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Phenotypic plasticity in response to light in the coffee tree

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ABSTRACT

Phenotypic plasticity to light availability was examined at the leaf level in field-grown coffee trees (*Coffea arabica*). This species has been traditionally considered as shade-demanding, although it performs well without shade and even out-yields shaded coffee. Specifically, we focused our attention on the morpho-anatomical plasticity, the balance between light capture and excess light energy dissipation, as well as on physiological traits associated with carbon gain. A wide natural light gradient, i.e., a diurnal intercepted photon irradiance differing by a factor of 25 between the deepest shade leaves and the more exposed leaves in the canopy, was explored. Responses of most traits to light were non-linear, revealing the classic leaf sun vs. leaf shade dichotomy (e.g., compared with sun leaves, shade leaves had a lower stomatal density, a thinner palisade mesophyll, a higher specific leaf area, an improved light capture, a lower respiration rate, a lower light compensating point and a limited capacity for photoprotection). The light-saturated rates of net photosynthesis were higher in sunlit than in shade leaves, although sun leaves were not efficient enough to use the extra light supply. However, sun leaves showed well-developed photoprotection mechanisms in comparison to shade leaves, which proved sufficient for avoiding photoinhibition. Specifically, a higher non-photochemical quenching coefficient was found in parallel to increases in: (i) zeaxanthin pools, (ii) de-epoxidation state of the xanthophyll cycle, and (iii) activities of some antioxidant enzymes. Intracanopy plasticity depended on the suite of traits considered, and was high for some physiological traits associated with photoprotection and maintenance of a positive carbon balance under low light, but low for most morpho-anatomical features. Our data largely explain the successful cultivation of the coffee tree in both exposed and shade environments, although with a poor resource-use efficiency in high light.

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1. Introduction

Local photosynthetically active radiation (PAR) conditions to which individual leaves are exposed vary tremendously throughout the canopy of a tree. Although light is a key limiting resource for photosynthesis, both low and high PAR can limit plant performance (Lusk et al., 2008). Therefore, to efficiently utilize the PAR energy while at the same time avoiding photodamage to their foliage, plants often exhibit a remarkable capacity to adjust their morphology and physiology to a particular set of light conditions by acclimation or, more broadly, phenotypic plasticity, i.e., the capacity of a given genotype to render different phenotypes under contrasting environmental conditions (Valladares et al., 2007; Valladares and Niinemets, 2008). Although the link between plasticity and sun-shade tolerance is a contentious issue (cf. Valladares et al., 2000; Rozendaal et al., 2006; Markesteijn et al., 2007), it is often assumed that leaf traits showing a high plasticity in response to PAR are more important to plant function in different environments than traits that show little or no plasticity (Bongers and Popma, 1988). Generally, shade-tolerant species display a greater phenotypic plasticity in morphological variables than in physiological variables (Valladares et al., 2005).

At the leaf level, acclimation may be expressed via morpho-anatomical and physiological adjustments in response to changes in the light environment (Evans and Poorter, 2001; Lusk et al., 2008) so that plants differentiate *sun* and *shade* leaves (Murchie and Horton, 1997). Sun leaves, compared with their shade counterparts, are generally thicker with an enhanced quantity of palisade mesophyll and denser stomata, larger N concentration per leaf area, less chlorophyll (Chl) per unit leaf mass (Chl_{mass}) with impoverishment of Chl *b*, higher rates of dark respiration and light-saturated photosynthesis, increased photoprotective pigments, as well as decreased susceptibility to photoinhibition of photosynthesis (Walters, 2005; Niinemets, 2007). Nonetheless, whenever the absorbed light energy exceeds the capacity of leaves to use the trapped energy through photosynthesis or to dissipate it as heat, damage to photosystem II (PSII) may occur. Protection against excess energy may be achieved by down-regulation of photochem-

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ical efficiency by way of the xanthophyll cycle or by maintenance of the electron flux involving alternative pathways such as photorespiration and the Mehler-peroxidase reaction (Ort and Baker, 2002; Logan et al., 2006).

Phenotypic plasticity to light is a classic topic in plant ecology and evolution, and the number of papers dealing with this subject has increased steadily over the last few years (Valladares and Niinemets, 2008). Nonetheless, few efforts have been undertaken in field conditions to examine plasticity to light in tropical crop species, such as coffee. Coffee is an important commodity in the international agricultural trade. It evolved in African forest understorys, and is thus considered to be a shade-requiring species. In many situations, however, coffee grows well without shade and even out-yields shaded coffee (DaMatta, 2004). It could be assumed, therefore, that coffee plants, regardless of their low rates of net carbon assimilation [(A; typically in the range of 4–11 μmol m^{-2} s^{-1} with current atmospheric CO_2 concentration and saturating light (DaMatta et al., 2007)] should have sufficient plasticity to acclimate themselves to contrasting light environments. However, by comparing the outer foliage of the lower crown and canopy top leaves (lower crown leaves intercepted 50–65% less irradiance than canopy top leaves), we demonstrated that neither physiological variables directly involved with photosynthetic carbon gain nor those involved with light capture were adjusted to match the capacity of the photosynthetic machinery to the average PAR supply (Araujo et al., 2008). Nevertheless, the low physiological responsiveness of coffee leaves to light could be due not only to low phenotypic plasticity, but also to the possibility that the average light intercepted by the shade leaves was not sufficiently low to trigger further leaf responses. A re-examination of phenotypic plasticity of coffee leaves over a wide light gradient should thus be addressed in order to improve our knowledge of the mechanisms involved in the sun–shade tolerance of the coffee tree.

In this study, we evaluate differences in several morpho-anatomical and physiological traits of coffee leaves from contrasting light environments. Specifically, we focused our attention on the morpho-anatomical plasticity, the balance between light capture and excess light energy dissipation, and on physiological traits associated with carbon gain. Based on the successful cultivation of the coffee tree at full sunlight, our working hypothesis was centered on the following question: would the coffee leaves have a greater phenotypic plasticity in physiological than in morpho-anatomical variables in response to varying PAR?

2. Materials and methods

2.1. Plant materials and experimental design

The experiment was conducted under field conditions with coffee trees (*Coffea arabica* L. 'Catuaí Vermelho IAC 44′; Rubiaceae) of approximately 13 years of age growing as a hedgerow (east-west orientation) on a Cambic Podzol, in Viçosa (20°45'S, 42°15'W, 650 m a.s.l.), southeastern Brazil. The trees were cultivated in full sunlight and were planted at a spacing of 3.0 m × 1.0 m. Routine agricultural practices for commercial coffee bean production were used. No supplemental irrigation was provided. In September 2006, the coffee plantation was subjected to drastic pruning of the lateral branches. In October 2007 (rainy, growing season), 30 trees (about 2 m tall) were initially selected for uniformity and vigor. From these trees several recently, fully expanded leaves from the third or fourth pair from the apex of primary and/or secondary plagiotropic branches from the basal and mid canopy were tentatively selected. Selections of leaves of similar ages, performed on cloudless days, were based on the integrated intercepted PAR (averages from 5 days with hourly PAR measurements from 07h30 to 16h30—solar time) by leaves at their natural angle using a photometer/radiometer (Li-185, Li-Cor, Nebraska, USA). Specifically, four classes of leaves, considered here as experimental treatments, were chosen, comprising leaves intercepting (mean ± SD) 1.19 ± 0.22, 2.97 ± 0.55, 11.87 ± 3.12, and 29.90 ± 8.67 mol photons m^{-2} d^{-1}. These treatments will be hereafter referred to T_1, T_2, T_3, and T_4, respectively. Therefore, leaf responses were examined over a wide natural light gradient (i.e., the intercepted PAR that differed by a factor of 25 between T_1 and T_4 leaves). At least 24 leaves from different trees per treatment were selected; relative position (azimuthal and vertical orientations) of leaves was taken into account so that for each treatment they were as similar as possible. A total of 24 leaves per treatment were used: six (one leaf per tree) for morphological analyses, six for anatomical assessments, six for photosynthetic measurements, and six leaves for biochemical analyses.

2.2. Morpho-anatomical features

The area of each leaf was computed using an allometric model based on two leaf dimensions developed by Antunes et al. (2008). The leaf was subsequently oven-dried for 72 h at 70 °C and weighted. The specific leaf area (SLA; leaf blade area per unit leaf mass, m^{-2} kg^{-1}) was then estimated.

For anatomical measurements, leaves were collected and fixed in FAA_{50} for 48 h, followed by storage in 70% (v/v) aqueous ethanol. Samples of the mean region of each leaf blade were embedded in methacrylate (Historesin–Leica Microsystems Nussloch, Heidelberg, Germany) according to the manufacturer. Transverse sections (7 μm thicknesses) were obtained with a rotary microtome (model RM2155, Leica Microsystems Inc., Deerfield, USA), stained with toluidine blue at pH 4.0 and mounted in synthetic resin (Permount®). Anatomical data were quantified using an image analysis program (Image Pro-Plus, version 4.5, Media Cybernetics, Silver Spring, USA). Video images were acquired using a video camera attached to an Olympus Microscope (AX70TRF, Olympus Optical, Tokyo, Japan). The following anatomical data were then assessed: (i) total leaf thickness; (ii) palisade and spongy mesophyll thickness; (iii) upper and lower epidermis thickness; (iv) stomatal density (according to DaMatta et al., 1997); (v) air space, computed as a percent of the total mesophyll tissue cross-sectional area; and (vi) leaf tissue density, calculated as the product of the inverse of SLA and the inverse of total leaf thickness.

2.3. Photosynthetic measurements

The net carbon assimilation rate (A) was measured using a portable open-flow gas exchange system (LCPro+, Analytical Development Company, Hoddesdon, UK). Photosynthetic light-response curves (A/PAR) were produced by increasing PAR in 12 steps from 0 to 1600 μmol (photons) m^{-2} s^{-1} at 25 °C. Initially, leaf tissue was exposed to an external CO_2 concentration of 50 μmol CO_2 mol^{-1} for 3 min to allow stomatal aperture; subsequently A/PAR curves were obtained at 380 μmol CO_2 mol^{-1}. Dark respiration rates (R_d), apparent quantum yield (Φ_a), light compensating point (LCP), light saturating point (LSP) and light-saturated A (A_{PAR}) were determined from these curves. Non-linear regression techniques for estimating these parameters were followed from Ögren and Evans (1993).

Chlorophyll *a* fluorescence parameters were gauged using a fluorometer (FMS2, Hansatech, King's Lynn, Norfolk, UK). Leaf tissue was placed in standard Hansatech leaf clips and PAR response curves were then constructed using the scripting facility of the fluorometer. Following dark-adaptation for 30 min, the leaf tissue was illuminated with a weak modulated measuring beam to obtain the initial fluorescence (F_0). A saturating white light pulse of 6000 μmol m^{-2} s^{-1} was applied during 1 s to ensure maximum fluorescence emission (F_m). The leaf tissue was exposed

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