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Morphological and physiological acclimations of coffee seedlings to growth over a range of fixed or changing light supplies

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ABSTRACT

Acclimations to low and high light levels are located in opposite extremes. We examined how the coffee plant (*Coffea arabica*), which is considered to be shade-demanding although it performs well under full sun exposure, can acclimate to a range of light regimens. We hypothesised that the growth and physiological performance depends on the total amount of light received by the plant per day and on the temporal order of diurnal variations in the light supply. The biomass accumulation and allocation and the key photosynthetic traits of pot-grown coffee seedlings were examined over a range of light treatments as follows: plants grown entirely under 100%, 40% or 10% sunlight; plants grown at either 40% or 10% sunlight from sunrise to midday and then submitted to full sunlight until sunset; and plants grown under full sunlight from sunrise to midday and then submitted to either 40% or 10% sunlight throughout the afternoon. The total biomass increased linearly with the increasing total light supply; however, plants receiving high amounts of light in the morning grew more than those receiving high amounts of light in the afternoon. Extensive morphological changes (e.g., specific leaf areas and leaf area ratios) primarily responsive to total light rather than diurnal light fluctuations or light quality, at a given light supply, were noted. In contrast, changes in the photosynthetic performance per unit leaf area among the treatments were narrower and apparently unrelated to carbohydrate accumulation or photoinhibition. Overall, we found a poor leaf-level physiological plasticity of traits to light. We suggest that adjustments in leaf number and leaf area, coupled with whole-plant physiological adjustments, could largely account for the differences in the biomass amongst treatments. We also suggest that coffee could be classified as a shade-tolerant species as its traits do not match the requirements of either a classic shade-avoiding or a classic shade-demanding species.

1. Introduction

Although light is a crucial environmental resource that drives photosynthesis and ultimately influences plant growth, both low and high sunlight can limit plant performance. On the one hand, the growth and survival can be compromised by low sunlight; on the other hand, desiccation, heat and light stress can occur under high sunlight conditions (Valladares and Niinemets, 2008). To cope with these stresses, plants have evolved a number of well-characterised biochemical, physiological and structural changes at the leaf and whole-plant levels that enable them to adjust to a particular set of light conditions (Boardman, 1977; Walters, 2005; Lusk et al., 2008; Niinemets, 2010). Many studies of the plant light response have aimed at unveiling the morphological and physiological mechanisms as well as the ecological implications of tolerance to extremes, such as tolerance to either sun or shade (Boardman, 1977). In these studies, although the plants may be constrained to different extents within their whole-plant allocation pattern, they tend to show universal plastic responses, such as increasing mass allocation to the shoots rather than to the roots when growing in the shade (Poorter et al., 2012). Irrespective, noticeably fewer studies have been conducted considering that the timing and duration of fluctuations of photosynthetically active radiation (PAR) can dramatically vary throughout plant canopies (Niinemets, 2007, 2010). In this context, the patterns of biomass accumulation and allocation in plants that are subjected to temporal variations in the PAR

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availability throughout the day have barely been explored (Ackerly, 1997).

The effects of the variable light environments are well characterised in the context of bursts of direct sunlight (i.e., sunflecks), in which the duration and frequency of light patches largely drive the carbon assimilation and growth (Way and Pearcy, 2012). However, very few studies (e.g., Wayne and Bazzaz, 1993; Watling et al., 1997) have compared plants grown under fluctuating light but receiving the same total daily PAR. Some evidence suggests that the whole plant carbon gain may be affected by the temporal scale of diurnal fluctuations in light environments, even when the total amount of PAR received is kept constant (Ackerly, 1997, and references therein), although this response may be species dependent (Watling et al., 1997). To the best of our knowledge, these few studies have been undertaken in the field of plant ecology and forest biology, and virtually nothing has been explored regarding the trends in the growth and physiological responses to temporal scales of diurnal variations in light availability in crop species.

Coffee is one of the most important commodities in the international agricultural trade. It evolved in the understory of the African forest and is traditionally considered to be a shade-demanding species. In early plantations, Arabica coffee (*Coffea arabica*) bushes were planted under taller shade trees to simulate their natural habitat. However, modern coffee cultivars can grow well and even produce greater yields in the sun than in the shade (DaMatta, 2004; DaMatta et al., 2010), which suggests that coffee plants should have sufficient plasticity to acclimate themselves to contrasting light environments (Matos et al., 2009; Cavatte et al., 2012). In any case, even in un-shaded plantations, the coffee plant may be subjected to pronounced temporal scales of diurnal variations in the PAR supply, which are frequently found in hilly zone plantations. Depending on the relative crop position on a hill, the plant may be mostly shaded during either the morning or afternoon (with terrain exposure facing west and east, respectively). We have empirically observed that, when shaded in the morning under field conditions, the growth (and production) of coffee plants may be depressed relative to plants that receive a more continuous diurnal light supply; we have noted an inverse relationship in plants grown under full sunlight in the morning and subjected to some degree of shade in the afternoon (personal observation). However, to the best of our knowledge, how the coffee plants adjust themselves, both structurally and physiologically, to cope with this type of temporal variation in the PAR supply to improve their fitness and hence biomass production have never been examined in this species.

We hypothesised that physiological performance, accumulation and biomass allocation patterns in coffee plants are dependent not only on the total amount of PAR received but also on the temporal scale of diurnal light availability. In this context, we further hypothesised that plants receiving greater amounts of PAR in the morning than in the afternoon, but receiving similar integrated daily photon flux, are able to accumulate more biomass, and these responses might be associated with increased carbon gains in combination with higher stomatal conductance in the morning when the PAR is non-limiting (Araújo et al., 2008; DaMatta et al., 2008; Batista et al., 2012). Finally, we also hypothesised that physiological (e.g., traits associated with photoprotection and maintenance of a positive carbon balance) rather than morphological (e.g., specific leaf area and leaf area ratio) adjustments are the major determinants for acclimations to temporal scale of diurnal light availability, as previously observed in coffee under fixed light supplies (Matos et al., 2009; Cavatte et al., 2012). To test these hypotheses, the biomass accumulation and allocation and the key photosynthetic traits of coffee plants were examined over a range of fixed or changing light supplies.

2. Materials and methods

2.1. Plant material, growth conditions and experimental design

The experiments were conducted in Viçosa (20°45′ S, 42°54′ W; 650 m in altitude) in southeastern Brazil. Uniform coffee seedlings (*C. arabica* L. cv. 'Red Catuaí IAC 44') were grown from seeds and transplanted after growing three leaf pairs (January 7, 2010) into 12 L pots containing a mixture of soil, sand and composted manure (4:1:1 v/v/v). After transplantation, the seedlings were randomly submitted to seven light treatments as follows: plants grown entirely under 100%, 40% or 10% sunlight (S-100, S-40 and S-10, respectively); plants grown every day at either 40% or 10% sunlight throughout the morning (from sunset to midday) and then submitted to full sunlight until sunrise (S-40/100 and S-10/100, respectively); and plants grown every day under full sunlight from sunrise to midday and then submitted to either 40% or 10% sunlight throughout the afternoon (S-100/40 and S-100/10, respectively). Every day, the shade shelter was removed or added at midday according to the treatment. All of these light treatment combinations were applied for 150 days. The shade shelters were provided by neutral density black nylon nettings. The light quality (blue/red and red/far red ratios) beneath the nettings as well as in the open (direct solar radiation) was checked in cloudless days at dawn, midday and dusk using a FieldSpec® spectroradiometer (ASD, Boulder, USA) following the recommendations of Smith (1982).

The plants were irrigated and fertilised as required, and no apparent restriction was observed in the root development at the end of the experiment. The pot positions were periodically randomised to minimise any variation within each light environment. The plants were distributed over a completely randomised design with 10 replicate plants per treatment, and the experimental plot consisted of one individual plant per pot. When the measurements were made on a single leaf (for photosynthetic parameters), the youngest, most fully expanded leaves from five individuals were used.

Throughout the experiment, the maximum and minimum average temperatures were 27.7 °C and 14.7 °C, respectively. The average air temperature was 21.4 ± 0.8 °C, and the relative humidity was 79.2%. The PAR was measured using LI-190SA quantum sensors (Li-Cor; Lincoln, NE, USA) that were positioned 0.5 m above the plant canopies. All sensors were installed at the experimental site and connected to an LI-1400 data logger (Li-Cor) that acquired data from the sensors every minute and stored them as 5-min averages. The day length corresponded approximately to 13.2 h at the beginning of the experiment and it was progressively shortened to approximately 10.8 h at the end of the study. The climate at the experimental site is classified as Cwa (mesothermal) by the Köppen system, with a rainy, warm season (October–March) followed by a dry, cool season (April–September).

2.2. Growth traits

At the end of the experiment, various morphological traits [heights, total leaf numbers per plant, numbers of plagiotropic branches and stem diameters (5 cm above ground)] were recorded. Total leaf areas were estimated by putting the maximum leaf widths and lengths into the equations described by Antunes et al. (2008). In addition, the plants were harvested and separated into orthotropic and plagiotropic branches, leaves and roots. The roots were washed thoroughly with tap water over a 0.5 mm screened sieve. The plant tissues were oven-dried at 70 °C for 72 h, after which the dry weights of the leaves, branches and roots were measured. Based on these data, the total biomasses, leaf mass fractions (LMF), orthotropic branch mass fractions (OMF), plagiotropic (lateral) branch mass fractions (PMF) and root mass fractions (RMF)