 1781-1787

Mendes AJT (1941) Cytological observations in *Coffea*. VI. Embryo and endosperm development in *Coffea arabica* L. *American Journal of Botany* **28**, 784-789

Mes MG (1957) Studies on the flowering of *Coffea arabica* L. *Portugaliae Acta Biologica* **4**, 328-356

Nunes MA, Bierhuizen JF, Ploegman C (1969) Studies on productivity of coffee III. Differences in photosynthesis between four varieties of coffee. *Acta Botanica Neerlandica* **18**, 420-424

Oliveira JG (2000) Efeitos fisiológicos da fotoinibição da fotossíntese em plantas jovens de cafeeiro (*Coffea arabica* L.). PhD thesis, Unicamp, 165 pp

Pearcy RW (1998) Aclimation to sun and shade. In: Raghavendra AS (Ed) *Photosynthesis: A Comprehensive Treatise*, Cambridge University Press, Cambridge, pp 250-263

Pinheiro HA, Da Matta FM, Chaves ARM, Fontes EPB, Loureiro MH, Ducatti C (2005) Drought tolerance is associated with rooting depth and stomatal control of water use in clones of *Coffea canephora*. *Annals of Botany* **96**, 101-108

Portères R (1946) Action de léau, après une période sèche, sur le déclenchement et la floraison chez *Coffea arabica*. *Agronomie Tropicale* **1**, 148-158

Ramalho, JC, Pons TL, Groeneveld HW, Nunes MA (1997) Photosynthetic responses of *Coffea arabica* leaves to a short-term high light exposure in relation to N availability. *Physiologia Plantarum* **101**, 229-239

Rena AB, Maestri M (1984) Fisiologia do cafeeiro. In: Rena AB, Malavolta E (Eds) *Cultura do Cafeeiro: Fatores que Afetam a Produtividade*, Associação Brasileira para a Pesquisa da Potassa e do Fosfato: Piracicaba, pp 13-85

Rena AB, Da Matta FM (2002) O sistema radicular do cafeeiro: morfologia e ecofisiologia. In: Laércio Zambolilm. (Org.). O estado da arte de tecnologias na produção de café. Universidade Federal de Viçosa, Viçosa, pp 11-92

Renard C, Karamaga P (1984) Etude des relations hydriques chez *Coffea arabica* L. III. Evolution de la conductance stomatique et des composantes du potentiel hydrique chez deux coultivars soumis a la secheresse en conditions controlees. *Café Cacao Thé* **28**, 155-163

Rogers WJ, Michaux S, Bastin M, Bucheli P (1999) Changes to the content of sugars, sugar alcohols, *myo*-inositol, carboxylic acids and inorganic anions in developing grains from different varieties of robusta (*Coffea canephora*) and arabica (*C. arabica*) coffees. *Plant Science* **149**, 115-123

Schulze E-D, Beck E, Müller-Holheintein K (2005) *Plant Ecology*, Springer, Berlin, Germany, 702 pp

Silva EA (2004) Influência de distintas condições edafoclimáticas e do manejo de irrigação no florescimento, produção e qualidade de bebida do café (*Coffea arabica* L.). PhD thesis, Unicamp, 70 pp

Silva EA, Da Matta FM, Ducatti C, Regazzi AJ, Barro RS (2004) Seasonal changes in vegetative growth and photosynthesis of Arabica coffee trees. *Field Crops Research* **89**, 349-357

Söndahl MR, Crocomo OJ, Sodek L (1976) Measurements of ^{14}C incorporation by illuminated intact leaves of coffee plants from gas mixtures containing $^{14}CO_2$. *Journal of Experimental Botany* **27**, 1187-1195

Söndahl MR, Nakamura T, Filho HPM, Carvalho A, Fazuoli LC, Costa WM (1984) Coffee. In: Ammirato PV, Evans DA, Sharp WR, Yamada Y (Eds) *Handbook of Plant Cell Culture (Vol 3) Crop Sciences*, Macmillan Inc., New York, pp 564-590

Tesha AJ, Kumar D (1979) Effects of soil moisture, potassium and nitrogen on mineral absorption and growth of *Coffea arabica* L. *Turrialba* **29**, 213-218

Venkataramanan D, Ramaiah PK (1987) Osmotic adjustments under moisture stress in coffee. X*II International Scientific Colloqium on Coffee, Montreux*; Association Scientifique International du Café, pp 493-500

Vieira LGE, Andrade AC, Colombo CA, Moraes AHA, Metha Â, Oliveira AC, Labate CA, Marino CL, Monteiro-Vitorello CB, Monte DC, Giglioti É, Kimura ET, Romano E, Kuramae EE, Lemos EGM, Almeida ERP, Jorge ÉC, Albuquerque ÉVS, Silva FR, Vinecky F, Sawazaki HE, Dorry HFA, Carrer H, Abreu IN, Batista JAN, Teixeira JB, Kitajima JP, Xavier KG, Lima LM, Camargo LEA, Pereira LFP, Coutinho LL, Lemos MVF, Romano MR, Machado MA, Costa MMC, Sá MFG, Goldman MHS, Ferro MIT, Tinoco MLP, Oliveira MC, van Sluys M-A, Shimizu MM, Maluf Mperez, Eira MTS, Guerreiro Filho O, Arruda P, Mazzafera P, Mariani PDSC, Oliveira RLBC, Harakava R, Balbao SF, Tsai SM, Mauro SMZ, Santos SN, Siqueira WJ, Costa GGL, Formighieri EF, Carazzolle MF, Pereira GAG (2006) Brazilian coffee genome project: an EST-based genomic resource. *Brazilian Journal of Plant Physiology* **18**, 95-108

Went FW (1957) The experimental control of plant growth. *Chronica Botanica* **17**, 164-168

Wrigley G (1988) *Coffee*, Longman Scientific and Technical, Essex, 639 pp