JUNIOR PASTOR PÉREZ MOLINA

IMPACTS OF DROUGHT ON COFFEE: INTEGRATING PHYSIOLOGICAL AND MORPHOLOGICAL PROCESSES FROM THE LEAF TO THE WHOLE-PLANT SCALE

Thesis submitted to the Plant Physiology Graduate Program of the Universidade Federal de Viçosa in partial fulfilment of the requirements for the degree of the Doctor Scientiae.

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DEDICATION

This thesis is dedicated to the brilliant researcher **Raquel Ghini**.
Her many works in science made her internationally recognized.
She was the bridge for my research achievements.

The scientific world regrets her loss, rests in peace **Raquel Ghini**.

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ABSTRACT

PÉREZ, Junior Pastor Molina, D.Sc., Universidade Federal de Viçosa, April, 2018. **Impacts of drought on coffee: integrating physiological and morphological processes from the leaf to the whole-plant scale.** Adviser: Fábio Murilo DaMatta.

The water deficit negatively impacts plant growth and development through morphophysiological alterations, either at the leaf level or at the whole plant level. This study focused on the dynamics of ecophysiological and canopy architecture traits of two coffee cultivars, cv. RUBI MG1192 (Rubi: drought sensitive) and cv. IAPAR59 (I59: drought tolerant). The trials were conducted over two years; three irrigation treatments were applied (irrigated and non-irrigated during the dry seasons, and irrigated during the second dry season only). Samplings and measurements were performed at six times (7-10 plants per treatment combination, totalling 211 plants). The following parameters were evaluated: relative growth rate, net primary productivity, leaf composition (C, N, and $\Delta^{13}C$), water-use efficiency, phenotypic plasticity, leaf water potential (Ψ_L), sap flow (SF), canopy conductance (g_C), total soil-to-leaf hydraulic conductance (g_L), branch setting (number and length), number of phytomers, leaf shedding and renewal, dynamics of leaf area and internode length; in addition, the patterns of light intercepted by the canopy was modelled. The cultivar which retained its leaves under severe drought (I59) proved to be more isohydric and more plastic for hydric functioning (SF, g_C, and g_L), demonstrating precocious adjustments to drought. In contrast, the leaf-shedding cultivar (Rubi) was more anisohydric and more plastic for late reactions to drought through, e.g. an increased root dry mass-to-leaf area ratio and leaf shedding with faster leaf renewal due to greater number of branches of second order. Despite marked differences in their hydric functioning, the two cultivars expressed similar vegetative growth, yield and recovery. Overall, drought had effects on all of the studied variables but no architectural trait appeared to be specifically responsive to water stress. Rubi displayed a greater proportion of higher order branches allowing a fast recovery of its leaf area from drought. This was associated with a high number of phytomers that in turn supported faster development of axillary buds (leaves and/or floral buds). The fitness of coffee plants submitted to climatic events depends on the adequacy of physiological and organo-morphogenetic features and, consequently, these aspects should be accounted for in breeding programs aimed at improving drought tolerance in coffee.

RESUMO

PÉREZ, Junior Pastor Molina, D.Sc., Universidade Federal de Viçosa, abril de 2018. **Impactos da seca em café: integrando processos fisiológicos e morfológicos, desde a folha à planta inteira.** Orientador: Fábio Murilo DaMatta.

O déficit hídrico impacta negativamente o crescimento e o desenvolvimento vegetal via alterações morfofisiológicas, desde o nível de folhas ao da planta inteira. Neste estudo, avaliaram-se a dinâmica de parâmetros ecofisiológicos e da arquitetura do dossel de duas cultivares (CV) de café, cv. RUBI MG1192 (Rubi: sensível à seca) e cv. IAPAR59 (I59: tolerante à seca). As avaliações foram feitas ao longo de dois anos, impondo-se três tratamentos de irrigação, IRR (irrigado e não irrigado durante as estações secas, e irrigado apenas durante a segunda estação seca). As amostragens foram feitas em seis épocas (7-10 plantas por cada combinação CVxIRR, perfazendo 211 plantas). Foram avaliados os seguintes parâmetros: taxa de crescimento relativo, produtividade primária líquida, composição foliar (C, N e Δ^{13}C), eficiência do uso da água, plasticidade fenotípica, potencial hídrico da folha (Ψ_L), fluxo de seiva (SF), condutância do dossel (g_C), condutância hidráulica total desde o solo à folha (g_L), número e comprimento de ramos, número de fitômeros, queda e renovação de folhas, dinâmica de área foliar e comprimento de entrenós; em adição, foi feita uma modelagem do padrão de interceptação de luz pelo dossel. A cultivar que manteve suas folhas sob seca severa (I59) provou-se mais isoídrica e mais plástica em termos de economia hídrica, fato associado a ajustes precoces sob seca (redução significativa de SF, g_C e g_L durante o período seco). Em contraste, a cultivar com queda de folhas (Rubi) mostrou-se mais anisoídrica e mais plástica, com reações mais tardias à seca, e.g., uma maior razão de massa seca de raiz/área foliar, e queda de folhas com renovação mais rápida devido ao maior número de ramos de segunda ordem. Apesar das diferenças marcantes no que respeita a economia hídrica, as duas cultivares foram similares em termos de crescimento vegetativo, rendimento e recuperação após o período seco. No geral, a seca afetou todas as variáveis estudadas; todavia, nenhuma característica da arquitetura da copa foi especificamente afetada pelo déficit hídrico. Rubi apresentou maior proporção de ramos de ordem superior, permitindo recuperação rápida de sua área foliar após a seca, devido ao fato de seu alto número de fitômeros permitir maior desenvolvimento de brotos axilares (folhas e/ou botões florais). O ajustamento das plantas de café submetidas a eventos climáticos depende da adequação de características fisiológicas e organo-morfogenéticas e, consequentemente, ambos os aspectos devem ser igualmente considerados em programas de melhoramento visando à tolerância à seca no cafeeiro.

GENERAL INTRODUCTION

Coffee, a widely marked worldwide commodity, is the source of income for approximately 80 developing countries in the tropics (Pay, 2009). Among more than 100 species of the Coffea genus, Coffea arabica L. (Arabica coffee) and Coffea canephora Pierre ex. A. Froehner (Robusta coffee) economically dominate the world coffee trade, and represent ca. 70% and 30% of the world's commercial production, respectively. Coffee crop involves some 500 million people to manage the product, from cultivation to final consumption (Rezende and Rosado, 2004), and livelihoods of about 25 million small producers globally depend on Arabica coffee (Pendergrast, 2010). Although coffee production is strongly affected by drought events, most of world's coffee has been cropped by smallholders in drought-prone regions where irrigation employment is an exception (DaMatta and Ramalho, 2006). Indeed, limited water supply is the major environmental stress affecting coffee production not only in Brazil but also in several other coffee growing countries (DaMatta, 2004). Selecting cultivars that could withstand severe drought spells with acceptable yields under drought conditions is therefore of utmost importance (DaMatta and Ramalho, 2006).

Coffee breeding programs have identified cultivars that present differential responses to water deficit (DaMatta, 2004). Physiological studies revealed that drought-tolerant cultivars are characterised by deep root systems (Pinheiro et al., 2004), improved tissue water status (DaMatta et al., 2003; Pinheiro et al., 2004) associated with maintenance of leaf area (DaMatta et al., 2003), adequate stomatal control of water use (Marraccini et al., 2011) and improved long-term water-use efficiency (WUE) as soil water becomes limiting (DaMatta and Ramalho, 2006). Under prolonged drought stress, reduced growth, reduced leaf area and altered assimilate partitioning among tree organs seems to be one of the causes responsible for decreased crop yields (DaMatta, 2003). In any case, during drought allocation shifts are often assumed to be accompanied by a reduction in growth rates and hence in net assimilation rate (NAR) and relative growth rate (RGR) (Cavatte et al., 2012a; Cavatte et al., 2012b; Dias et al., 2007). Notably, RGR is a prominent indicator of plant strategy with respect to productivity as related to environmental stresses (Shipley, 2002); also, NAR allows standardizing net primary productivity (NPP) treatments according to their leaf area (Charbonnier et al., 2017).

In terms of plants' strategies facing drought, there is a trade-off between water savings and carbon starvation (Choat et al., 2012). Isohydric cultivars regulate stomatal conductance (g_s) so that variations in water potential (Ψ) are minimum, thus avoiding xylem cavitation caused by excessive tension in the plant hydraulic system (McDowell et al., 2008; Negin and Moshelion, 2016; Roman et al., 2015). Nonetheless, a consequence of this strategy is that such plants close their stomata in response to even mild water stress (e.g., decrease in soil water potential, or increase in vapour pressure deficit, VPD), thereby reducing carbon uptake. In contrast, anisohydric cultivars allow their Ψ to decrease during drought by sustaining relatively high g_s (and thus C assimilation); this strategy leads to rapid declines in soil water availability, xylem cavitation, and leaf water supply which ultimately may affect a range of physiological processes, including photosynthetic capacity (Kursar et al., 2009; McDowell et al., 2008; Negin and Moshelion, 2016; Roman et al., 2015).

Phenotypic plasticity is defined as the ability of an individual to modify its phenotypic expression in response to changes in the environment (Valladares et al., 2006; West-Eberhard, 2003). Whenever changes in distribution caused by climate change are projected using correlated models of bioclimatic envelope (Hampe, 2004), these changes can be overestimated when plasticity is ignored (Assad et al., 2004; Thuiller et al., 2005). Some effort has been made to evaluate how plasticity contributes to drought tolerance in some cultivars, but most research has been restricted to short-term periods, without consecutive drought events (thus avoiding acclimation to occur), and under limited growth conditions (containers). To our knowledge, there is limited information of how phenotypic plasticity could contribute to drought tolerance in coffee cultivars in real field conditions and for various scales, from organ to the whole-plant level, including the belowground.

A comprehensive analysis of morphological traits from plants facing long-term droughts remains therefore poorly explored. Studies of morphological changes when plants are facing drought are commonly confined to some global variables such as plant height, leaf area per plant, number of branches or biomass (Dias et al., 2007; Matos et al., 2009) whereas the parameters of the plant structure are ignored. The emphasis is therefore put here on the growth parameters that are involved in the building of the plant structure, namely the growth process in terms of number of nodes and the ramification process. The 3D plant structure is a key piece to integrate and understand the relationships between the functions of different organs at the level of the entire plant (Dauzat et al., 2008; Fourcaud et al., 2008; Guo et al., 2011). This has become a major challenge in the last decade to model and simulate the architecture of plants within different climatic scenarios (Fourcaud et al., 2008; Guo et al., 2011; Matsunaga et al., 2016). However, using 3D structure of plants for simulating biophysical processes is only one aspect of functional-structural plant modelling (FSPM). Indeed, the concept of plant architecture goes beyond of the plant structure at a given time but deals with the dynamics of plants along their ontological and phenological stages (Barthélémy and Caraglio, 2007). Description of plant structure at a given stage does not give proper information for analysing the effects of drought events if the trajectory of plant development is not accounted for. Actually, one has to address the organogenetic (e.g. phyllochrone and branching) and morphogenetic (e.g. leaf expansion) responses to drought to really understand what are the effects of physiological stress at a given time.

The present study mostly targets in plasticity of the ecophysiological and canopy architecture traits of two commercial coffee (C. arabica L.) cultivars (cv. IAPAR59 and RUBI-MG1192, tolerant and sensitive to drought, respectively) when submitted to drought events and their capacity to recover from drought stress. To this aim, comprehensive ecophysiological and architectural descriptions of individuals of these cultivars were performed at six sampling dates. From this database I aimed **(i)** to compare growth, allocation patterns (i.e., to above- vs. below-ground compartments), yield and WUE; **(ii)** to elucidate cultivar differences in terms of hydric strategies (leaf Ψ, whole-plant transpiration, canopy and hydraulic conductance); **(iii)** to assess which groups of variables express high phenotypic plasticity under iso/aniso-hydric strategies; **(iv)** to explore the effect of seasons and drought events on organogenetic processes (phyllochrone, ramifications) as well as on morphogenetic processes (internode length and leaf area) in different branching order levels and positions in axis from analysis of plant architecture; and **(v)** to evaluate the interception of light by 3D mock-ups of observed plants as a first step towards linking physiological and architectural features. Finally, the strategies of the two cultivars to overcome temporary water deficits are compared and discussed.

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CHAPTER 1

Is anisohydry an asset for crop growth and yield under moderate drought? Not for Coffea arabica L.

RESEARCH PAPER

Is anisohydry an asset for crop growth and yield under moderate drought? Not for *Coffea arabica* L.

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Highlight

Despite marked differences in their hydric functioning under moderate drought, two coffee cultivars expressed similar vegetative growth and yield, suggesting that anisohydry is not necessarily an asset.

Abstract

It is often assumed that anisohydric crops perform better under moderate water stress. To elucidate relationships among growth, water-use strategies, plasticity and recovery after a moderate drought, we grew two Coffea arabica cultivars of contrasting drought tolerance in the field, for two years and under three irrigation treatments (irrigated vs non-irrigated during both dry seasons; irrigated during the second dry season only). We sampled whole coffee plants on six dates, comparing the cultivars' relative growth rate, net primary productivity, leaf composition (C, N, and $\Delta^{13}C$), water-use efficiency, phenotypic plasticity and hydric functioning (leaf water potential: Ψ_L; sap flow: SF; canopy conductance: g_C; and soil-to-leaf total hydraulic conductance: g_L). The cultivar known already to retain its leaves under severe droughts (I59) showed here more plasticity for early adjustments to drought (SF, g_C, and g_L), and was more isohydric. In contrast, the cultivar Rubi, known to shed leaves under severe drought was more anisohydric and more plastic for late reactions to drought through, e.g. an increased root dry mass-to-leaf area ratio. In spite of such marked differences in their hydric strategies, the two cultivars expressed similar vegetative growth, yield and recovery, suggesting that compensation mechanisms occur and that anisohydry is not necessarily an asset for crops under moderate drought.

Key words: canopy and hydraulic conductance / carbon-isotope discrimination / leaf water potential / sap flow / water-use efficiency.

Abbreviations

ADM: aboveground dry mass (g);
BA: basal area of the stem (cm^2);
BLR: basal area of trunk-to-leaf area ratio (m^2_{BA} m^{-2}_{TLA}), a proxy for hydraulic conductance;
C/N: carbon-to-nitrogen ratio in leaf;
CV: Coffee variety (I59 vs. Rubi);
ET_0: potential evapotranspiration (mm_{H2O} d^{-1});
FDM: fruit dry mass (g);
FLA: fruit dry mass-to-leaf area ratio (g_{FDM} m^{-2}_{TLA}), indicator of source-to-fruit sink ratio;
FMR: fruit-to-total dry mass ratio;
g_c: canopy conductance (m s^{-1});
g_L: soil-to-leaf total hydraulic conductance (kg_{H2O} $plant^{-1}$ h^{-1} MPa^{-1});
H: height (m);
I: irrigated;
I59: IAPAR59 coffee cultivar, non-leaf shedding under drought, and crossed with Robusta (C. arabica cv. Villa Sarchi x HT 832/2 Introgression of Canephora);
IRR: irrigation factor (I, NI or NI_I);
LAR: leaf area-to-total dry mass ratio (m^2_{TLA} kg^{-1}_{TDM});
LDM: leaf dry mass (g);
LMR: leaf-to-total dry mass ratio;
NAR: net assimilation rate (g_{TDM} m^{-2}_{TLA} d^{-1});
NI: non-irrigated;
NI_I: non-irrigated during the 1st dry season and irrigated during the 2nd dry season;
NPP: net primary productivity;
PAR: photosynthetically active incident radiation (MJ m^{-2} d^{-1});
PP: phenotypic plasticity;
PPI_m: phenotypic plasticity index based on maximum and minimum means (Valladares et al., 2000);
R: rainfall (mm_{H2O} d^{-1});
RBR: root dry mass-to-basal area ratio (g_{RDM} cm^{-2}_{BA}), proxy for the inverse of hydraulic conductance;

RDM: root dry mass (g);

RDPI: relative distance plasticity index (Valladares et al., 2006);

RGR: relative growth rate ($g_{TDM}\ g^{-1}_{TDM}\ d^{-1}$);

Rh: relative humidity of the air (%);

RLA: root dry mass-to-leaf area ratio ($g_{RDM}\ m^{-2}_{TLA}$);

RMR: root-to-total dry mass ratio;

Rubi: RUBI-MG1192 coffee cultivar, sensitive-drought, and 100% Arabica (C. arabica cv. Mundo Novo x C. arabica cv. Catuai);

S: sampling date (S1, S2, S3, S4, S5 and S6);

SDM: shoot dry mass (g);

SF: sap flow (kg_{H2O} plant^{-1} d^{-1});

SLA: specific leaf area ($m^2_{TLA}\ kg^{-1}_{LDM}$);

SMR: shoot-to-total dry mass;

Ta: air temperature (°C);

TDM: total dry mass (g);

TLA: total leaf area (m^2);

VPD: vapor pressure deficit of the air (hPa);

WUE: water-use efficiency ($\Delta g_{(SDM+RDM)}\ kg_{H2O}^{-1}$ plant^{-1}).

Symbols

$\Delta^{13}C$: carbon isotope discrimination (‰);

$\Delta\Psi$: leaf water potential difference between predawn and midday (MPa);

Ψ_L: leaf water potential (MPa);

Ψ_{md}: leaf midday water potential (MPa);

Ψ_{pd}: leaf predawn water potential (MPa).

Introduction

Hydric strategies of plants facing drought is a trade-offs between water savings (to preserve the integrity of the hydraulic system) and growth needs (Choat et al., 2012). The leaf water potential (Ψ_L) is the core of the iso/anisohydry conceptual framework and is assumed to be regulated both by transpiration and hydraulic conductance (Martínez-Vilalta and Garcia-Forner, 2017). Broadly, isohydric species adjust their stomata to keep their midday (daily minimum) water potential (Ψ_{MD}) stable under environmental changes, whereas anisohydric species show no threshold of their Ψ_{MD}, which tracks environmental fluctuations. The iso/anisohydry concept typically opposes plants that tend to reduce transpiration early during drought (water savers) and water spenders (Jones, 1980; Ludlow, 1989; Shantz, 1927; Turner, 1979). It should be seen rather like a gradient than a dichotomy, though.

The downside of the isohydric strategy is that plants may close their stomata in response to even mild water stress (e.g., decrease of soil Ψ, or increase in vapour pressure deficit, VPD), thereby reducing carbon (C) uptake and ultimately compromising crop yields. On the other end of the gradient, anisohydric cultivars are considered more drought-resistant, they allow Ψ to decrease during drought by sustaining relatively high g_s (and thus high C assimilation). Therefore, isohydric cultivars are often assumed to increase their water-use efficiency (WUE) under moderate water stress, whereas anisohydric ones express lower WUE associated with greater g_s and wasteful water consumption (Ainsworth and Rogers, 2007; Sade et al., 2012). Now considering prolonged or extreme drought stress, the isohydric strategy is often assumed to induce mortality through C starvation, while anisohydric plants may die from embolism (Kursar et al., 2009; McDowell et al., 2008; Negin and Moshelion, 2016; Roman et al., 2015). However, the iso/aniso-hydric strategies and their consequences on C assimilation and mortality remain largely a matter of debate (Garcia-Forner et al., 2017). Even its metrics are not fixed yet and there is a still an active debate on how to rank plants along this gradient, comparing: (i) the seasonal minimum midday leaf water potential (Ψ_{MD}, more negative, more anisohydry); (ii) the seasonal variability of Ψ_{MD}; (iii) empirical linear relationships between predawn leaf water potential (Ψ_{pd}) and Ψ_{MD} (Martínez-Vilalta et al., 2014), where intercept characterizes the maximum transpiration rate per unit of hydraulic transport capacity, and slope measures the relative sensitivity of the transpiration rate and plant hydraulic conductance to declining water availability; (iv) inspired by the former, but restricts the correlation to the dry portion of the relationship, discarding wet data where Ψ_{MD} fluctuates independently of Ψ_{pd} (according to light conditions mainly) and extremely dry data as well, allowing to compute an hydroscape area as a novel indicator (Meinzer et al., 2016); (iv) correlations between Ψ_{pd} and delta of leaf water potential ($\Delta\Psi = \Psi_{MD} - \Psi_{pd}$), either linearly (Garcia-Forner et al., 2015) or after log transformation of $\Delta\Psi$ (Meinzer et al., 2016). Indeed, the comparison results may depend largely upon the chosen indicator. New case-studies are required, both under moderate and extreme drought to disentangle the underlying processes affecting crop growth and yield according to their iso/aniso-hydric strategies. Therefore, we propose here to assess a large bunch of isohydric indicators, together with concurrent important criteria of vulnerability to drought, such as root development, transpiration during wet and dry periods, leaf area index dynamics, water-use efficiency and proxies of the hydraulic conductivity before concluding.

Coffee is one of the most heavily globally agricultural traded commodities. The world coffee trade is supported by two species, Coffea arabica L. (Arabica coffee) and C. canephora Pierre ex A. Froehner (Robusta coffee), which account for ca. 99% of coffee production worldwide. Coffee productivity is strongly affected by drought events, nevertheless the crop has been extensively cultivated in drought-prone regions where irrigation is an exception (DaMatta and Ramalho, 2006). Selection of cultivars that could cope both with moderate water deficit with acceptable yields and severe water deficits without mortality is therefore of paramount importance. As reviewed by DaMatta and Ramalho (2006), a major component of differential adaptation to drought among coffee genotypes seems to be behavioral, and may be governed by the rates of water use and/or efficiency of extraction of soil water. This characterizes a strategy of dehydration postponement, and could largely explain why isohydric cultivars show later leaf wilting and shedding than their drought-resistant counterparts (DaMatta and Ramalho, 2006). Here, we selected two contrasted coffee cultivars (I59 and Rubi), known respectively to keep their leaves or shed them under severe drought conditions. We assumed that such traits would translate into water functioning, iso/anisohydry strategies and crop performance under moderate drought.

Moderate, not extreme droughts prevail in several coffee producing regions. It is questioned here whether supposedly drought-resistant anisohydric coffee cultivars, that keep opening their stomata for longer, also express higher growth and yield under moderate drought, or not. This question is linked to the hypothetical correlation between stomatal opening, assimilation and growth, which is actually often disrupted due to respiration, allocation or reserve dynamics. Here in particular, we investigated allocation and relative growth rate (RGR) patterns, together with phenotypic plasticity (PP). Although above- and below-ground biomass, net primary productivity (NPP) and yield of coffee plants have been described extensively according to a shade gradient in a recent paper by Charbonnier et al. (2017), little is known about shifts in dry-matter partitioning during moderate droughts. Therefore, monitoring experiments are required. RGR is a prominent indicator of plant strategy with respect to productivity as related to environmental stress and disturbance regimes (Shipley, 2002), whereas net assimilation rate (NAR) enables to standardize NPP treatments according to leaf area (Charbonnier et al., 2017). A common assumption is that during droughts, allocation shifts are accompanied by reductions in NAR and RGR (Cavatte et al., 2012a; Cavatte et al., 2012b; Dias et al., 2007) and we searched how this would differentially affect iso- vs. aniso-hydric coffee cultivars. PP is defined as the ability of an individual to modify its phenotypic expression in response to changes in the environment (Valladares et al., 2006; West-Eberhard, 2003). Whenever changes in species distribution caused by climate change are projected using correlated models of bioclimatic envelope (Hampe, 2004), the reduction of suitable areas can be overestimated if plasticity is ignored (Assad et al., 2004; Thuiller et al., 2005). We questioned which families of traits express high PP under drought, according to iso/aniso-hydric strategies.

In the literature regarding plants facing drought, we see a nexus between at least three key paradigms: performance/yield, iso/aniso-hydric strategies and phenotypic plasticity (Franks et al., 2007; Klein, 2014; Kursar et al., 2009). How do such paradigms complete, corroborate or exclude each other? Can monitoring experiments in the field take advantage of cultivars' contrasting responses to drought to elucidate some links between those paradigms, at least specifically? Furthermore, in the case of coffee, several authors have described the large variability in genetic factors that affect plants' drought tolerance at the leaf scale, and under controlled conditions (Cavatte et al., 2012b; Dias et al., 2007; Lima et al., 2002; Praxedes et al., 2006), but rarely on the whole-plant scale (above- and below-ground), or under real long-term field conditions. No study performed to date documents if PP contributes to coffee plant's drought tolerance under plantation conditions and for various scales, from the organ to the whole-plant levels including the root system, to avoid biases from small-containers and provide enough time for acclimation. This would allow for example to examine if and to what extent there would be trade-offs between productivity and water use upon dry spells. Furthermore, most studies concerning drought effects on coffee have been performed during one drought spell only, without recovery, and nothing is known about differential recovery of iso/anisohydric coffee plants. Here, we compared two coffee cultivars of contrasting drought tolerance, during two years under field conditions, with or without irrigation during the dry season and adding a recovery treatment (irrigation during the second year only). Specifically, we aimed (i) to compare growth, allocation patterns (i.e., to above- vs. below-ground compartments), yield and WUE in coffee cultivars contrasting for leaf shedding after drought in the field; (ii) to elucidate their hydric strategies (leaf Ψ, whole-plant transpiration, canopy and hydraulic conductance); and (iii) to assess which groups of variables express high PP under iso/aniso-hydric strategies.

Materials and Methods

Site and microclimate

The experiment was conducted from January 2008 to March 2010 at Embrapa Cerrados (15°35'S, 45°43'W), located 30 km from Brasilia, Central Brazil. Rainfall, air temperature, relative humidity, and photosynthetically active radiation (PAR) were recorded every 30 min by a weather station (Davis Instruments Ltd., Hayward, USA) near the experimental plot. The site is characterized by a wet season (from October to April) during which more than 90 % of annual precipitation (800-2000 mm) falls and by a dry season (from May to September), June and July being the driest months. The average annual minimum and maximum temperatures are 18 and 28 °C, respectively (Ratter et al., 1997). During the experiment, the total annual precipitation and potential evapotranspiration (ET_0: method in Allen et al. (1998)) were respectively 1844 mm and 1774 mm in 2008, and 2208 mm and 1643 mm in 2009 (Fig. 1A, B). We observed that between rains, VPD and ET_0 increased with each passing day, reaching a maximum VPD of 25 hPa and a maximum ET_0 of 8 mm_{H2O} d^{-1} (Fig. 1B).

Plant material, experimental design, and plant sampling

It should be stressed first that Arabica coffee comes from elevated and cool plateaus of eastern Africa, while Robusta is much more exposed to heat and drought in lowlands of central Africa and developed specific adaptations to drought and higher yield in most progenies. We compared two cultivars of Coffea arabica: CV. IAPAR59 (hereafter referred to as I59, F4 generation coming from a cross between C. arabica cv. Villa Sarchi x C. arabica Timor Hybrid (TH) CIFC 832/2), and CV. RUBI-MG1192 (hereafter referred as Rubi, coming from a cross between C. arabica cv. Mundo Novo x C. arabica cv. Catuai), that did not present recent introgression with Robusta genomic DNA (Carvalho et al., 2008). During prolonged and severe droughts, I59 is actually much better able to maintain its leaf area (Fig. S1A) than Rubi (Fig. S1B), as has been observed in preliminary trials in Central Brazil (Marraccini et al., 2011).

In December 2007, five-month-old seedlings of both cultivars were planted (3.0 x 0.7 m spaced) in the experimental plot under full-sunlight conditions. This plot measured approximately 0.4 ha (21 m x 155 m) with SE/NW row direction, with 17 subplots, each containing 78 plants (i.e. 39 plants for each genotype), distributed on three rows, with 13 plants per row (Fig. 1C). At planting, the soil was fertilized and limed according to routine agronomic practices for the coffee crop in Brazil. Weeds were manually controlled.

Irrigation was supplied by sprinklers (1.5 m high), monthly during the wet season and weekly during the dry season to maintain the soil moisture close to field capacity, as monitored using PR2 profile probes (Delta-T Devices Ltd., Burwell, UK). We had three irrigation treatments (IRR) (Fig. 1C): (i) irrigated during both dry seasons 2008 and 2009 (I); (ii) non-irrigated during dry seasons (NI); (iii) non-irrigated during the first dry season (2008) but irrigated during the second dry season (2009) (NI_I). This latter treatment was applied to examine plant recovery after the first dry season.

We harvested 5-10 whole coffee plants per CV for each IRR treatment at six sampling dates (S1 to S6; S1, S3, S4 and S6 represent samplings after the rainy seasons; S2 and S5 represent samplings after the dry seasons, see Fig. 1D). At S1, there was no irrigation difference irrespective of treatments and we just compared the two CV. The NI_I treatment was established only after 352 days after planting (DAP). We assumed that NI_I was the same as NI during the first year; hence, plants from NI_I were sampled only from S4 onward. All of the leaf samplings and measurements were done using fully expanded leaves from plagiotropic branches in the upper third of the plant canopy.

Growth and allometric traits

Each sampled plant's height (H) and basal area of the stem at soil level (BA) were measured, after which the plants were oven-dried for one week at 80°C. The dried plants, and each compartment thereof, were then weighed to determine each plant's leaf dry mass (LDM); shoot dry mass (SDM); root dry mass (RDM); fruit dry mass (FDM); aboveground vegetative dry mass (AVM); and total dry mass (TDM). Roots from each of those plants were sampled by excavating layers of soil from 70 cm x 70 cm squares centered on the plants' stems (Fig. S2). For S1 and S2, roots were dug down to 0.5 m deep only (roots confined to this soil depth). For S3 to S6, roots were dug down to 1 m deep, and two additional lateral sampling volumes were excavated between the planting lines (L4 and L5 = 0-20 cm, Fig. S2). Indeed, 90% of the roots were distributed from L1 to L3, as assessed in a preliminary test. Roots were washed thoroughly (1.0 mm screen sieve).

Total leaf area per plant (TLA) was obtained by scanning every leaf with a leaf-area meter (model AAC 400, Hayashi Denkoh, Tokyo, Japan). Specific leaf area (SLA) was computed as the ratio of TLA to LDM, at the whole-plant scale. We computed the DM partitioning as: leaf mass ratio (LMR: LDM/TDM); shoot mass ratio (SMR: SDM/TDM); root mass ratio (RMR: RDM/TDM); fruit mass ratio (FMR: FDM/TDM); and leaf area ratio (LAR: TLA/TDM). We also computed some candidate proxies for hydraulic conductance, in order to evaluate whether they can be used reliably where hydraulic-conductance data are not available. Those candidate proxies were: the ratios RDM-to-TLA (RLA); BA-to-TLA (BLR); and RDM-to-BA (RBR). Additionally, a source-to-fruit sink ratio (FLA: FDM/TLA) was calculated by a method similar to those used on coffee in previous reports (Charbonnier et al., 2017; Vaast et al., 2006). Finally, relative growth rate (RGR) and net assimilation rate (NAR) were calculated, based on total vegetative DM, following Hunt et al. (2002).

Leaf water potential

Throughout the two dry seasons, leaf water potential (Ψ_L) was measured weekly during predawn hours (Ψ_{pd}) (04:00 to 06:00 h) and at midday (Ψ_{md}) (12:00-13:00 h) using a Scholander-type pressure chamber (Model 1000, PMS Instruments, Albany, NY, USA). Measurements were conducted from 3 to 9 plants for each CV*IRR combination. Data from three leaves per plant were averaged.

Sap flow, canopy and hydraulic conductances

Sap flow (SF) is the product of sap-flux density (dF) and sapwood area (SA). We calculated SF values (kg_{H2O} plant^{-1} h^{-1}) as described in Roupsard et al. (2006) and Battie-Laclau et al. (2016), using data collected from pairs of home-built thermal dissipative probes (TDP) (Granier, 1987). The TDPs were 1 cm long and were inserted into the sapwood radially, about 20 cm above the soil. To derive dFs from the TDP data, we used the following empirical relationship, which Rapidel and Roupsard (2009) calibrated on potted coffee plants, using the gravimetric method as a reference: $dF=\alpha \cdot K^{\beta}=17.64 \cdot [(\Delta T_M-\Delta T_U)/\Delta T_U]^{1.231}$, where dF is sap flux density (l dm^{-2} h^{-1}); α and β are empirical coefficients; K is the sap flow index; and ΔT_M and

ΔT_U are the temperature differences between the two probes (°C), at minimum and current sap flow, respectively. We measured SA on the cross section of the heated probe at harvest, corrected for kinetics of diameter growth during the sap flow experiment from the S1 to S6 for each CV*IRR. SF was calculated only for treatments I and NI, on four plants from each combination of treatment and cultivar. We verified that natural thermal gradients could be neglected. Due to lightning, TDP data for the NI treatment during the time near the end of the 2009 dry season was lost. At the daily time step, we assumed that SF was equal to transpiration (Cruiziat, 1978; Schulze et al., 1985).

The canopy conductance (g_c) was evaluated daily from SF and climatic data using the simplified formula proposed by Pérez-Priego et al. (2010), assuming similar net radiation between treatments.

We computed soil-to-leaf total hydraulic conductance (g_L) as the ratio of SF to $\Delta\Psi$ ($\Delta\Psi = \Psi_{pd} - \Psi_{md}$), according to Roupsard et al. (1999).

Water-use efficiency and carbon-isotope discrimination

WUE was estimated at the whole-plant level between S4 and S5 (i.e., during the second dry season) as the ratio of NPP to SF. We omitted LDM values from the computation NPP here to avoid uncertainty due to litterfall. Given that NPP was measured on different plants than SF, we used the average WUE per CV or per IRR only to correlate with $\Delta^{13}C$ and did not perform other statistics on WUE. In addition, as we missed SF data by the end of the dry season for NI, we assume that trends (slopes of linear regression SF vs. time) remained constant until the end of the period.

The carbon isotope discrimination ($\Delta^{13}C$) was measured according to Farquhar and Richards (1984), where the carbon isotope composition in the air (δ_{air}) was estimated from maize plants grown within the experimental plot and harvested at each sampling date following Marino and McElroy (1991). δ_{air} remained rather constant during our experiment (-8.54 ‰ ± 0.33 SE, n=18), close to typical air values (-8.00 ‰, Farquhar et al. (1989)).

Five harvested plants from each CV*IRR*S combination (Fig. 1D) were analysed to determine their values of leaf $\Delta^{13}C$; leaf carbon and nitrogen contents (C and N); and C/N ratios. $^{13}C/^{12}C$ ratios were determined by mass spectrometry (Thermo Delta Plus, Finnigan MAT, Bremen, Germany coupled to a Carlo Erba NC2500 elemental analyzer (CE Instruments, Milan, Italy)) in the CENA-Brazil.

Phenotypic plasticity (PP) indices

As indicators of the coffee cultivars' phenotypic responses to drought, we calculated and contrasted PP indices for irrigation treatments I and NI. For the variables LDM, RDM, SDM, TDM, TLA, SLA, RLA, and BLR, we used the relative distance plasticity index (RDPI, obtained according to Valladares et al. (2006)). We could not use that index for values of hydric traits (SF, g_C, g_L, WUE, Ψ_{pd}, and Ψ_{md}) because those values were daily averages of measurements made over the course of each dry season. Instead, we used the PP index based upon maximum and minimum means (PPI_m, obtained according to Valladares et al. (2000)). Values of both indices range from 0 (no plasticity) to 1 (maximal plasticity). PPI_m values for SF, g_C, g_L, and WUE were calculated for the 2009 dry season, using daily average values from June to August 2009. PPI_m for Ψ_{pd} and Ψ_{md} were computed as the average between values from the first (2008) and second (2009) dry seasons.

Statistical analysis

Data on DM per compartment; DM partitioning; hydraulic conductance proxies; FLA; and for leaves' compositions and carbon-isotope discriminations were evaluated by three-way ANOVA for the following factors: CV (I59 vs. Rubi), IRR (I vs. NI_I and NI), and sampling date (S1 to S6), with a posteriori comparison between means with Tukey's HSD test ($\alpha= 0.05$). Ψ_{pd} and Ψ_{md} were evaluated using a two-way ANOVA for factors CV and IRR. Due to non-normal distribution of Ψ_L of differences between Rubi and I59 for the Ψ_{pd} and Ψ_{md}, we performed bootstrap effect sizes to find confidence intervals mean with 2000 interactions (package "*bootES*" into R: Gerlanc and Kirby (2015); more details in Kirby and Gerlanc (2013)). The relationship between mean values of WUE and $\Delta^{13}C$, for all CV*IRR combinations, was analysed with linear regression ($\alpha= 0.05$). Time-sequences of SF, g_C, and g_L for each CV*IRR combination were separated into three seasons (different rain regimes) in 2009 (specifically, March to May=wet; June to August=dry; September to October=wet), then evaluated with linear regressions and compared through ANCOVA. RGR and NAR differences were assessed via two-way ANOVA for each time interval ([S1 to S2], …, [S5 to S6]) with factors CV and IRR. Differences between the cultivars' RDPIs for each sampling date were analysed using the Tukey's HSD test ($\alpha= 0.05$). All statistical analyses were performed with R programming language, version 3.4.0 (RCoreTeam, 2017).

Results

Growth partitioning, and leaf composition

Irrespective of cultivar by irrigation (CV*IRR) treatments, H (Fig. 2A), RDM (Fig. 2E), ADM (Fig. 2G), SDM (Table S1), and BA (Table S1) increased rather steadily from S1 to S6. Regarding TLA (Fig. 2C), cultivar I59 irrigated (I59*I) remained steady during the dry season from S4 to S5 but decreased dramatically for cultivar Rubi irrigated (Rubi*I). LDM (Fig. 2D) increased for I59*I during the dry season (S4 to S5), but Rubi*I showed no significant changes, indicating SLA adjustments (Fig. 2B). Overall, differences between cultivars for a given irrigation treatment remained relatively small considered at S6 (end of the experiment): I59 was similar to Rubi for BA, LDM, ADM and TDM (Table S1). However, I59 outperformed Rubi for yield (Fig. 2F), SLA and TLA whatever the irrigation treatment, whereas Rubi was superior to I59 only for RDM (Fig. 2E) and only for I (Table S1).

In absence of irrigation (NI), drought affected growth strongly in most cases (down to a 50% reduction at S6 in TDM for instance; Fig. 2H). For all NI plants, TLA decreased significantly between S4 and S5 (Fig. 2C), but even more drastically in Rubi. Overall, we observed a significant seasonal effect upon SLA, which increased during the two wet seasons (between S3 and S4, and between S5 and S6), and decreased during the dry seasons (S1 to S2, and S4 to S5).

Results for the recovery treatment (NI_I) confirmed that irrigation during the second dry season made possible an efficient but uncomplete recovery, and NI_I plants ended-up ca. half-way between I and NI at S6 (Fig. 2). The only interaction found between CV and IRR was for H, SDM, FMR, RLA, FLA, C, N, and C/N (Table S1).

We stress that during drought, Rubi increased its allocation to roots, to the detriment of leaves (Fig. 3): RLA increased significantly during both periods of drought for Rubi*NI (ca. 38% more than for I plants), whereas the increases for I59*NI remained not significant.

Trends for RGR and NAR were similar and decreased throughout the experiment for all CV*IRR combinations (Fig. 4). They dropped during the second drought (S4 to S5), with some recovery during the following wet season (S5 to S6). Significant differences among the CV*IRR combinations were found only between dates S2 and S3, with higher RGR and NAR values in the I treatment. Such differences vanished afterwards.

Effects of CV and IRR upon DM partitioning were not large either, with the exception of LMR and FMR (Table S1, Fig. 5A). Under treatments I and NI_I, both cultivars showed similar trends for DM partitioning among leaves, shoots and roots: hence, DM results for NI_I are not presented here. Effects of treatment NI (Fig. 5B) were quite different from those of I: Rubi's decreases in LMR were steeper than I59's during both dry seasons (S1 to S2, and S4 to S5). We found no cultivar effects upon RMR even during drought, where both cultivars' RMRs tended to increase similarly. DM partitioning at S6 was very similar for both cultivars, regardless of IRR, with the notable exception of fruit yield (FMR), being generally higher for I59.

We did not find significant increases between S1 and S6 for leaf C (from 47% to 49%, Fig. S3A), nor were changes in leaf N, which averaged 3.5% (Fig. S3C). Δ^{13}C were significantly different only between IRR at the end of the first dry season in S3, where I expressed higher Δ^{13}C values than NI (Fig. S3B).

Leaf water potential

Ψ_{pd} under treatment I remained close to -0.22 MPa, even during the dry seasons (Fig. 6A). NI_I's Ψ_{pd} values were similar to NI's during the first year, and to treatment I's during the second year (data not shown). However, Rubi's Ψ_{pd} dropped under NI (-1.88 MPa), especially during 2008-the drier of the two years-while I59's Ψ_{pd} decreased moderately (-0.79 MPa). For both cultivars, Ψ_{md} remained close to -1.1 MPa under treatment I, even during the dry seasons (Fig. 6B). Under NI, Ψ_{md} decreased to -2.4 MP during the dry season; although Rubi's Ψ_{md} was lower than I59's, the difference was not statistically significant. Note that after treatment NI's unirrigated 2008 dry season, it took a long time during succeeding wet seasons for both cultivars' Ψ_{pd} and Ψ_{md} values to become comparable to treatment I's. On average, the difference between the cultivars' Ψ_{pd} values under NI was -0.22 MPa during the first dry season (with one marked difference at one date only), and -0.32 MPa during the second dry season (Table 1).

Sap flow, canopy and hydraulic conductances

For all irrigation treatments, I59's SF (Fig. 7A, B) was almost constant throughout the first rainy season (March to May 2008) at approximately 1.8 kg_{H2O} $plant^{-1}$ day^{-1}. During the same period, Rubi had increased to 3-5 kg_{H2O} by the season's end. By the end of the dry season (June to August 2009), I59*I's SF had increased to 7 kg_{H2O} $plant^{-1}$ d^{-1}, and Rubi*I's to 8 kg_{H2O} $plant^{-1}$ d^{-1}. However, I59*NI's SF decreased significantly during drought, whereas Rubi*NI's remained nearly steady (Fig. 7A, B; Table 2). During the next rainy season (September to October 2009), SF increased significantly for all CV*IRR combinations with the exception of Rubi*I. At the end of the experiment, I59 and Rubi expressed similar SF.

Over the course of the first rainy season, g_C (Fig. 7C, D) averaged on ca. 0.25 m s^{-1}. Contrasting patterns for g_C were found according to treatments: g_C diminished in I59, increased in Rubi*I and remained unchanged in Rubi*NI (Table 2). During the dry season, g_C decreased to a remarkably greater extent in I59*NI than in Rubi*NI, which is in good agreement with the steeper reduction in SF. During the second rainy season, NI plants from both cultivars displayed a rapid g_C recovery to values comparable to those of their I counterparts.

g_L (Fig. 7E, F) remained constant in I59 independently of irrigation during the first rainy season (around 0.18 kg_{H2O} $plant^{-1}$ MPa^{-1} h^{-1}), but increased significantly for Rubi (0.5 and 0.4 kg_{H2O} $plant^{-1}$ h^{-1} MPa^{-1} at the end of May 2009 for I and NI, respectively) (Table 2). During the 2008 dry season, g_L under I treatment increased consistently in both cultivars, reaching approximate values of 0.5 (I59) and 0.8 (Rubi) kg_{H2O} $plant^{-1}$ MPa^{-1} h^{-1} at the end of August 2009; in NI plants, in contrast, g_L decreased over time in I59, while remaining invariant in Rubi. Finally, during the second rainy season, I plants from both cultivars displayed a clear reduction in g_L, whereas g_L remained unchanged in their NI counterparts. At the end, plants from NI and I treatments reached similar g_L values, though slightly higher in Rubi.

Relationship between water-use efficiency and carbon isotope discrimination

WUE integrated at the plant scale (Fig. 8) was on average about two times higher in I59 (0.6 $g_{DM}\ kg_{H2O}^{-1}$) than in Rubi (0.3 $g_{DM}\ kg_{H2O}^{-1}$), and 1.5 times higher in Rubi*NI than in Rubi*I. The apparent $\Delta^{13}C$ reduction in NI as compared to I was not significant at S5 (Fig. 8). It is stressed here that leaf $\Delta^{13}C$ did not correlate significantly with whole-plant WUE (Fig. 8): unexpectedly, WUE remained approximately 9% lower in I59*NI than in I59*I, whereas Rubi expressed an increase in WUE during drought.

Phenotypic plasticity for drought

Regarding growth and allocation variables, plasticity indexes and ranking between CV fluctuated strongly according to the season. For instance, RDPI for LDM, RDM, SDM, TDM, TLA, and SLA, and proxies for hydraulic conductance as RLA and BLR, was less than 0.15 at the first drought (S2), with no significant cultivar differences (Fig. 9). Subsequently, in sampling S3, I59 showed the highest RDPI for LDM, TLA, RDM, SDM, TDM, and BLR. That result was reversed in S4, where Rubi proved to have the highest RDPI for all of the tested variables. At the end of the second drought (S5), Rubi's RDPIs were still higher than I59's for LDM, TLA, SLA, RLA, and BLR. In S6, Rubi's RDPIs for RDM and SDM were higher than I59's.

The differences appeared much more clearly regarding hydric traits: plasticity indices (PPI_m) were higher in I59 than in Rubi for SF, g_C, and g_L, whereas the contrary was observed for Ψ_{pd}, Ψ_{md}, and WUE (Table 3).

Discussion

To the best of our knowledge, how the coffee plants adjust themselves (morphologically and physiologically) to cope with prolonged, fluctuating drought stress under plantation conditions had never been examined in coffee. Despite little differences expressed for growth and allocation, the coffee cultivars studied here did demonstrate contrasted hydric strategies. Are such results case-specific or do they have a more general value? A broad comparison of our results with other investigations on coffee cultivars facing drought is shown in Table S2, while particular aspects are discussed below.

Main cultivar differences for growth, allocation and yield

When irrigated during the dry seasons, we overall encountered little cultivar differences for growth and partitioning of DM. Major cultivar differences were fundamentally restricted to the higher I59's yield as revealed by FDM, which was accompanied by a higher TLA. Rubi, which shed leaves under prolonged drought, consistently demonstrated a higher fluctuation of TLA under moderate drought, decreasing by approximately 23% after the second dry season, possibly as a consequence of VPD. A higher TLA (up to 46% larger) in irrigated, non-leaf shedding coffee cultivars is commonly reported in the literature (Table S2). Regarding fruits, I59's yield was 24% greater at S6 than Rubi's, likely a consequence of I59's introgression with highly productive Robusta coffee. At the same time, I59's RDM remained constant, indicating a clear priority to reproductive growth in I59, while Rubi's RDM continued to increase. Such competition between fruit and vegetative growth has been reported by Vaast et al. (2005), who found that reduced fruit load in the coffee branches (non-ring-barked) provoked an increase in branch growth for three months.

Under drought, we demonstrated that Rubi had a greater canopy conductance, with presumably greater carbon assimilation. We also noted the classic shifts in biomass allocation in plants grown under limited water supply, from leaves and stems to roots and fruits, as has extensively been reported elsewhere (e.g., Fernández and Reynolds (2000); Ekta and Singh (2004); Nagakura et al. (2004); Otieno et al. (2005)). Indeed we showed that during the second drought, I59's RMR increased by 8% as its LMR decreased by 10%, and that Rubi's RMR increased by 10% as its LMR decreased by 30%. We can infer that under dry conditions, both cultivars reduced their TLA to probably prevent further water loss, while also increasing their water-uptake capacity (as reflected by higher RDMs). Plants often invest more resources in the root system at the expense of leaves during droughts (Pinheiro et al., 2005; Poorter and Nagel, 2000; Silva et al., 2013). Our RLA results (RDM-to-TLA ratios) are consistent with that pattern: Rubi increased its RLA, as a late reaction to drought, in contrast to I59, which adjusted its g_C first. A comparable result was reported by Dias et al. (2007), who found higher RLA in leaf-shedding than in non-leaf-shedding coffee cultivars (Table S2). Moreover, in our study, the changes of SMR in response to drought were either undetectably small or negligible for all CV*IRR combinations, thus suggesting that allocation to stems remained rather conservative. Indeed, Charbonnier et al. (2017) showed that allocation to stems was conserved whatever the fruit demand, which the plant met by reducing allocation to leaves, essentially. Last, we found that both cultivars had similar NAR and RGR values, both decreasing during the second drought. This result is consistent with other studies of coffee plants under drought conditions, which show that allocation shifts are often accompanied by reductions in RGR and NAR (Cavatte et al., 2012a; Cavatte et al., 2012b; Dias et al., 2007).

To our knowledge, previous studies have not attempted a detailed study of the mechanisms by which two coffee cultivars of contrasting drought tolerance recover after a drought event in the field. Actually, we observed little difference between our cultivars for their recovery capacities, in spite of their contrasting water-use strategies under drought. NI_I's effects upon both cultivars observed at the end of the experiment were intermediate between those of treatments I and NI.

Main cultivar differences for water relations and drought tolerance

Despite displaying only moderate differences in growth and allocations, the cultivars did demonstrate contrasted hydric strategies. Our ranges of $\Psi_{L,}$ SF, g_C, and g_L values were comparable to those reported for other coffee cultivars (Table S2). Rubi's Ψ_{pd} decreased gradually during drought, as expected for anisohydric behaviour, reaching a minimum value that can be considered as moderate as compared with coffee plants submitted to a severe drought stress (Pinheiro et al., 2005; Praxedes et al., 2006; Silva et al., 2013). During the same period, I59's Ψ_{pd} decreased only slightly. In addition, we found that the constant difference between Ψ_{pd} and Ψ_{md} in the time-course for I59 (data not shown) corresponded to an isohydrodynamic behaviour (Franks et al., 2007). Accordingly, I59's clear decrease in transpiration in the absence of irrigation, as indicated by values of SF, g_C, and g_L, reflected an earlier and much more efficient stomatal regulation than for Rubi. As a result, I59 had a higher WUE integrated at the whole plant scale. When cumulated over time, Rubi transpired more than I59 during both wet (6.4% more) and dry seasons (27% more), which is again typical of anisohydry. Finally, I59's g_C decreased much more quickly than Rubi's, a result that explains most of the I59's reduction in sap flow. Indeed, I59's TLA was often larger than Rubi's regardless of the season. Reduction in leaf area during drought (as was the case for Rubi) may increase the canopy's boundary-layer conductance to some degree (Jarvis and McNaughton, 1986), thus compensate somehow for the reduction of transpiration.

It is generally considered that isohydric genotypes, such as I59 here, regulate their Ψ_L and transpiration during drought, resulting in decreased C gains, whereas anisohydric genotypes like Rubi sustain their transpiration (greater g_s), thereby sustaining growth under moderate stress (Meinzer et al., 2016; Negin and Moshelion, 2016; Roman et al., 2015). However, our research does not support such a widespread idea, given that I59 and Rubi maintained similar rates of biomass gain during both drought periods. In support to our results, Garcia-Forner et al. (2017) have recently provided some evidence that a Mediterranean tree species that is relatively more isohydric and more prone to mortality than its counterpart, expressed similar seasonal patterns for gas exchanges, reserves dynamics and embolism under severe drought. Here for coffee, neither RGR nor recovery could explain how the isohydric cultivar could grow similarly to its counterpart when submitted to moderate drought stress.

We here propose three alternative interpretations for explaining similar growth despite contrasting iso/aniso-hydric strategies: i) the increased water use efficiency in I59 compensated for the reduction of its stomatal conductance, allowing to maintain high levels of assimilation: indeed Charbonnier et al. (2017) already demonstrated that an increase in LUE could compensate for the reduction of light availability under shade; it would worth studying how this applies, or not, to WUE under drought; ii) soil water availability decreased rapidly for Rubi, leading to xylem cavitation, thereby decreasing its water supply (Kursar et al., 2009; McDowell et al., 2008; Negin and Moshelion, 2016; Roman et al., 2015), and, ultimately, its photosynthetic capacity and growth; and iii) I59 sustained growth during drought through greater depletion of reserves. Further experimentation is needed to document the former hypothesis, for instance providing hydraulic curves (to test the vulnerability of the cultivars to cavitation) and dynamics of reserves.

Does phenotypic plasticity contribute to drought tolerance?

We here highlight some contrasting ecophysiological drivers for drought resistance in Arabica coffee, as based upon the PP indices calculated in this study: the non-leaf shedding cultivar I59 displayed an isohydric behaviour with greater plasticity of hydraulic traits (SF, g_C, and g_L) which were adjusted early during drought and result in lower consumption of soil water, ultimately leading to a low drop in Ψ_L. In contrast, the drought-sensitive cultivar Rubi was revealed anisohydric and more plastic especially for morphological traits, as denoted by its late reactions to drought associated with shifts in biomass allocation to roots together with leaf shedding. Rubi displayed higher water consumption during drought, higher plasticity in Ψ_L, DM adjustments (LDM, TLA), and in proxies for hydraulic conductance such as RLA and BLR. We suggest that isohydry could be more related to the physiological plasticity of traits linked to early water conservation whereas anisohydry could be more related to the morphological plasticity. We therefore conclude that plasticity was the key for understanding the cultivars' strategies against a moderate water stress, provided that early physiological adjustments are distinguished from late morphological ones. Nevertheless, we consider that changes in biomass or yield are fundamental indicators of a plant's ability to respond to and take advantage of varying resource (water) availability (Dawson et al., 2012). As there was no major change in growth rates here despite contrasting strategies for water use, we assume that such strategies overall compensated with time. Further experimentation is needed to search for the drought threshold (intensity or duration) beyond which growth and yield clearly diverge.

Synthesis regarding strategies for drought tolerance and breeding

I59 and Rubi have markedly different strategies for coping with water-stress, as summarized in Table 3.

Given that the water stress was not pronounced in I59, adjustments in C allocation at the whole-plant scale remained small: we observed only a slight decrease in LMR, and a slight increase in RMR and SMR. We conclude here that I59 did not experience profound drought stress, and, consequently, did not appreciably modify its patterns of biomass allocation.

In sharp contrast, Rubi's strategy was not related to early physiological adjustments or to leaves' anatomical aspects. Instead, Rubi invested more in roots (higher RMR and RLA) to the detriment of TLA. As a consequence, g_L or its proxies appeared to be higher. Rubi's investment in roots enabled it to sustain larger variations in Ψ_L, and thereby to sustain a larger g_C during drought as well. As a consequence, Rubi's transpiration (SF) did not decrease. During the dry season, the soil water deficit around Rubi's root system became more severe than around I59's, forcing Rubi to adjust its main morphological traits. Under prolonged drought, a drop in Ψ_L led Rubi to shed its leaves significantly (Fig. S1), with great consequence for its recovery, and probably also for its balance of reserve compounds (upon which leaf renewal will depend).

Although whole-plant integrated WUE and leaf $\Delta^{13}C$ behaved globally consistently with the theory, expressing increased WUE and decreased $\Delta^{13}C$ under drought (Farquhar and Richards, 1984), and increased WUE in the isohydric cultivar (Sade et al., 2012), we obtained no significant negative correlation between WUE and $\Delta^{13}C$: therefore, leaf $\Delta^{13}C$ may indicate whole-plant integrated WUE but does not appear reliable enough to rank cultivars for WUE. Such a discrepancy is likely due to scaling issues, from leaf to whole-plant. It would be worth testing whole-plant $\Delta^{13}C$ but the cost of analyzing samples per compartment or to grind whole mature could plants could be prohibitive for standard breeding programs.

It has often been reported that leaf-shedding coffee cultivars like Rubi are drought-sensitive, while its counterparts (like I59) are drought-tolerant (DaMatta et al., 2003). We argue here that such sensitive/tolerant classification remains vague regarding the actual processes underpinning coffee hydric strategies: considering the results presented here, we suggest that ranking cultivars along an iso/aniso-hydric gradient (Ainsworth and Rogers, 2007; Garcia-Forner et al., 2017) is more appropriate. By definition, the isohydric cultivar (I59) can be considered as more drought avoidant (conserving water), whereas Rubi is more drought-resistant (enduring larger Ψ_L drops).

The main requirements for a successful breeding program for coffee cultivars under drought should be to develop cultivars that survive severe periods of drought, and also produce acceptable yields under moderate water-limiting conditions (Silva et al., 2013). However, in line with what has been proposed from potted coffee plants experiments (DaMatta, 2018), we here suggest that no single trait has sufficient predictive power. Moreover, we consider that even characterizations of growth and allocation together are not sufficient to detect the consequences of drought stress, and should be completed with a full survey of water relation traits (in particular vulnerability to cavitation) and reserves dynamics, leading to a broader PP separation between physiological and morphological responses and hopefully, to a better understanding of the compensation effects.

Supplementary data

Table S1. ANOVAs

Table S2. Literature

Figure S1. Photos under severe drought

Figure S2. Root extraction

Figure S3. Leaf composition

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Tables

Table 1. Differences of leaf water potential (Ψ_L) between Rubi and I59 (Rubi<I59) in the non-irrigated treatment for two successive dry seasons (2008 and 2009).

Ψ_L	Year	Difference: Rubi – I59 (Ψ_L, MPa)	Lower C.I. 95%	Upper C.I. 95%	P
Predawn	2008	-0.22	-0.358	-0.023	*
	2009	-0.32	-0.516	-0.088	*
	Average	-0.26	-0.393	-0.109	*
Midday	2008	-0.26	-0.627	0.251	n.s.
	2009	-0.25	-0.579	0.166	n.s.
	Average	-0.25	-0.566	0.152	n.s.

We used Bootstrap effect sizes to find confidence intervals mean with number of interactions= 2000; C.I.: Confident interval; *: $p<0.05$; n.s.: not significantly different

Table 2. Trends (slopes of linear regression vs. time) of sap flow (SF, kg$_{H2O}$ plant^{-1} day^{-1}), canopy conductance (g$_C$, m s^{-1}), and hydraulic conductance (g$_L$, kg$_{H2O}$ plant^{-1} h^{-1} MPa^{-1})

			Irrigated		**Non-irrigated**	
Variable	**Period**	**Season**	**I59**	**Rubi**	**I59**	**Rubi**
Sap flow (SF)	Mar. to May	Wet	0.002 ± 0.003 $^{n.s.}$ A	0.073 ± 0.008 *** B	0.010 ± 0.004 $^{n.s.}$ A	0.035 ± 0.006 *** B
	Jun. to Aug.	Dry	0.049 ± 0.004 *** A	0.044 ± 0.005 *** A	-0.024 ± 0.006 *** A	-0.010 ± 0.005 $^{n.s.}$ B
	Sep. to Oct.	Wet	0.039 ± 0.014 *** B	0.024 ± 0.022 $^{n.s.}$ A	0.026 ± 0.008 ** A	0.029 ± 0.012 * A
Canopy conductance (g$_C$) x 10^{-3}	Mar. to May.	Wet	-2.39 ± 1.3 * A	4.42 ± 1.5 ** B	-2 ± 0.9 * A	2.17 ± 1.1 $^{n.s.}$ B
	Jun. to Aug.	Dry	0.68 ± 0.57 $^{n.s.}$ B	-2.02 ± 0.87 * A	-4.59 ± 1.1 *** A	-4.59 ± 0.92 *** A
	Sep. to Oct.	Wet	5.22 ± 1.64 ** A	6.46 ± 2.06 ** A	10.2 ± 0.17 *** A	17 ± 0.31 *** A
Hydraulic conductance (g$_L$) x 10^{-3}	Mar. to May.	Wet	-0.10 ± 0.28 $^{n.s.}$ A	5.13 ± 0.56 *** B	0.22 ± 0.28 $^{n.s.}$ A	2.56 ± 0.39 *** B
	Jun. to Aug.	Dry	1.41 ± 0.53 * A	2.21 ± 0.66 ** B	-2.67 ± 0.65 *** A	1.51 ± 1.09 $^{n.s.}$ B
	Sep. to Oct.	Wet	-2.54 ± 1.13 * B	-3.96 ± 1.68 * A	-0.32 ± 0.63 $^{n.s.}$ A	-0.10 ± 0.97 $^{n.s.}$ A

Measurements were performed between March and October 2009, for cultivars I59 and Rubi, treatments irrigated during the dry season (I) and non-irrigated (NI). Slope ± SE; n.s.: slope not significant; *: $p<0.05$; **: $p<0.01$; ***: $p<0.001$. Uppercase letters compare slopes of regressions between cultivars I59 and Rubi under same season (wet and dry) and treatment (I and NI), using ANCOVA.

Table 3. Phenotypic plasticity for hydraulic traits, between irrigated and non-irrigated treatment into dry season

Variable (abbreviation, unit)	I59	Rubi
Hydraulic traits ^{PPIm}		
Sap flow (SF, kg_{H2O} plant^{-1} day^{-1}) $^{\zeta}$	**0.93**	0.79
Canopy conductance (g_C, cm s^{-1}) $^{\zeta}$	**0.94**	0.78
Hydraulic conductance (g_L, kg_{H2O} plant^{-1} MPa^{-1} h^{-1}) $^{\zeta}$	**0.95**	0.74
Water-use efficiency (WUE, $\Delta g_{(SDM+RDM)}$ kg_{H2O}^{-1} plant^{-1})	0.10	**0.30**
Predawn leaf water potential (Ψ_{pd}, MPa) †	0.67	**0.86**
Midday leaf water potential (Ψ_{md}, MPa) †	0.44	**0.60**

Letters in bold highlight the highest value between cultivars to each traits.

^{PPIm}: Phenotypic plasticity index based on maximum and minimum means (Valladares et al., 2000). This index was applied hydraulic traits because were measurements of time-course, using maximum and minimum daily averages (Fig. 6, 7, 8);

$^{\zeta}$: These were computed for the period of the second drought from June to August 2009, due to datalogger breakdown after lightning, we missed data by the end of the dry season in the NI treatment;

†: These were computed as the average between first and second drought.

Table 4. Synthesis of main contrasts for strategies facing drought in cultivars I59 and Rubi

Variable (abbreviation)	I59	Rubi
Genes		
Genetic origin [α]	C. arabica cv. Vila Sarchi x HT 832/2 Introgression of Canephora (robusta)	C. arabica cv. Mundo Novo x C. arabica cv. Catuai 100% Arabica
Lipid-transfer protein (nsLTP) genes [β]	highly up-regulated	not up-regulated
Dry mass partitioning at transition from wet to dry season		
Leaf (LMR)	Slow decrease and low plasticity	Fast decreases and high plasticity, until shedding
Root (RMR)	Slow increase and low plasticity	Fast increase and high plasticity
Shoot (SMR)	Slow increase and low plasticity	Fast increase and high plasticity
Leaf characteristics		
Specific leaf area (SLA) [γ]	Higher, less plasticity	Less, higher plasticity
Cuticle thickness [δ]	+25%	0%
Spongy parenchym [δ]	+5.4%	0%
Proxies		
Leaf area-to-total dry mass ratio (LAR)	higher	less
Root dry mass-to-leaf area (RLA)	less	higher
Basal area trunk-to-leaf area ratio (BLR)	less	higher
Hydraulic traits at transition from wet to dry season		
Leaf predawn water potential (Ψ_{pd})	decreases slowly, low plasticity, isohydric	decreases quickly, high plasticity, anisohydric
Sap flow (SF)	decreases quickly, high plasticity	without changes, low plasticity
Canopy conductance (g_C)	decreases quickly, high plasticity	decreases slowly, low plasticity
Total hydraulic conductance (g_L)	decreases quickly, high plasticity	without changes, low plasticity

[α]: see Carvalho et al. (2008);

[β]: corresponds to proteins involved in signal transduction pathways, as well as ABA and lipid metabolism (e.g. cuticle), see Mofatto et al. (2016);

[γ]: a significant difference was found only for the first dry season;

[δ]: see Mofatto et al. (2016).

Figures

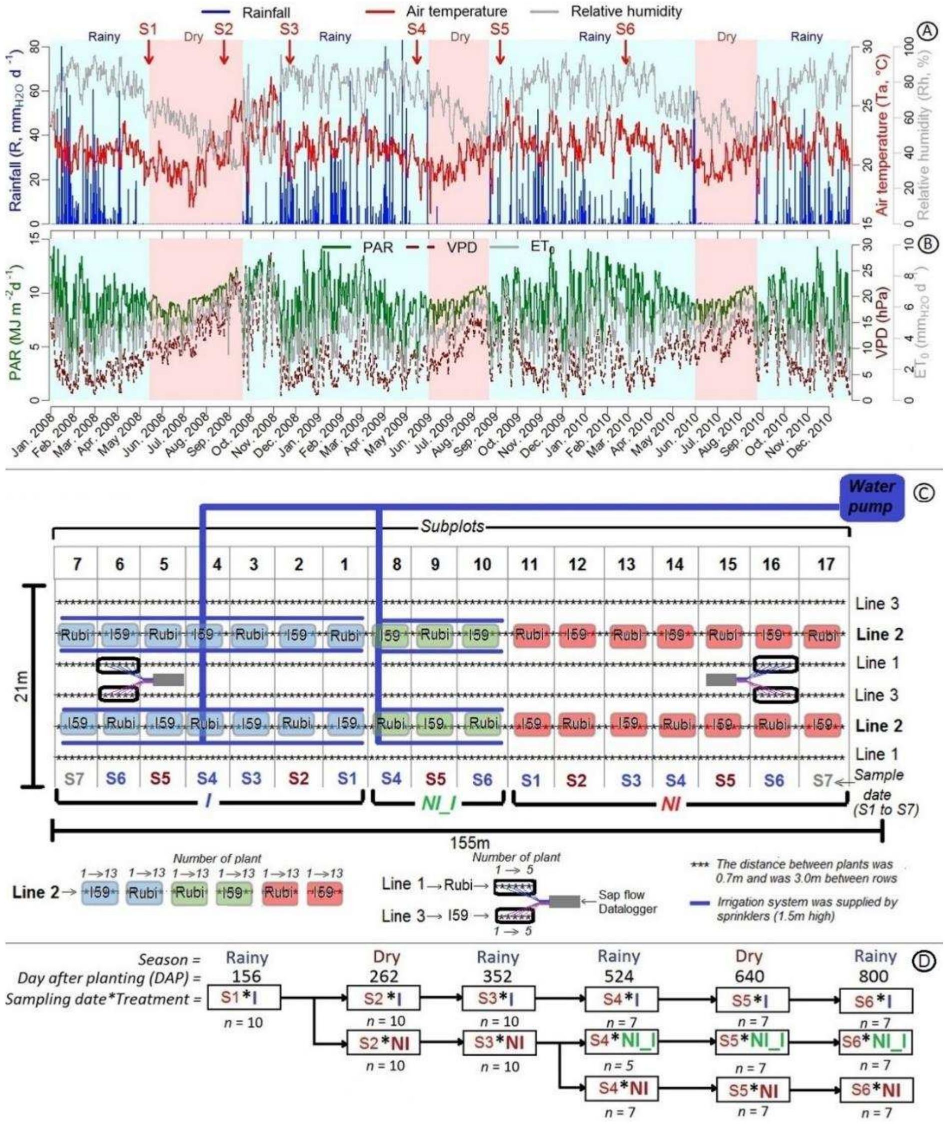

Fig. 1. Microclimate and experimental design at Embrapa-Cerrado, Brasilia, Brazil: A) Daily rainfall, air temperature, and relative humidity; B) Daily PAR (photosynthetically active radiation), VPD (vapour pressure deficit); and ET$_0$ (potential evapotranspiration; Allen et al. (1998)). Study period 2008-2010. Arrows show the coffee plant sampling dates (S1 to S6); blue area: wet season; pink area: dry season; C) Experimental plot, comprising 17 subplots, each defined as the area formed by the two genotypes (CV: I59 and Rubi), under one given irrigation treatment IRR (I, NI_I, or NI): and for one given sampling date (S). Subplots 1 to 7 were irrigated during the dry seasons (I, in blue), subplots 8 to 10 were non-irrigated during dry season of year 1 and irrigated during dry season of year 2 (NI_I, in green), and subplots 11 to 17 were non-irrigated during the dry seasons (NI, in red). Each subplot contains 78 plants, i.e. 39 plants for each CV, each distributed on 3 lines (13 plants per line). Line 1 and 3 were meant for borders only. Lines 2 include 10 plants that were used for destructive dry mass partitioning. S7 was for reserve only (not used here); D) Sketch of the factors and their treatments studied throughout the experiment, with indication of dry and wet seasons for each sampling date: (i) CV (cultivars I59 vs. Rubi); (ii) IRR (I, NI_I, or NI); and (iii) sampling date (S1 to S6); n is the number of sampled plants.

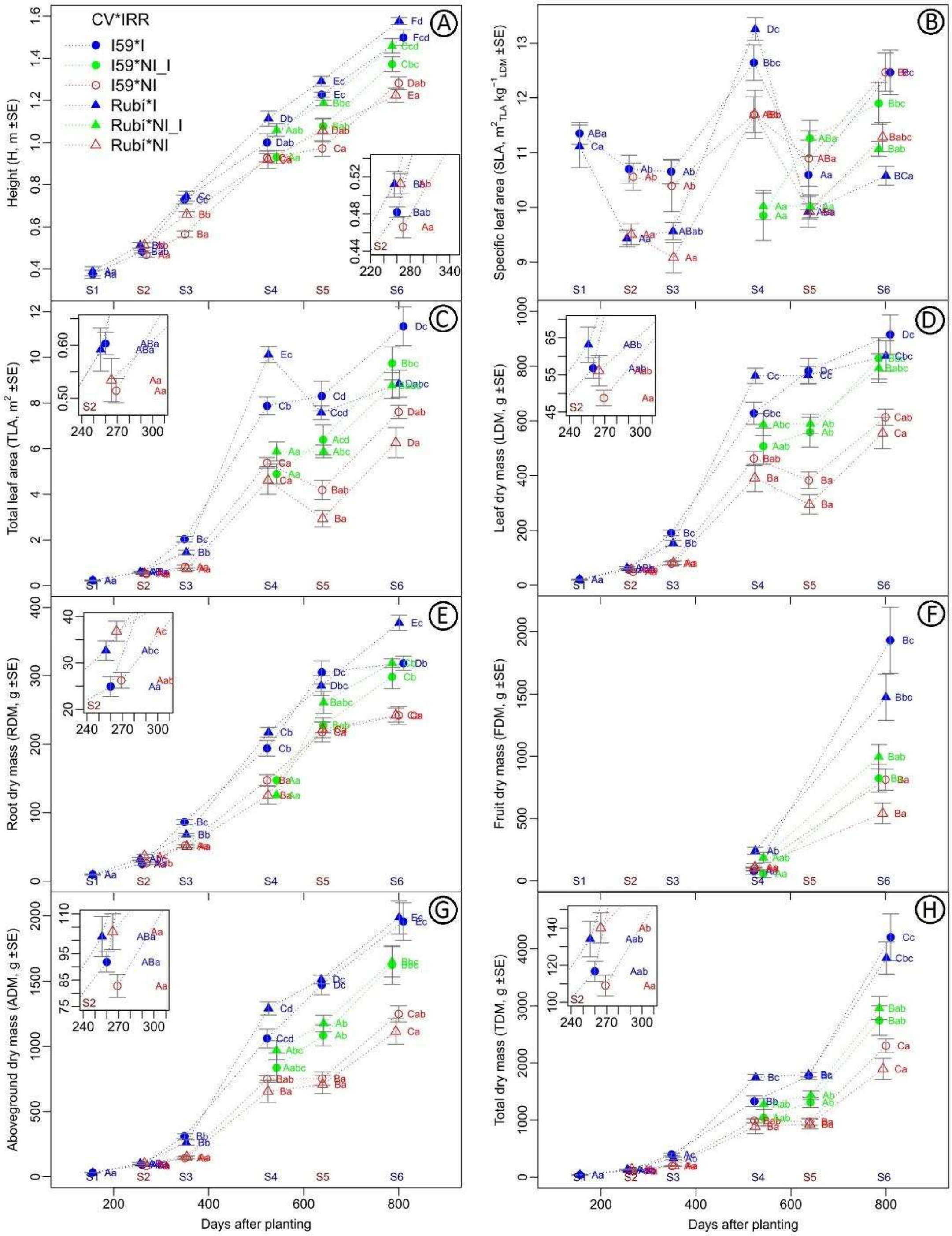

Fig. 2. State variables at sampling dates S1 to S6, for cultivars I59 and Rubi (filled and empty circles, respectively), irrigated during the dry season (I, in blue), non-irrigated year 1 and irrigated during the dry season year 2 (NI_I, in green), or non-irrigated during the dry season (NI, in red). Uppercase letters indicate significant differences over time for a given CV*IRR combination, whereas lowercase letters indicate significant differences between CV*IRR combinations at a given sampling date, according to the Tukey's HSD test, p<0.05.

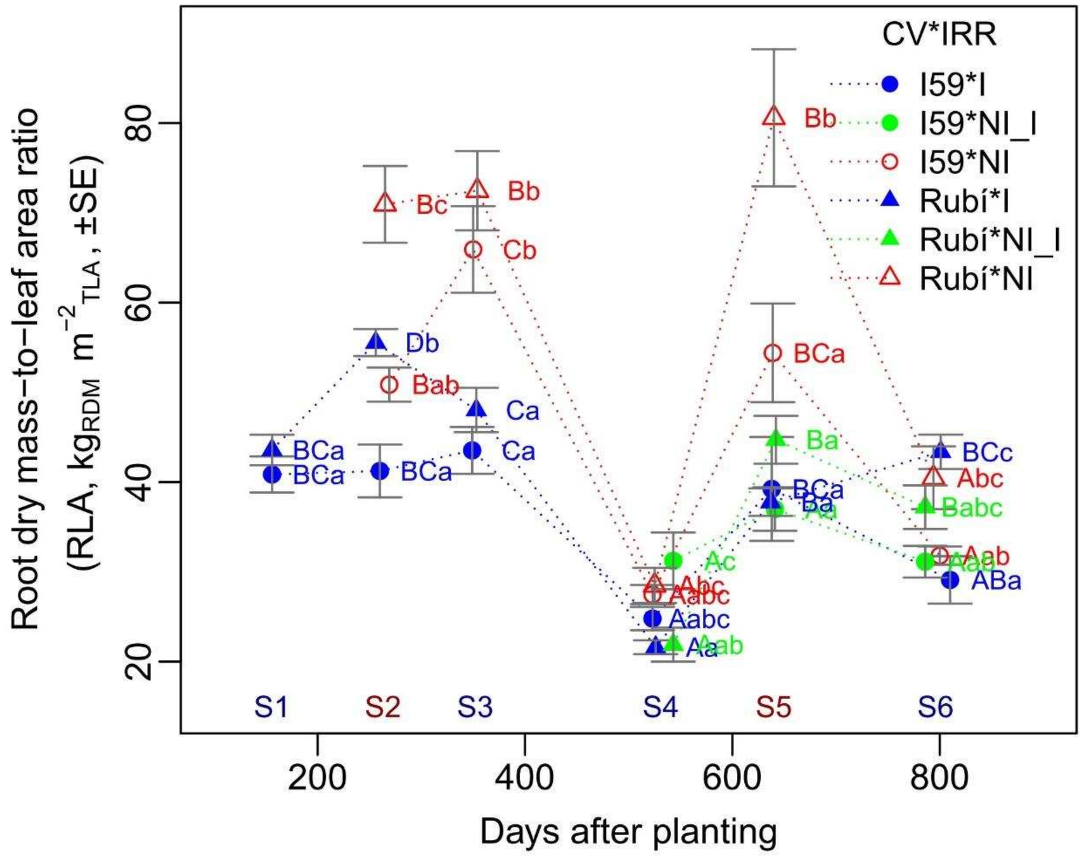

Fig. 3. Root dry mass-to-leaf area ratio (RLA) from S1 to S6 for cultivars I59 and Rubi, irrigated during the dry season (I, in blue), non-irrigated year 1 and irrigated during the dry season year 2 (NI_I, in green), or non-irrigated during the dry season (NI, in red). Uppercase letters indicate significant differences over time for a given CV*IRR combination, whereas lowercase letters indicate significant differences between CV*IRR combinations at a given sampling date, according to the Tukey's HSD test, p<0.05.

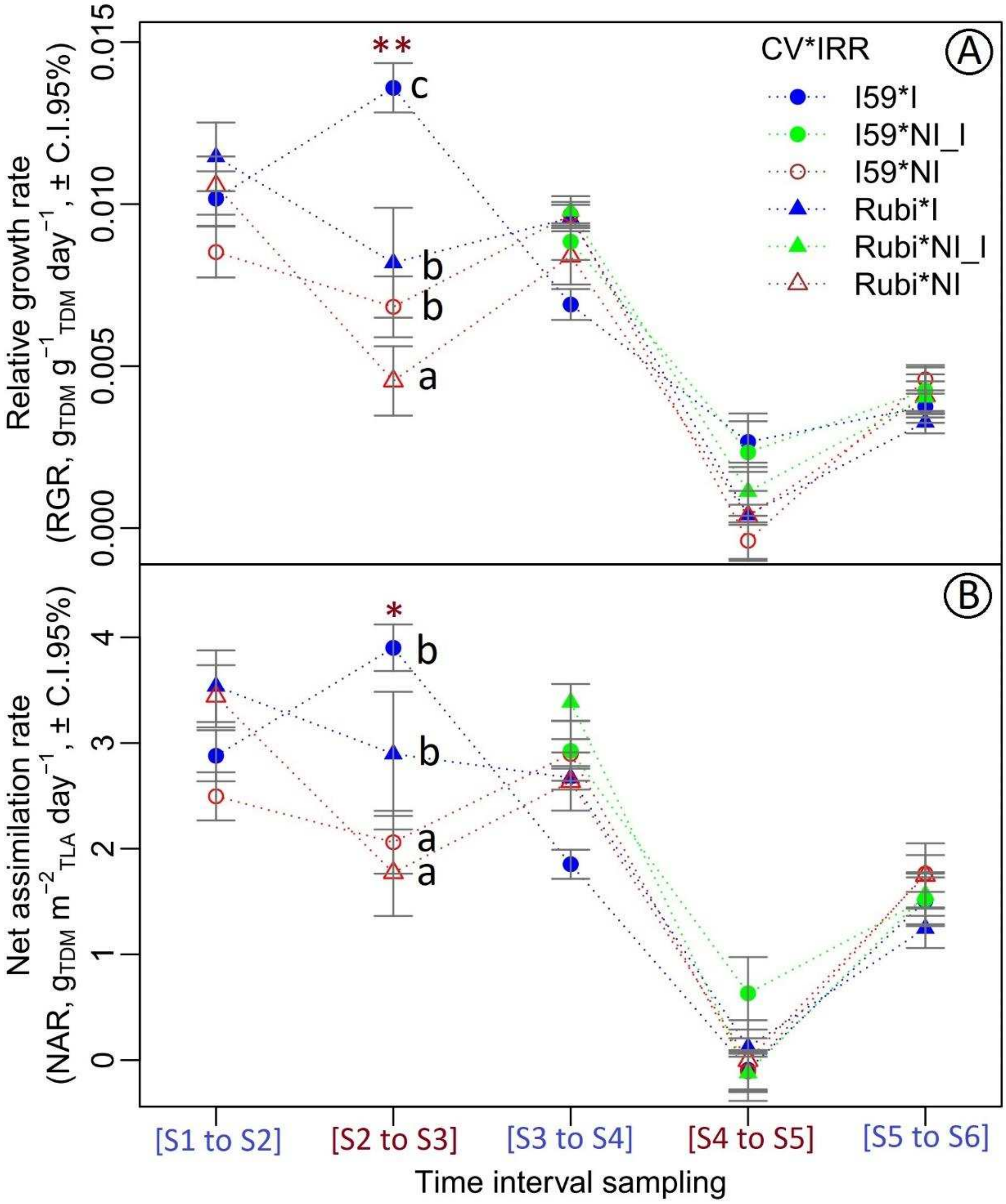

Fig. 4. A) Relative growth rate (RGR), and B) net assimilation rate (NAR). Asterisk highlights the significance of ANOVA, *: p<0.05, **: p<0.01. Different letters indicate significant differences between combinations of CV*IRR. We applied the Tukey's HSD test, p<0.05. Transitions in blue (S1 to S2, S3 to S4, and S5 to S6) and in red (S2 to S3 and S4 to S5) correspond to rainy and dry periods, respectively. C.I.: Confidence interval.

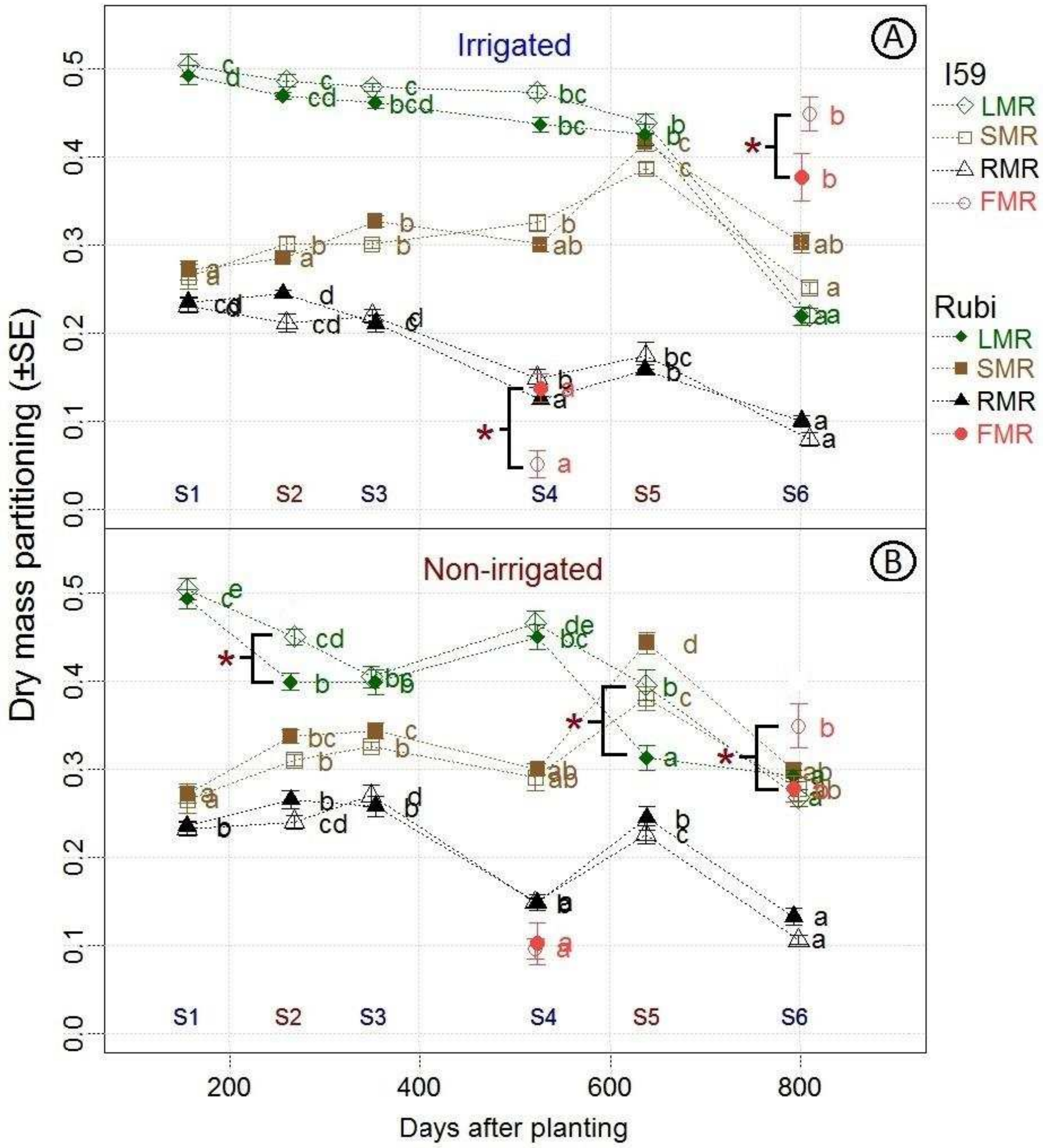

Fig. 5. Dry mass partitioning monitored from sampling dates S1 to S6, for cultivars I59 and Rubi (filled and empty circles, respectively) irrigated during the dry season (I, top) and non-irrigated at all (NI, below). Non-irrigated year 1 and irrigated year 2 (NI_I) behaves similarly to I treatment (data not shown). Letters are from comparison between means with Tukey's HSD test for each compartment and CV*IRR throughout sampling dates, p<0.05. Asterisks and brackets highlight differences between CV within sampling date for each compartment, comparing means with Tukey's HSD test, p<0.05.

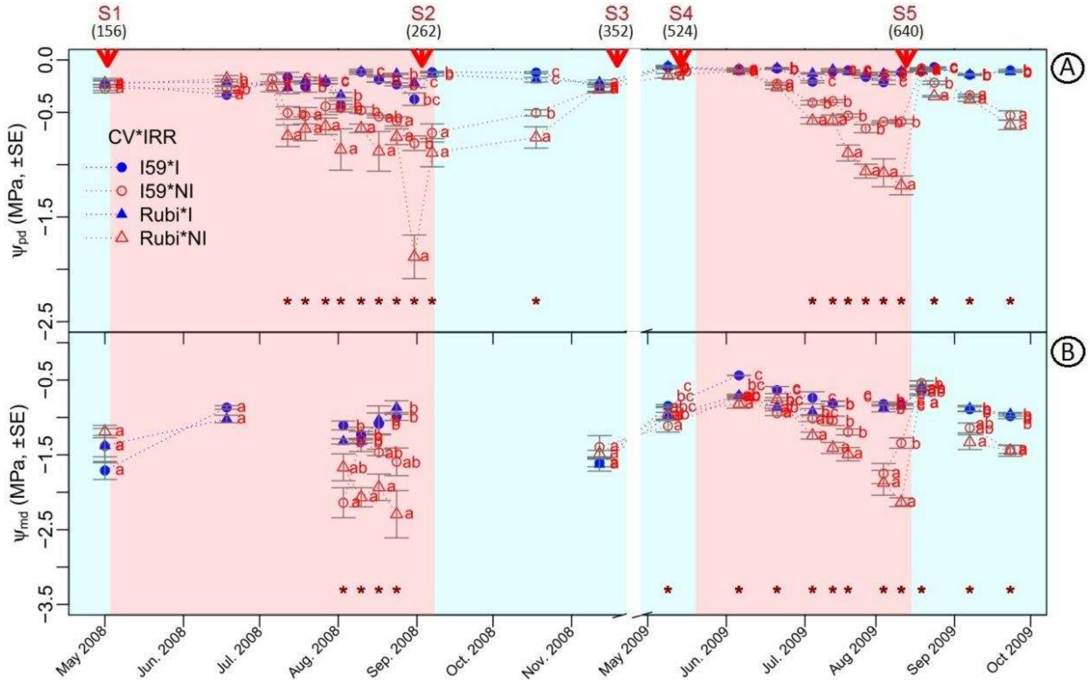

Fig. 6. Time-course of leaf water potential measured throughout the wet (blue areas) and dry (pink areas) seasons of 2008 and 2009. A) Predawn leaf water potential (Ψ_{pd}, MPa) and B) midday leaf water potential (Ψ_{md}, MPa) for two coffee cultivars (I59: filled; and Rubi: empty circles) under three irrigated treatment (I: irrigated; NI: non-irrigated). NI_I behaved similarly to NI during the first year and to I during the second year (data not shown). Arrows show the coffee plant sampling dates (S1 to S5), and numbers in parenthesis are for days after planting. Letters compare the four combinations of 2 cultivars x 2 water treatments for each given sampling date. We applied the Tukey's HSD test, $p<0.05$. Asterisk highlights differences between combinations of treatment.

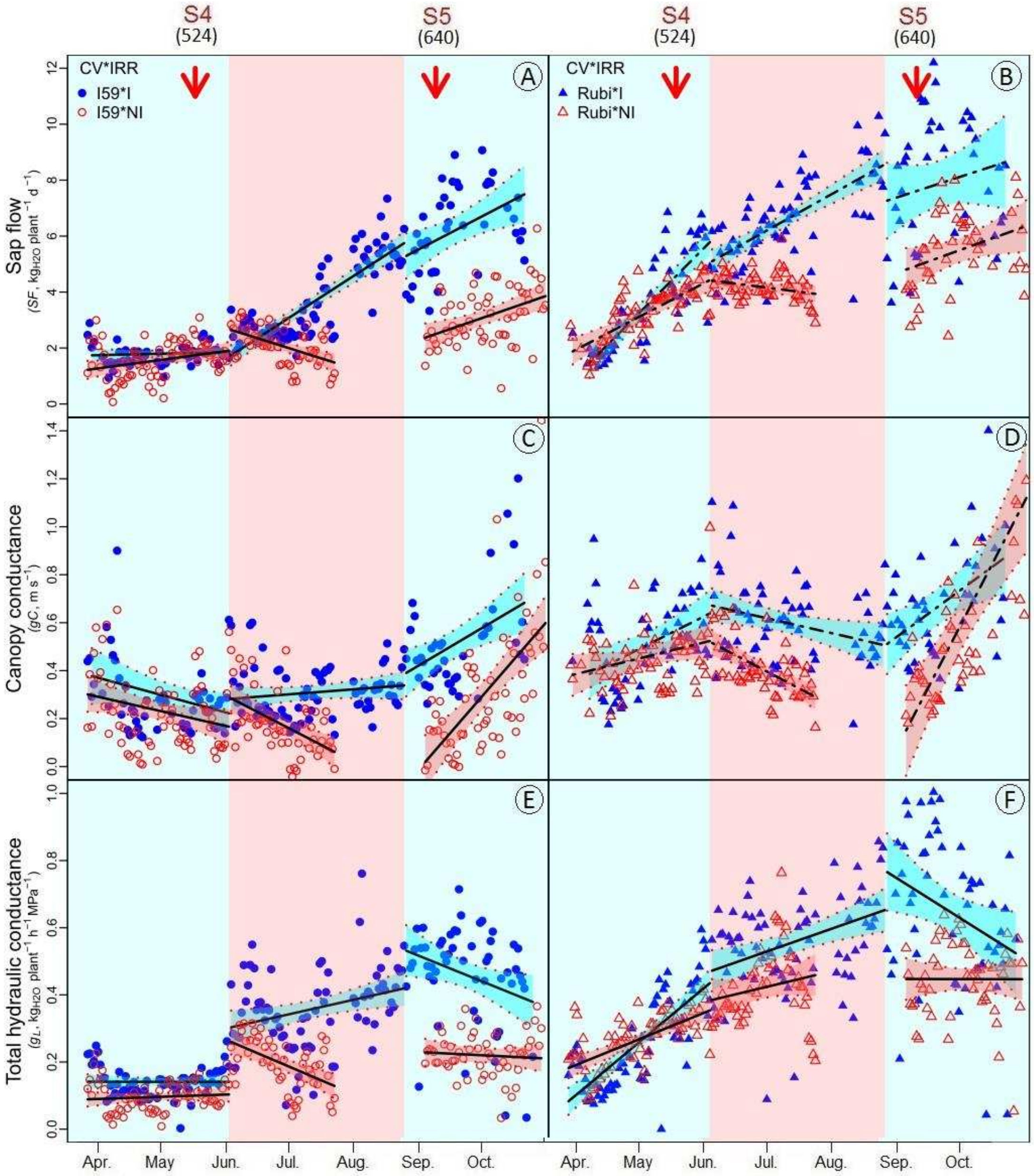

Fig. 7. Time-course of sap flow (A and B), canopy conductance (C and D), and total hydraulic conductance (E and F). Measurements were made between March and October 2009 for cultivars I59 (left side) and Rubi (right side) either irrigated during the dry season (I) or non-irrigated (NI). Wet season in blue; dry season in pink; Solid and dashed line are adjusted linear regressions given with confidence 95% intervals. Arrows show the coffee plant sampling dates (S4 and S5), and numbers in parenthesis are for days after planting. Due to lightning, we lost data by the end of the dry season in the NI treatment.

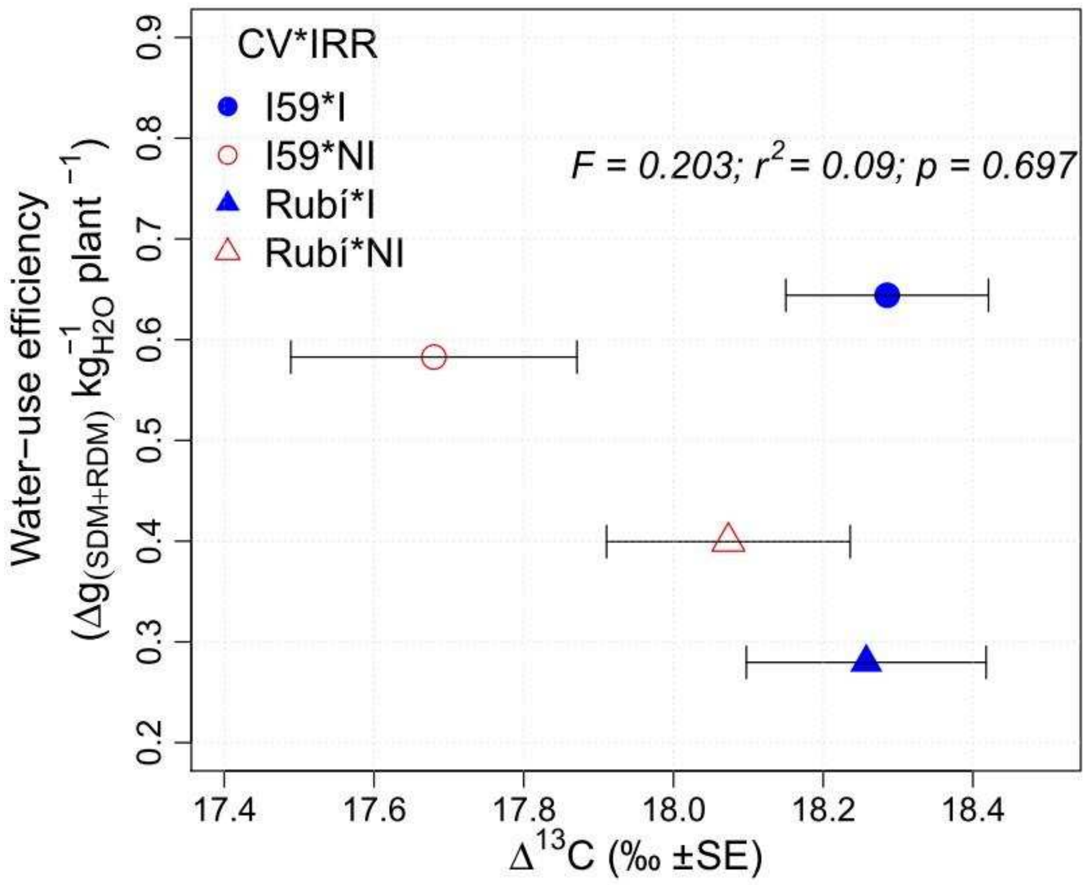

Fig. 8. Relationship between water-use efficiency and carbon isotopic discrimination for second dry season (NI_I was not measured here). WUE was computed between S4 and S5 as (SDM+RDM)/SF, where SDM is the shoot dry mass (without leaves), RDM is the root dry mass, and SF is the sap flow. Linear regression for all CV*IRR; F: Fisher´s value; r^2: Pearson´s correlation coefficient; P: probability model.

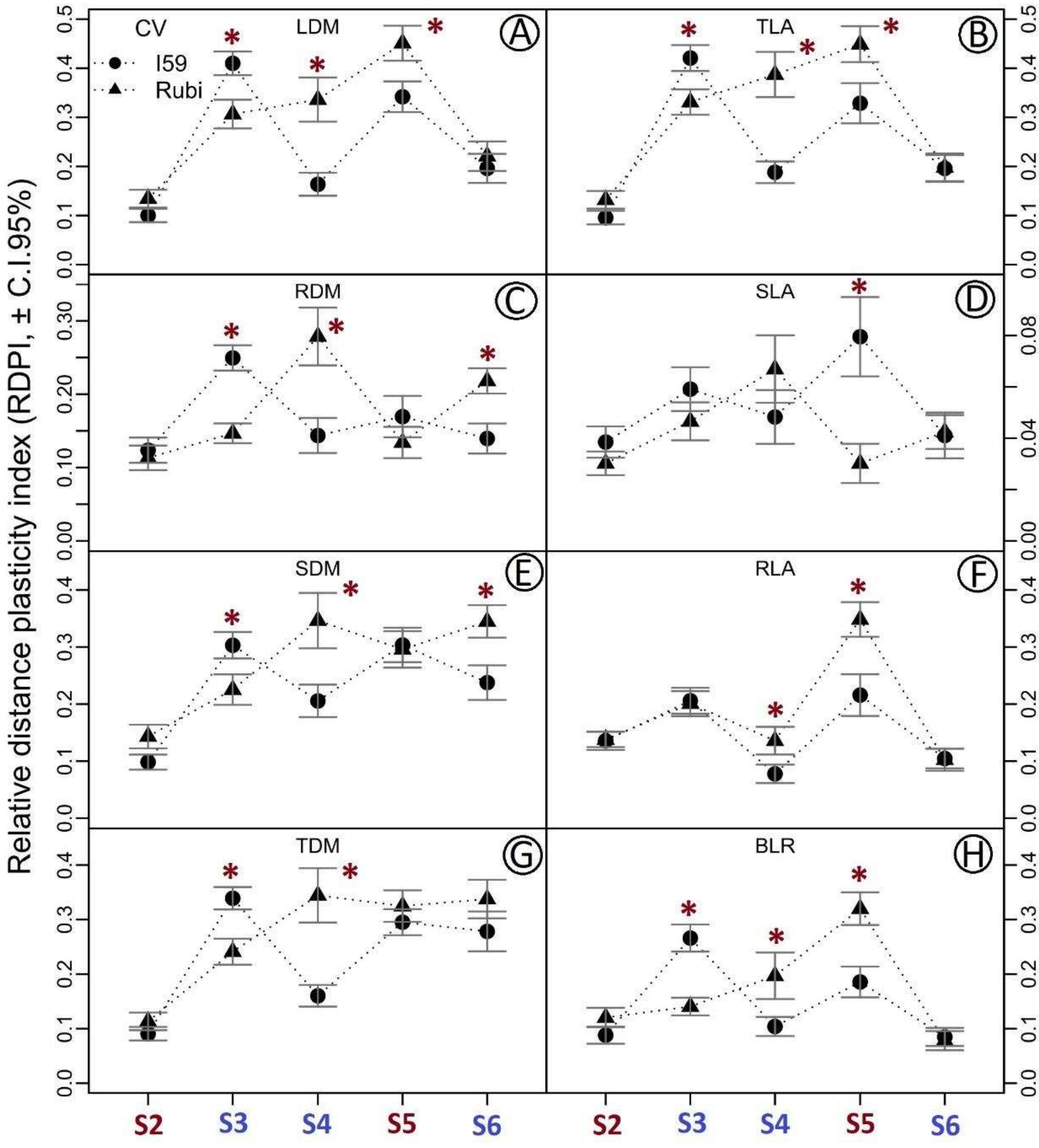

Fig. 9. Time-course of relative distance plasticity index between irrigated and non-irrigated treatment, expressed for DM per compartment (Leaf: LDM, root: RDM; shoot: SDM, and total: TDM), total leaf area (TLA), specific leaf area (SLA), RDM-to-TLA ratio (RLA), and basal area of stem-to-TLA (RLR). Data from S2 to S6 for cultivars I59 and Rubi. Asterisks indicate significant differences between cultivars (Tukey's HSD test, $p<0.05$. C.I.: Confidence interval).

SUPPLEMENTARY DATA

Supplementary tables

Table S1. ANOVA results for growth per compartment, dry mass partitioning, hydraulic conductance proxies, fruit dry mass-to-leaf area ratio, and leaf composition, for two cultivars (CV: I59 and Rubi), under three irrigation treatments (IRR: irrigated during the dry season= I, non-irrigated= NI, or non-irrigated year 1 and irrigated year 2= NI_I), from six sampling date (S: S1 to S6).

Variable (abbreviation, unit)	S	I59*I		I59*NI		I59*NI_I		Rubi*I		Rubi*NI		Rubi*NI_I		CV		IRR			S	CVx IRR	CVx IRRxS	F	R^2	P
														I59	Rubi	I	NI	NI_I						
Growth per compartment																								
Height (H, m)	S1	0.37(0.019)	Aa					0.39(0.022)	Aa						***	***			***	*	***	**204.64**	**0.97**	***
	S2	0.48(0.006)	Bab	0.47(0.012)	Aa			0.51(0.014)	Bb	0.51(0.011)	Ab													
	S3	0.73(0.021)	Cc	0.57(0.015)	Ba			0.75(0.023)	Cc	0.66(0.012)	Bb													
	S4	1(0.041)	Dab	0.93(0.019)	Ca	0.93(0.031)	Aa	1.11(0.036)	Db	0.92(0.042)	Ca	1.06(0.03)	Aab											
	S5	1.23(0.012)	Ec	0.97(0.037)	Ca	1.08(0.038)	Bab	1.29(0.023)	Ec	1.06(0.054)	Dab	1.19(0.012)	Bbc											
	S6	1.5(0.036)	Fcd	1.28(0.03)	Dab	1.37(0.035)	Cbc	1.58(0.017)	Fd	1.22(0.034)	Ea	1.46(0.035)	Ccd											
Basal area trunk (BA, cm²)	S1	0.9(0.07)	Aa					0.9(0.07)	Aa					n.s.		***			***	n.s.	***	**93.26**	**0.93**	***
	S2	2.1(0.06)	Aa	1.9(0.15)	Aa			2.1(0.15)	ABa	2.3(0.12)	Aa													
	S3	4.3(0.3)	Bb	2.9(0.17)	Aa			4.1(0.35)	Bb	2.6(0.22)	Aa													
	S4	9.8(0.74)	Cab	8(0.28)	Bab	8.5(0.81)	Aab	11.1(1.27)	Cb	6.5(0.42)	Ba	9.3(1.23)	Aab											
	S5	12.7(0.61)	Db	8.7(0.57)	Ba	12.6(1.31)	Bb	11.6(0.52)	Cab	8.5(0.58)	Ca	10.7(0.49)	Aab											
	S6	15.1(0.72)	Ebc	11.7(0.53)	Ca	14.3(0.73)	Bbc	16.6(0.73)	Dc	11.3(0.39)	Da	13.3(0.45)	Bab											
Leaf dry mass (LDM, g)	S1	20.5(1.62)	Aa					20.2(2.14)	Aa					n.s.		***			***	n.s.	***	**90.74**	**0.93**	***
	S2	56.8(2.75)	Aab	48.8(2.1)	Aa			63.1(4.77)	ABb	56.1(4.09)	Aab													
	S3	190.6(10.71)	Bc	79.4(6.25)	Aa			152.9(11.36)	Bb	80.7(6.88)	Aa													
	S4	627.8(40.3)	Cbc	462.2(25.92)	Bab	507.3(65.79)	Aab	764.6(27.82)	Cc	391.2(49.41)	Ba	586.6(40.86)	Abc											
	S5	782.6(45.51)	Dc	383.2(30.18)	Ba	558.7(54.3)	Ab	766.6(32.94)	Cc	294.7(35.47)	Ba	589.5(34.3)	Ab											
	S6	915.1(71.33)	Dc	613.2(29.31)	Cab	828.3(75.39)	Bbc	836.9(55.85)	Cbc	555.4(57.32)	Ca	792.9(52.58)	Babc											
Root dry mass (RDM, g)	S1	9.5(0.97)	Aa					9.6(0.91)	Aa						*	***			***	n.s.	***	**192.07**	**0.96**	***
	S2	24.9(2.15)	Aa	26.2(1.71)	Aab			32.7(2.1)	Abc	36.8(2.14)	Ac													
	S3	86.3(3.36)	Bc	51.7(2.16)	Aa			67.9(1.93)	Bb	50.6(1.78)	Aa													
	S4	194.1(11.48)	Cb	147.4(7.98)	Ba	147.4(0)	Aa	217.6(7.28)	Cb	125.5(13.22)	Ba	125.5(0)	Aa											
	S5	305(16.87)	Dc	217.7(14.35)	Ca	227.7(11.06)	Bab	285.6(14.33)	Dbc	221.8(12.11)	Ca	261.1(16.07)	Babc											
	S6	318.4(10.3)	Db	242.2(13.01)	Ca	298.5(17.27)	Cb	377.5(11.02)	Ec	242.5(10.28)	Ca	318.7(6.05)	Cb											
Shoot dry mass (SDM, g)	S1	10.86(1.032)	Aa					10.81(0.727)	Aa						*	***			***	n.s.	***	**119.32**	**0.94**	***
	S2	35(1.28)	Aa	34(2.29)	Aa			38.3(2.89)	ABab	47.1(2.93)	Ab													
	S3	119.9(7.55)	Ab	63.4(3.66)	Aa			108.8(8.95)	Bb	68.8(4.69)	Aa													
	S4	432.9(33.43)	Bbc	286.1(14.15)	Ba	328.9(46.3)	Aab	526.9(21.93)	Cc	264.2(35.37)	Ba	383.6(36.32)	Aab											
	S5	689(32.1)	Cde	369.6(28.32)	Ca	525(29.57)	Abc	746.8(13.14)	De	412.9(37.26)	Cab	587(29.96)	Bcd											
	S6	1042.7(76.92)	Dcd	635.9(37.23)	Dab	796.3(75.06)	Babc	1153(72.57)	Ed	559.3(42.17)	Da	855.9(64.11)	Cbc											
Fruit dry mass (FDM, g)	S4	76.1(23.93)	Aa	95.9(12.67)	Aa	57.7(31.92)	Aa	241.1(29.59)	Ab	107.5(31.41)	Aa	185.5(40.81)	Aab	*		***			***	n.s.	***	**28.62**	**0.82**	***
	S6	1932.3(266)	Bc	812.2(84.2)	Ba	822.1(110.24)	Ba	1475(185.05)	Bbc	540.8(82.55)	Ba	996.2(97.58)	Bab											
Aboveground dry mass (ADM, g)	S1	31.4(2.45)	Aa					31(2.76)	Aa					n.s.		***			***	n.s.	***	**109.13**	**0.94**	***
	S2	91.8(3.85)	ABa	82.8(4.28)	Aa			101.4(7.59)	ABa	103.3(6.76)	Aa													
	S3	310.4(18.08)	Bb	142.7(9.69)	Aa			261.7(20.14)	Bb	149.6(10.74)	Aa													
	S4	1060.7(71.62)	Ccd	748.3(25.56)	Bab	836.2(111.7)	Aabc	1291.5(49.23)	Cd	655.4(84.18)	Ba	970.2(73.28)	Abc											
	S5	1471.7(76.4)	Dc	752.8(51.95)	Ba	1083.8(80.69)	Ab	1513.4(33.11)	Dc	707.6(69.88)	Ba	1176.6(63.12)	Ab											
	S6	1957.8(144.15)	Ec	1249.1(61.91)	Cab	1624.6(149.15)	Bbc	1989.9(126.97)	Ec	1114.7(98.16)	Ca	1648.8(115.8)	Bbc											

Variable (abbreviation, unit)	S	I59*I		I59*NI		I59*NI_I		Rubi*I		Rubi*NI		Rubi*NI_I		CV		IRR			S	CVx IRR	CVx IRRxS	F	R^2	P
														I59	Rubi	I	NI	NI_I						
Total dry mass (TDM, g)	S1	40.9(3.33)	Aa					40.6(3.63)	Aa					n.s.		***			***	n.s.	***	99.79	0.93	***
	S2	116.7(5.41)	Aab	109.1(5.68)	Aa			134.1(9.63)	Aab	140.1(8.13)	Ab													
	S3	396.8(20.74)	Ac	194.4(10.94)	Aa			329.6(21.41)	Ab	200.2(11.71)	Aa													
	S4	1330.9(94.85)	Bb	991.7(35.08)	Bab	1041.4(141.53)	Aab	1750.1(54.18)	Bc	888.4(126.38)	Ba	1281.2(98.83)	Aab											
	S5	1776.7(62.96)	Bc	970.6(62.17)	Ba	1311.5(90.79)	Ab	1799.1(41.14)	Bc	929.4(80.23)	Ba	1437.7(73.15)	Ab											
	S6	4208.4(409.48)	Cc	2303.5(119.01)	Ca	2745.3(259.52)	Bab	3842.3(281.35)	Cbc	1898(185.74)	Ca	2963.8(204.57)	Bab											
Total leaf area (TLA, m^2)	S1	0.23(0.016)	Aa					0.22(0.015)	Aa					**		***			***	n.s.	***	103.16	0.93	***
	S2	0.6(0.021)	ABa	0.51(0.023)	Aa			0.59(0.041)	ABa	0.53(0.041)	Aa													
	S3	2.03(0.127)	Bc	0.82(0.069)	Aa			1.45(0.093)	Bb	0.72(0.052)	Aa													
	S4	7.87(0.395)	Cb	5.38(0.233)	Ca	4.89(0.427)	Aa	10.13(0.356)	Ec	4.61(0.615)	Ca	5.88(0.414)	Aa											
	S5	8.3(0.648)	Cd	4.19(0.419)	Bab	6.39(0.653)	Acd	7.58(0.302)	Ccd	2.93(0.359)	Ba	5.88(0.276)	Abc											
	S6	11.36(0.848)	Dc	7.61(0.293)	Dab	9.74(0.717)	Bbc	8.85(0.601)	Dabc	6.26(0.661)	Da	8.77(0.566)	Babc											
Specific leaf area (SLA, m^2_{TLA} kg^{-1}_{LDM})	S1	11.3(0.2)	ABa					11.1(0.39)	Ca					***		***			***	n.s.	***	11.07	0.61	***
	S2	10.7(0.25)	Ab	10.6(0.25)	Ab			9.4(0.15)	Aa	9.5(0.19)	Aa													
	S3	10.7(0.23)	Ab	10.4(0.47)	Ab			9.6(0.16)	ABab	9.1(0.28)	Aa													
	S4	12.6(0.32)	Bbc	11.7(0.33)	ABb	9.8(0.46)	Aa	13.3(0.21)	Dc	11.7(0.44)	Bb	10(0.25)	Aa											
	S5	10.6(0.63)	Aa	10.9(0.5)	ABa	11.3(0.33)	ABa	9.9(0.28)	ABa	9.9(0.14)	Aa	10(0.2)	Aa											
	S6	12.5(0.41)	Bc	12.5(0.35)	Bc	11.9(0.39)	Bbc	10.6(0.17)	BCa	11.3(0.27)	Babc	11.1(0.13)	Bab											

Dry mass partitioning

Leaf-to-total dry mass ratio (LMR)	S1	0.5(0.012)	Ca					0.49(0.011)	Da					***		***			***	n.s.	***	62.71	0.90	***
	S2	0.49(0.007)	Cc	0.45(0.009)	CDb			0.47(0.004)	CDbc	0.4(0.01)	Ba													
	S3	0.48(0.005)	Cb	0.4(0.012)	BCa			0.46(0.006)	BCDb	0.4(0.014)	Ba													
	S4	0.47(0.007)	BCa	0.47(0.014)	Da	0.49(0.01)	Ca	0.44(0.008)	BCa	0.45(0.014)	Ca	0.46(0.016)	Ca											
	S5	0.44(0.011)	Bb	0.39(0.017)	Bb	0.42(0.014)	Bb	0.43(0.012)	Bb	0.31(0.014)	Aa	0.41(0.009)	Bb											
	S6	0.22(0.008)	Aa	0.27(0.01)	Ab	0.3(0.005)	Ac	0.22(0.01)	Aa	0.29(0.006)	Abc	0.27(0.006)	Ab											
Root-to-total dry mass ratio (RMR)	S1	0.23(0.008)	Da					0.24(0.006)	CDa					n.s			***		***	n.s.	***	39.64	0.85	***
	S2	0.21(0.01)	CDa	0.24(0.008)	CDab			0.25(0.004)	Db	0.26(0.01)	Bb													
	S3	0.22(0.007)	Dab	0.27(0.012)	Dc			0.21(0.01)	Ca	0.26(0.011)	Bbc													
	S4	0.15(0.011)	Bb	0.15(0.005)	Bb	0.15(0.019)	ABb	0.12(0.004)	Aab	0.15(0.01)	Ab	0.1(0.01)	Aa											
	S5	0.17(0.015)	BCa	0.23(0.01)	Cbc	0.18(0.006)	Ba	0.16(0.006)	Ba	0.24(0.014)	Bc	0.18(0.009)	Bab											
	S6	0.08(0.008)	Aa	0.11(0.005)	Aabc	0.11(0.007)	Abc	0.1(0.006)	Aab	0.13(0.01)	Ac	0.11(0.007)	Aabc											
Shoot-to-total dry mass ratio (SMR)	S1	0.26(0.014)	Aa					0.27(0.011)	Aa						***		**		***	**	***	26.72	0.79	***
	S2	0.3(0.008)	Bab	0.31(0.006)	ABb			0.29(0.004)	Aa	0.34(0.007)	Bc													
	S3	0.3(0.005)	Ba	0.33(0.004)	Bb			0.33(0.006)	Bb	0.34(0.009)	Bb													
	S4	0.33(0.009)	Ba	0.29(0.015)	ABa	0.31(0.005)	Aa	0.3(0.008)	ABa	0.3(0.007)	Aa	0.3(0.014)	Aa											
	S5	0.39(0.006)	Ca	0.38(0.014)	Ca	0.4(0.01)	Bab	0.42(0.009)	Cab	0.44(0.012)	Cb	0.41(0.003)	Bab											
	S6	0.25(0.007)	Aa	0.28(0.013)	Aab	0.29(0.011)	Aab	0.3(0.012)	ABb	0.3(0.008)	Ab	0.29(0.006)	Aab											
Fruit-to-total dry mass ratio (FMR)	S4	0.05(0.015)	Aa	0.1(0.011)	Aab	0.05(0.02)	Aa	0.14(0.016)	Ab	0.1(0.023)	Aab	0.14(0.028)	Ab	n.s		***			***	**	***	50.77	0.89	***
	S6	0.45(0.019)	Bd	0.35(0.025)	Bc	0.29(0.018)	Bab	0.38(0.027)	Bbc	0.28(0.015)	Bab	0.33(0.012)	Bab											
Leaf area-to-total dry mass ratio (LAR, m^2_{TLA} kg^{-1}_{TDM})	S1	5.71(0.136)	CDa					5.45(0.161)	Ca					***		***			***	n.s.	***	40.47	0.85	***
	S2	5.2(0.134)	BCc	4.74(0.09)	Bb			4.43(0.072)	Bb	3.79(0.111)	Ba													
	S3	5.11(0.137)	BCc	4.2(0.206)	Bb			4.41(0.084)	Bb	3.6(0.101)	ABa													
	S4	5.99(0.199)	Db	5.43(0.162)	Cab	4.82(0.267)	Ba	5.79(0.12)	Cb	5.26(0.258)	Cab	4.6(0.068)	Ca											
	S5	4.65(0.288)	Bb	4.28(0.226)	Bb	4.82(0.219)	Bb	4.2(0.088)	Bb	3.1(0.138)	Aa	4.09(0.069)	Bb											
	S6	2.75(0.137)	Aab	3.32(0.083)	Acd	3.6(0.13)	Ad	2.32(0.088)	Aa	3.3(0.131)	ABcd	2.97(0.059)	Abc											

Variable (abbreviation, unit)	S	I59*I		I59*NI		I59*NI_I		Rubi*I		Rubi*NI		Rubi*NI_I		CV		IRR			S	CVx IRR	CVx IRRxS	F	R^2	P
														I59	Rubi	I	NI	NI_I						
Hydraulic conductance proxies																								
Root dry mass-to-leaf area ratio (RLA, $g_{RDM}\ m^{-2}_{TLA}$)	S1	40.9(2.01)	BCa					43.6(1.7)	BCa						***		***		***	**	***	22.19	0.75	***
	S2	41.2(2.94)	BCa	50.9(1.9)	Bab			55.5(1.5)	Db	70.9(4.28)	Bc													
	S3	43.5(2.61)	Ca	65.9(4.83)	Cb			48(2.47)	Ca	72.5(4.42)	Bb													
	S4	24.8(1.3)	Aabc	27.5(1.07)	Aabc	31.2(3.16)	Ac	21.6(0.77)	Aa	28.5(1.95)	Abc	21.9(1.89)	Aab											
	S5	39.2(5.78)	BCa	54.4(5.49)	BCa	37(2.42)	Aa	37.8(1.53)	Ba	80.6(7.64)	Bb	44.7(2.67)	Ba											
	S6	29.1(2.64)	ABa	31.8(1.02)	Aab	31.1(1.76)	Aab	43.4(1.91)	BCc	40.5(3.5)	Abc	37.2(2.43)	Babc											
Basal area trunk-to-leaf area ratio (BLR $x10^{-4}$)	S1	3.8(0.3)	Ca					4.2 (0.14)	Ea						***	***			***	n.s.	***	35.41	0.83	***
	S2	3.5(0.12)	Ca	3.6(0.22)	Bab			3.6 (0.18)	Da	4.4(0.26)	Cb													
	S3	2.1(0.12)	Ba	3.7(0.25)	Bc			2.8 (0.12)	Cb	3.7(0.19)	BCc													
	S4	1.2(0.51)	Aa	1.5(0.67)	Aa	1.8(0.15)	Aa	1.1(0.12)	Aa	1.6(0.28)	Aa	1.(0.15)	Aa											
	S5	1.6(0.2)	ABa	2.1(0.87)	Aa	2.0(0.22)	Aa	1.5(0.75)	ABa	3.1(0.22)	Bb	1.8(0.97)	Aa											
	S6	1.4(0.72)	ABa	1.5(0.6)	Aabc	1.5(0.99)	Aab	1.9(0.80)	Bc	1.9(0.12)	Abc	1.6(0.93)	Aabc											
Root dry mass-to-basal area trunk ratio (RBR, g_{RDM} $cm2_{BA}$)	S1	11.57(1.451)	Aa					10.57(0.42)	Aa						*		*		***	n.s.	**	12.45	0.63	***
	S2	11.85(1.01)	Aa	14.56(1.301)	Aab			15.76(0.736)	Bb	16.3(0.821)	Ab													
	S3	20.8(0.94)	Ba	18(1.07)	ABa			17.4(1.1)	BCa	20.3(1.67)	Aa													
	S4	20.3(1.66)	Ba	18.5(0.8)	ABa	17.9(1.73)	Aa	20.8(2.06)	CDa	19.1(1.49)	Aa	14.4(1.63)	Aa											
	S5	24.5(2.1)	Bab	25.3(1.57)	Cab	19(1.63)	Aa	24.6(0.59)	Dab	26.5(1.69)	Bb	24.3(0.86)	Bab											
	S6	21.3(1.15)	Ba	20.8(0.69)	BCa	21.1(1.25)	Aa	22.9(0.98)	Da	21.6(0.72)	ABa	24(0.68)	Ba											
Source-to-sink rate																								
Fruit dry mass-to-leaf area ratio (FLA, $g_{FDM}\ m^{-2}_{TLA}$)	S4	9.1(2.72)	Aa	18.1(2.48)	Aab	10.5(5.24)	Aa	24(3.04)	Aab	20(4.74)	Aab	30.4(6.26)	Ab	n.s.		***			***	*	***	43.58	0.88	***
	S6	167.5(15.63)	Bb	106.3(9.64)	Ba	82.4(6.49)	Ba	166.6(18.39)	Bb	85.1(6.71)	Ba	112.8(5.95)	Ba											
leaf composition																								
Carbon content (C, %)	S1	47(0.19)	Aa					47.3(0.13)	ABa					*			***		***	*	**	9.11	0.65	***
	S2	47.1(0.28)	Aa	48.1(0.26)	Ba			47.8(0.13)	Ca	48.1(0.37)	Aa													
	S3	48.4(0.1)	Aab	49.4(0.19)	ABc			47.7(0.27)	ABa	48.9(0.12)	Cbc													
	S4	49.7(0.21)	Aa	50.7(0.72)	Aa			49.4(0.37)	Aa	49.4(0.31)	ABa													
	S5	49.5(0.23)	ABa	49.3(0.32)	ABa	49(0.24)	Ba	49(0.34)	BCa	49.6(0.41)	Aa	49.4(0.18)	ABa											
	S6	49.9(0.35)	Ab	49.8(0.17)	Cb	48.5(0.18)	Ca	48.4(0.28)	Ba	48.9(0.19)	ABCab	49(0.25)	Aab											
Nitrogen content (N, %)	S1	3.56(0.089)	Ba					3.46(0.128)	ABa					n.s			***		***	*	***	8.25	0.63	***
	S2	3.37(0.061)	Ba	3.37(0.068)	Ba			3.46(0.111)	Aa	3.2(0.12)	Aa													
	S3	3.26(0.065)	Bab	3.53(0.067)	ABab			3.23(0.112)	Ba	3.58(0.084)	Ab													
	S4	3.3(0.042)	ABa	3.1(0.119)	ABa			3.26(0.069)	Aa	3.26(0.036)	ABa													
	S5	2.89(0.123)	Bab	3.69(0.178)	Bc	3.03(0.076)	Aab	3.04(0.118)	ABab	3.35(0.095)	Abc	2.6(0.064)	ABa											
	S6	2.78(0.076)	Aa	3.21(0.104)	Bbc	2.99(0.062)	ABab	2.89(0.123)	ABab	3.48(0.054)	Ac	2.96(0.054)	Bab											
Cabon-to-nitrogen ratio (C/N)	S1	13.2(0.34)	Aa					13.7(0.47)	Ba					n.s.			***		***	**	***	10.45	0.69	***
	S2	14(0.21)	Aa	14.3(0.29)	Aa			13.9(0.42)	Ba	15.1(0.56)	Ba													
	S3	14.9(0.28)	Aa	14(0.25)	Aa			14.8(0.54)	Aa	13.7(0.33)	Ba													
	S4	15.1(0.14)	ABa	16.5(0.39)	ABCb			15.2(0.36)	Aa	15.2(0.09)	ABa													
	S5	17.3(0.74)	ABbc	13.6(0.83)	Aa	16.2(0.44)	Bb	16.2(0.66)	BCb	14.8(0.38)	Aab	19.1(0.45)	ABc											
	S6	18(0.49)	ABc	15.6(0.51)	Aab	16.3(0.3)	ABCbc	16.9(0.71)	ABbc	14.1(0.22)	Ca	16.6(0.23)	Abc											

Variable (abbreviation, unit)	S	I59*I		I59*NI		I59*NI_I		Rubi*I		Rubi*NI		Rubi*NI_I		CV		IRR			S	CVx IRR	CVx IRRxS	F	R^2	P
														I59	Rubi	I	NI	NI_I						
^{13}C isotopic discrimination (Δ13C, ‰)	S1	17.6(0.11)	ABb					17.1(0.13)	Ba					***		**			***	n.s.	***	14.64	0.75	***
	S2	17.3(0.1)	ABa	17.3(0.15)	CDa			16.9(0.1)	BCa	17.1(0.06)	Aa													
	S3	18.9(0.12)	ABb	18(0.12)	Aa			18.4(0.09)	Ab	17.6(0.12)	Da													
	S4	17.1(0.49)	Aa	17.9(0.12)	CDa			17.5(0.1)	Aa	17.8(0.1)	Ba													
	S5	18.3(0.14)	Aab	17.7(0.38)	ABa	18.9(0.22)	Ab	18.3(0.16)	Cab	18.1(0.16)	Aab	17.9(0.18)	Ca											
	S6	19.4(0.22)	Ab	19(0.1)	Aab	19.3(0.2)	Bb	18.9(0.11)	BCab	18.4(0.18)	Da	19(0.24)	Bab											

Three-way ANOVA for growth per compartment, dry mass partitioning, hydraulic conductance proxies, fruit dry mass-to-leaf area ratio, and leaf composition (factor: CV, IRR, S, and interaction CVxIRR, CVxIRRxS),
n.s.: not significant; *: $p<0.05$.; **: $p<0.01$; ***: $p<0.001$; asterisks´s position inside columns CV and IRR marks greater trend; F: Fisher´s value; R^2: determination coefficient; P: probability model; mean (SE);
Letters at the right of the mean show comparison using Tukey's HSD test, same uppercase letters indicate no significant differences between sampling date for each CV*IRR, same lowercase letters indicate no significant differences between CV*IRR into same sampling date, $p<0.05$.

Table S2. Comparison of state variables and ecophysiology traits with studies on coffee crops under irrigation treatments.

Variable	Abbreviation	Unit	Our range	Range in the coffee literature	Coffee cultivar literature	Age after planting	Coffee literature sources $^{\alpha}$	Comments to literature sources
Height	H	m	$1.2^{\mathrm{Rubi*NI}}$ – $1.58^{\mathrm{Rubi*I}}$	$0.78a^{I}$	Robusta, clone 14 ^{DT}	1 year	Pinheiro et al. (2004); Pinheiro et al. (2005)	
				$0.94b^{I}$	Robusta, clone 120 ^{DT}			
				$0.73a^{I}$	Robusta, clone 46 ^{DS}			
				$0.92b^{I}$	Robusta, clone 109A ^{DS}			
Basal area of stem	BA	cm^2	$11.3^{\mathrm{Rubi*NI}}$ – $16.6^{\mathrm{Rubi*I}}$					
Shoot dry mass	SDM	g	$559^{\mathrm{Rubi*NI}}$ – $1153^{\mathrm{Rubi*I}}$	5.28^{NI} – 6.51^{I}	Catuacaí 785-15 (a hybrid between Arabica, cv. Catucaí and the hybrid Icatu (C. arabica x C. canephora) ^{DS}	6 months	Dias et al. (2007)	(1) These averages were calculated by us as the multiplication of TDM and SMR, LMR or RMR, as appropriate.
				8.43^{NI} – 11.17^{I}	Siriema (a hybrid of C. arabica x C. racemosa) ^{DT}			
				55.68^{NI} – 84^{I}	Robusta, clone 02 ^{MDT}	1 year	Silva et al. (2013)	(1)
				60.45^{NI} – 105^{I}	Robusta, clone 03 ^{MDT}			
				27.69^{NI} – 32.56^{I}	Robusta, clone 14 ^{DT}			
				43.75^{NI} – 99.53^{I}	Robusta, clone 16 ^{MDT}			
				42.3^{NI} – 74.8^{I}	Robusta, clone 22 ^{MDT}			
				54.45^{NI} – 79.5^{I}	Robusta, clone 48 ^{DT}			
				22.05^{NI} – 41.6^{I}	Robusta, clone 109 ^{DS}			
				31.28^{NI} – 36.8^{I}	Robusta, clone 120 ^{DT}			
				51.3^{NI} – 72.6^{I}	Robusta, clone 201 ^{DS}			
				31.0^{2NI} – 71^{I}	Robusta, Apoatã ^{EDS}			
Leaf dry mass	LDM	g	$555^{\mathrm{Rubi*NI}}$ – $915^{\mathrm{I59*I}}$	10.29^{NI} – 13.23^{I}	Catuacaí 785-15 (a hybrid between Arabica, cv. Catucaí and the hybrid Icatu (C. arabica x C. canephora) ^{DS}	6 months	Dias et al. (2007)	(1)
				15.07^{NI} – 24.3^{I}	Siriema (a hybrid of C. arabica x C. racemosa) ^{DT}			
				72.96^{NI} – 120^{I}	Robusta, clone 02 ^{MDT}	1 year	Silva et al. (2013)	(1)
				42.9^{NI} – 115.5^{I}	Robusta, clone 03 ^{MDT}			
				23.43^{NI} – 39.6^{I}	Robusta, clone 14 ^{DT}			
				41.25^{NI} – 96.84^{I}	Robusta, clone 16 ^{MDT}			
				56.4^{NI} – 88^{I}	Robusta, clone 22 ^{MDT}			
				72.6^{NI} – 129.85^{I}	Robusta, clone 48 ^{DT}			
				23.31^{NI} – 66.3^{I}	Robusta, clone 109 ^{DS}			
				35.88^{NI} – 57.5^{I}	Robusta, clone 120 ^{DT}			
				40.5^{NI} – 92.4^{I}	Robusta, clone 201 ^{DS}			
				76.14^{NI} – 144.84^{I}	Robusta, Apoatã ^{EDS}			
Root dry mass	RDM	g	$242^{\mathrm{I59*NI}}$ – $318^{\mathrm{Rubi*I}}$	4.97^{NI} – 6^{I}	Catuacaí 785-15 (a hybrid between Arabica, cv. Catucaí and the hybrid Icatu (C. arabica x C. canephora) ^{DS}	6 months	Dias et al. (2007)	(1)
				6.82^{NI} – 9.2^{I}	Siriema (a hybrid of C. arabica x C. racemosa) ^{DT}			

Variable	Abbreviation	Unit	Our range	Range in the coffee literature	Coffee cultivar literature	Age after planting	Coffee literature sources $^{\alpha}$	Comments to literature sources
				61.44^{NI} – 96^{I}	Robusta, clone 02 ^{MDT}	1 year	Silva et al. (2013)	
				91.65*^{NI} – 129.5^{I}	Robusta, clone 03 ^{MDT}			
				19.17*^{NI} – 15.84^{I}	Robusta, clone 14 ^{DT}			
				40*^{NI} – 72.63^{I}	Robusta, clone 16 ^{MDT}			
				42.3^{NI} – 57.2^{I}	Robusta, clone 22 ^{MDT}			
				36.3^{NI} – 55.65^{I}	Robusta, clone 48 ^{DT}			
				17.64*^{NI} – 20.8^{I}	Robusta, clone 109 ^{DS}			
				24.84*^{NI} – 19.55^{I}	Robusta, clone 120 ^{DT}			
				43.2*^{NI} – 52.8^{I}	Robusta, clone 201 ^{DS}			
				35.25^{NI} – 68.16^{I}	Robusta, Apoatã ^{EDS}			
				176b^{I}	Robusta, clone 14 ^{DT}	1 year	Pinheiro et al. (2004); Pinheiro et al. (2005)	Root depth (m) significantly highest in clones DT (mean= 0.76) than in DS (0.51)
				268ab^{I}	Robusta, clone 120 ^{DT}			
				187b^{I}	Robusta, clone 46 ^{DS}			
				251a^{I}	Robusta, clone 109A ^{DS}			
Fruit dry mass ^{S5}	FDM	g	541 ^{I59*NI} – 1932 ^{I59*I}	2050	Arabica, cv. Catuaí Vermelho IAC44 ^{DS}	10 years	DaMatta et al. (2008)	No supplemental irrigation was provided, but there was abundant rain during the weeks preceding measurements. It receives an average rainfall annual of 1200 mm, chiefly distributed from October to March.
				2006= 2 300^{NI} 2007= 200^{NI} 2008= 3000^{NI}	Arabica, cv. Catuaí Vermelho IAC99 ^{UD}	7 year	Chaves et al. (2012)	The experiment, carried out under field conditions, began in 2006 with seven-year-old, ca. 2m tall coffee trees. No supplemental irrigation was provide, but there were abundant rains during the growing season (rainfall annual 1300 mm, mainly distributed from September to March, growing season). Here you can see the biennial harvest (2006-2008)
Aboveground dry mass	ADM	g	1114 ^{Rubi*NI} – 1990 ^{Rubi*I}	15.56b^{NI} – 19.74^{I}	Catuacaí 785-15 (a hybrid between Arabica, cv. Catucaí and the hybrid Icatu (C. arabica x C. canephora) ^{DS}	6 months	Dias et al. (2007)	These averages were calculated by us as the difference of TDM and RMR.
				23.51^{NI} – 35.46^{I}	Siriema (a hybrid of C. arabica x C. racemosa) ^{DT}			
				130.6a*^{NI} – 204b^{I}	Robusta, clone 02 ^{MDT}	1 year	Silva et al. (2013)	
				103.3a*^{NI} – 220.5a^{I}	Robusta, clone 03 ^{MDT}			
				51.8c*^{NI} – 72.2e^{I}	Robusta, clone 14 ^{DT}			
				85b*^{NI} – 196.4c^{I}	Robusta, clone 16 ^{MDT}			
				98.7b*^{NI} – 162.8d^{I}	Robusta, clone 22 ^{MDT}			
				128.7a*^{NI} – 209.3c^{I}	Robusta, clone 48 ^{DT}			
				45.4a*^{NI} – 109.2b^{I}	Robusta, clone 109 ^{DS}			
				67.2c*^{NI} – 95.4e^{I}	Robusta, clone 120 ^{DT}			
				91.8b*^{NI} – 167.2d^{I}	Robusta, clone 201 ^{DS}			
				105.8b*^{NI} – 215.8c^{I}	Robusta, Apoatã ^{EDS}			
Total dry mass	TDM	g	1898 ^{Rubi*NI} – 4208 ^{I59*I}	434b^{I}	Robusta, clone 14 ^{DT}	1 year	Pinheiro et al. (2004); Pinheiro	
				645a^{I}	Robusta, clone 120 ^{DT}			

Variable	Abbreviation	Unit	Our range	Range in the coffee literature	Coffee cultivar literature	Age after planting	Coffee literature sources ^{a}	Comments to literature sources
				$455b^{I}$	Robusta, clone 46 ^{DS}		et al. (2005)	
				$744a^{I}$	Robusta, clone 109A ^{DS}			
				$20.53b*^{NI}$ – $25.74b^{I}$	Catuacaí 785-15 (a hybrid between Arabica, cv. Catucaí and the hybrid Icatu (C. arabica x C. canephora) ^{DS}	6 months	Dias et al. (2007)	
				$30.33a*^{NI}$ – $44.66a^{I}$	Siriema (a hybrid of C. arabica x C. racemosa) ^{DT}			
				$192a*^{NI}$ – $300b^{I}$	Robusta, clone 02 ^{MDT}	1 year	Silva et al. (2013)	
				$195a*^{NI}$ – $350a^{I}$	Robusta, clone 03 ^{MDT}			
				$71c*^{NI}$ – $88e^{I}$	Robusta, clone 14 ^{DT}			
				$125b*^{NI}$ – $269c^{I}$	Robusta, clone 16 ^{MDT}			
				$141b*^{NI}$ – $220d^{I}$	Robusta, clone 22 ^{MDT}			
				$165a*^{NI}$ – $265c^{I}$	Robusta, clone 48 ^{DT}			
				$63a*^{NI}$ – $130b^{I}$	Robusta, clone 109 ^{DS}			
				$92c*^{NI}$ – $115e^{I}$	Robusta, clone 120 ^{DT}			
				$135b*^{NI}$ – $220d^{I}$	Robusta, clone 201 ^{DS}			
				$141b*^{NI}$ – $284c^{I}$	Robusta, Apoatã ^{EDS}			
Total leaf area	TLA	m^2	6.3 ^{Rubi*NI} – 11.4 ^{I59*I}	$0.147b*^{NI}$ – $0.203b^{I}$	Catuacaí 785-15 (a hybrid between Arabica, cv. Catucaí and the hybrid Icatu (C. arabica x C. canephora) ^{DS}	6 months	Dias et al. (2007)	
				$0.220a*^{NI}$ – $0.373a^{I}$	Siriema (a hybrid of C. arabica x C. racemosa) ^{DT}			
				$1.89a^{I}$	Robusta, clone 14 ^{DT}	1 year	Pinheiro et al. (2004)	
				$2.51a^{I}$	Robusta, clone 120 ^{DT}			
				$1.91a^{I}$	Robusta, clone 46 ^{DS}			
				$2.36b^{I}$	Robusta, clone 109A ^{DS}			
				$11.5b^{NI}$ – $12.1a^{I}$	Robusta, clone 120 ^{DT}	2 years	DaMatta et al. (2003)	
				$5.1a*^{NI}$ – $11.5a^{I}$	Robusta, clone 46 ^{DS}			
Shoot-to-total dry mass	SMR		0.25 ^{I59*I} – 0.30 ^{Rubi*I}	$0.257a^{NI}$ – $0.253a^{I}$	Catuacaí 785-15 (a hybrid between Arabica, cv. Catucaí and the hybrid Icatu (C. arabica x C. canephora) ^{DS}	6 months	Dias et al. (2007)	
				$0.278a*^{NI}$ – $0.250a^{I}$	Siriema (a hybrid of C. arabica x C. racemosa) ^{DT}			
				$0.29c^{NI}$ – $0.28c^{I}$	Robusta, clone 02 ^{MDT}	1 year	Silva et al. (2013)	
				$0.31c^{NI}$ – $0.30c^{I}$	Robusta, clone 03 ^{MDT}			
				$0.39a^{NI}$ – $0.37a^{I}$	Robusta, clone 14 ^{DT}			
				$0.35b^{NI}$ – $0.37a^{I}$	Robusta, clone 16 ^{MDT}			
				$0.30c*^{NI}$ – $0.34b^{I}$	Robusta, clone 22 ^{MDT}			
				$0.33b*^{NI}$ – $0.30c^{I}$	Robusta, clone 48 ^{DT}			
				$0.35b*^{NI}$ – $0.32b^{I}$	Robusta, clone 109 ^{DS}			
				$0.34b^{NI}$ – $0.32b^{I}$	Robusta, clone 120 ^{DT}			
				$0.38a*^{NI}$ – $0.33b^{I}$	Robusta, clone 201 ^{DS}			
				$0.22d*^{NI}$ – $0.25d^{I}$	Robusta, Apoatã ^{EDS}			
Leaf-to-total dry mass ratio	LMR		0.22 ^{Rubi*I} – 0.30 ^{Rubi*NI}	$0.501a^{NI}$ – $0.514a^{I}$	Catuacaí 785-15 (a hybrid between Arabica, cv. Catucaí	6 months	Dias et al. (2007)	

Variable	Abbreviation	Unit	Our range	Range in the coffee literature	Coffee cultivar literature	Age after planting	Coffee literature sources $^{\alpha}$	Comments to literature sources
					and the hybrid Icatu (C. arabica x C. canephora) ^{DS}			
				$0.497a^{*NI} – 0.544a^{I}$	Siriema (a hybrid of C. arabica x C. racemosa) ^{DT}			
				$0.38c^{NI} – 0.40c^{I}$	Robusta, clone 02 ^{MDT}	1 year	Silva et al. (2013)	
				$0.22f^{*NI} – 0.33e^{I}$	Robusta, clone 03 ^{MDT}			
				$0.33d^{*NI} – 0.45b^{I}$	Robusta, clone 14 ^{DT}			
				$0.33d^{*NI} – 0.36d^{I}$	Robusta, clone 16 ^{MDT}			
				$0.40c^{NI} – 0.40c^{I}$	Robusta, clone 22 ^{MDT}			
				$0.44b^{*NI} – 0.49a^{I}$	Robusta, clone 48 ^{DT}			
				$0.37e^{*NI} – 0.51a^{I}$	Robusta, clone 109 ^{DS}			
				$0.39c^{*NI} – 0.50a^{I}$	Robusta, clone 120 ^{DT}			
				$0.30c^{*NI} – 0.42c^{I}$	Robusta, clone 201 ^{DS}			
				$0.54a^{NI} – 0.51a^{I}$	Robusta, Apoatã ^{EDS}			
				$0.39^{NI} – 0.35^{I}$	Arabica, cv. Catuaí Vermelho IAC 44 ^{DS}	1 year	Cavatte et al. (2012a)	
Root-to-total dry mass ratio	RMR		$0.08^{I59*I} – 0.13^{Rubi*NI}$	$0.242a^{NI} – 0.233a^{I}$	Catuacaí 785-15 (a hybrid between Arabica, cv. Catucaí and the hybrid Icatu (C. arabica x C. canephora) ^{DS}	6 months	Dias et al. (2007)	
				$0.225a^{NI} –0.206a^{I}$	Siriema (a hybrid of C. arabica x C. racemosa) ^{DT}			
				$0.32b^{NI} – 0.32c^{I}$	Robusta, clone 02 ^{MDT}	1 year	Silva et al. (2013)	
				$0.47a^{*NI} – 0.37b^{I}$	Robusta, clone 03 ^{MDT}			
				$0.27c^{*NI} – 0.18b^{I}$	Robusta, clone 14 ^{DT}			
				$0.32b^{*NI} – 0.27a^{I}$	Robusta, clone 16 ^{MDT}			
				$0.30b^{NI} – 0.26b^{I}$	Robusta, clone 22 ^{MDT}			
				$0.22d^{NI} – 0.21b^{I}$	Robusta, clone 48 ^{DT}			
				$0.28c^{*NI} – 0.16b^{I}$	Robusta, clone 109 ^{DS}			
				$0.27c^{*NI} – 0.17b^{I}$	Robusta, clone 120 ^{DT}			
				$0.32b^{*NI} – 0.24b^{I}$	Robusta, clone 201 ^{DS}			
				$0.25d^{NI} – 0.24b^{I}$	Robusta, Apoatã ^{EDS}			
				$0.37^{NI} – 0.35^{I}$	Arabica, cv. Catuaí Vermelho IAC 44 ^{DS}	1 year	Cavatte et al. (2012a)	
Fruit-to-total dry mass ratio	FMR		$0.29^{Rubi*NI} – 0.45^{I59*I}$					
Leaf area-to-total dry mass ratio	LAR	$m^{2}_{TLA}\ kg^{-1}_{TDM}$	$2.3^{Rubi*I} – 3.6^{I59*NI\_I}$	$7.18a^{NI} – 7.81a^{I}$	Catuacaí 785-15 (a hybrid between Arabica, cv. Catucaí and the hybrid Icatu (C. arabica x C. canephora) ^{DS}	6 months	Dias et al. (2007)	
				$7.01a^{*NI} – 8.44a^{I}$	Siriema (a hybrid of C. arabica x C. racemosa) ^{DT}			
				$4.81^{NI} – 4.33^{I}$	Arabica, cv. Catuaí Vermelho IAC 44 ^{DS}	1 year	Cavatte et al. (2012a)	
Specific leaf area	SLA	$m^{2}_{TLA}\ kg^{-1}_{LDM}$	$10.6^{Rubi*I} – 12.5^{I59*I}$	11.4	Arabica, cv. Caturra ^{DS}	28 year	Charbonnier et al. (2017)	The climate is tropical humid with no dry season (Peel et al., 2007). Rainfall annual is approximately 2860 mm. Mean of SLA from coffee

Variable	Abbreviation	Unit	Our range	Range in the coffee literature	Coffee cultivar literature	Age after planting	Coffee literature sources $^{\alpha}$	Comments to literature sources
								agroforestry system under light environment in the open.
				$14.72a^{NI}$ – $15.46a^{I}$	Catuacaí 785-15 (a hybrid between Arabica, cv. Catucaí and the hybrid Icatu (C. arabica x C. canephora) ^{DS}	6 months	Dias et al. (2007)	
				$14.17a^{NI}$ – $15.43a^{I}$	Siriema (a hybrid of C. arabica x C. racemosa) ^{DT}			
				10.9^{NI} – 11^{I}	Arabica, cv. Catuaí Vermelho IAC 44 ^{DS}	1 year	Cavatte et al. (2012b)	
				$11.2b^{NI}$ – $10.9b^{I}$	Robusta, clone 02 ^{MDT}	1 year	Silva et al. (2013)	
				$9.67c^{NI}$ – $10.4c^{I}$	Robusta, clone 03 ^{MDT}			
				$12.7a^{NI}$ – $12.9a^{I}$	Robusta, clone 14 ^{DT}			
				$12.3a^{NI}$ – $12.3a^{I}$	Robusta, clone 16 ^{MDT}			
				$12.4a^{NI}$ – $12.5a^{I}$	Robusta, clone 22 ^{MDT}			
				$11.0b^{NI}$ – $10.1c^{I}$	Robusta, clone 48 ^{DT}			
				$10.3c^{NI}$ – $11b^{I}$	Robusta, clone 109 ^{DS}			
				$11.3b^{NI}$ – $11.2b^{I}$	Robusta, clone 120 ^{DT}			
				$11.2b^{NI}$ – $11.7b^{I}$	Robusta, clone 201 ^{DS}			
				$10.9b^{*NI}$ – $13.4a^{I}$	Robusta, Apoatã ^{EDS}			
				6.54	Arabica, cv. Costa Rica 95 ^{UD}	6 years	Vaast et al. (2005)	The experimental plot was located at 1180 m elevation, and has a mean annual temperature of 22 °C and a mean annual rainfall of 2200mm (no apparent water stress). Cultivar 'Costa Rica 95' is a dwarf cultivar with a maximum height not exceeding 2.5 m after four to five years of growth.
Root dry mass-to-leaf area ratio, indicating capacity to use water	RLA	$g_{RDM}\ m^{-2}_{TLA}$	29^{I59*I} – 43^{Rubi*I}	33.8^{NI} – 29.6^{I}	Catuacaí 785-15 (a hybrid between Arabica, cv. Catucaí and the hybrid Icatu (C. arabica x C. canephora) ^{DS}	6 months	Dias et al. (2007)	These averages were calculated by us as the RDM-to-TLA ratio.
				31^{NI} – 24.7^{I}	Siriema (a hybrid of C. arabica x C. racemosa) ^{DT}			
				$93.5a^{I}$	Robusta, clone 14 ^{DT}	1 year	Pinheiro et al. (2005)	
				$107.2a^{I}$	Robusta, clone 120 ^{DT}			
				$113a^{I}$	Robusta, clone 46 ^{DS}			
				$120.8a^{I}$	Robusta, clone 109A ^{DS}			
Basal area trunk-to-leaf area ratio x 10^{-4}, a proxy for hydraulic conductance	BLR	$m^{2}_{BA}\ m^{-2}_{TLA}$	1.4^{I59*I} – 1.9^{Rubi*I}					
Root dry mass-to-basal area ratio,	RBR	$g_{RDM}\ cm^{-2}_{BA}$	21^{I59*NI} – $24^{Rubi*NI\_I}$					

Variable	Abbreviation	Unit	Our range	Range in the coffee literature	Coffee cultivar literature	Age after planting	Coffee literature sources ^{a}	Comments to literature sources
proxy for the inverse of hydraulic conductance								
Fruit dry mass-to-leaf area ratio, indicator of source-to-fruit sink ratio ^{S5}	FLA	$g_{FDM}\ m^{-2}_{TLA}$	$82^{\mathrm{I59*NI\_I}}$ – $167^{\mathrm{I59*I}}$					
Percent carbon leaf	C	%	$48.4^{\mathrm{Rubi*I}}$ – $49.8^{\mathrm{I59*I}}$	46.3^{NI}	Arabica, cv. Caturra ^{DS}	28 year	Charbonnier et al. (2017)	
Percent nitrogen leaf	N	%	$2.78^{\mathrm{I59*I}}$ – $3.48^{\mathrm{Rubi*NI}}$	3.15^{NI}	Arabica, cv. Catuaí Vermelho IAC44 ^{DS}	10 years	DaMatta et al. (2008)	
				2.96^{NI}	Arabica, cv. Catuaí Vermelho IAC 44 ^{DS}	13 years	Matos et al. (2009)	The experiment was conducted under field conditions and non-irrigated treatment.
				3.36^{NI}	Arabica, cv. Caturra ^{DS}	28 year	Charbonnier et al. (2017)	This was calculated by us as the multiplication between SLA (m^2_{TLA} kg^{-1}_{LDM}) and nitrogen content (kgN m^{-2}_{LA})*100.
				3^{NI}	Arabica, cv. Catuaí Vermelho IAC99 ^{UD}	7 years	Chaves et al. (2012)	
Carbon-to-nitrogen percent leaf	C/N		$14^{\mathrm{Rubi*NI}}$ – $18^{\mathrm{I59*I}}$	13.78^{NI}	Arabica, cv. Caturra ^{DS}	28 year	Charbonnier et al. (2017)	This was calculated by us from the provided information of %C and %N leaf.
Carbon 13 isotope discrimination	$\Delta^{13}C$	‰	$18.9^{\mathrm{Rubi*NI}}$ – $19.4^{\mathrm{I59*I}}$	$-22.3*^{\mathrm{I}}$ – -24.6^{NI}	Arabica, cv. Catuaí Vermelho IAC 44 ^{DS}	1 year	Cavatte et al. (2012b); Cavatte et al. (2012a)	(2) Measurement of $\delta^{13}C$
				-29.42^{NI}	Arabica, cv. Catuaí Vermelho IAC99 ^{UD}	7 years	Chaves et al. (2012)	(2)
				-26.5^{NI} – -27.5^{I}	Robusta, clone 02 ^{MDT} Robusta, clone 03 ^{MDT} Robusta, clone 14 ^{DT} Robusta, clone 16 ^{MDT} Robusta, clone 22 ^{MDT} Robusta, clone 48 ^{DT} Robusta, clone 109 ^{DS} Robusta, clone 120 ^{DT} Robusta, clone 201 ^{DS} Robusta, Apoatã ^{EDS}	1 year	Silva et al. (2013)	(2) Mean approximate for all clones
				$[16.5 – 20]^{\mathrm{NI}}$ – $[18.5 – 20.5]^{\mathrm{I}}$ $[17.5 – 21]^{\mathrm{NI}}$ – $[19 – 21]^{\mathrm{I}}$	Robusta, clone 120 ^{DT} Robusta, clone 46 ^{DS}	2 years	DaMatta et al. (2003)	$\Delta^{13}C$ of leaves in relation to their position on a plagiotropic branch, between first node of attachment of expanding leaves (c. half final size) and five node successively older leaves [1st – 5thnode]. Mean of six replicates; the standard error did not

Variable	Abbreviation	Unit	Our range	Range in the coffee literature	Coffee cultivar literature	Age after planting	Coffee literature sources ^{a}	Comments to literature sources
								exceed 1.5% of the mean value.
				[17.98 – 18.78]^{NI} – [20.29 – 19.41]^{I} [16.05 – 18.05]^{NI} – [20.06 – 19.33]^{I} [16.10 – 18.60]^{NI} – [19.38 – 18.89]^{I} [16.65 – 18.97]^{NI} – [18.49 – 18.67]^{I} [16.29 – 18.38]^{NI} – [18.53 – 18.22]^{I}	Arabica, cv. San Ramon ^{DT} Arabica, cv. Moka ^{UD} Arabica, cv. Yellow Caturra ^{DS} Arabica, cv. Guatemalan ^{UD} Arabica, cv. Catuaí ^{DS}	6 months	Meinzer et al. (1990)	Leaves in different states [Expanding – Mature]
Leaf predawn water potential^{WS}	Ψ_{pd}	MPa	-0.2 ^{I59*I} – -1.9 ^{Rubi*NI}	-1.8 ^{NI} – -0.5 ^{I} -1 ^{NI} – -0.3 ^{I} -1.1 ^{NI} – -0.3 ^{I}	Arabica, cv. Typica^{DS} Arabica, cv. San Ramon^{DT} Arabica, cv. Yellow Caturra^{DT}	10 years	Tausend et al. (2000a)	
				-1.43b*^{NI} – -0.17a^{I} -0.65a*^{NI} – -0.10a^{I}	Catuacaí 785-15 (a hybrid between Arabica, cv. Catucaí and the hybrid Icatu (C. arabica x C. canephora) ^{DS} Siriema (a hybrid of C. arabica x C. racemosa) ^{DT}	6 months	Dias et al. (2007)	
				-2.93a*^{NI} – -0.05a^{I} -2.95a*^{NI} – 0.05a^{I} -2.95a*^{NI} – 0.08a^{I} -2.97a*^{NI} – 0.06a^{I}	Robusta, clone 14^{DT} Robusta, clone 120 ^{DT} Robusta, clone 46 ^{DS} Robusta, clone 109A ^{DS}	1 year	Pinheiro et al. (2004)	
				-0.60b^{NI} – 0.05a*^{I} -1.48a^{NI} – 0.05a*^{I}	Robusta, clone 120 ^{DT} Robusta, clone 46 ^{DS}	2 years	DaMatta et al. (2003)	
				-2.7^{NI} – -0.2^{I}	Robusta, cv. Kouillou ^{DT} Arabica, cv. Red Catuaí ^{DS}	14 months	DaMatta et al. (1997)	
				EDS= -3*^{NI} – <-0.02^{I} DS= [-2 – -1.8]*^{NI} – [<-0.02]^{I} MDT= [-2.5 – -1.5]*^{NI} – [<-0.02]^{I} DT= [-2 – -0.5]*^{NI} – [<-0.02]^{I}	Robusta, clone 02 ^{MDT} Robusta, clone 03 ^{MDT} Robusta, clone 14 ^{DT} Robusta, clone 16 ^{MDT} Robusta, clone 22 ^{MDT} Robusta, clone 48 ^{DT} Robusta, clone 109 ^{DS} Robusta, clone 120 ^{DT} Robusta, clone 201 ^{DS} Robusta, Apoatã ^{EDS}	1 year	Silva et al. (2013)	Lower and upper limits [low – upper] of all cultivars by irrigation condition (I vs NI) and category sensitivity to drought (EDS, DS, MDT, or DT).
Leaf midday water potential^{WS}	Ψ_{md}	MPa	-0.7 ^{I59*I} – -2.4 ^{Rubi*NI}	-2.5 ^{NI} – -1.5 ^{I} -1.7 ^{NI} – -1.1 ^{I} -1.7 ^{NI} – -1.3 ^{I}	Arabica, cv. Typica^{DS} Arabica, cv. San Ramon^{DT} Arabica, cv. Yellow Caturra^{DT}	10 years	Tausend et al. (2000a)	
				-2.49b*^{NI} – -0.80a^{I} -1.85a*^{NI} – -0.73a^{I}	Catuacaí 785-15 (a hybrid between Arabica, cv. Catucaí and the hybrid Icatu (C. arabica x C. canephora) ^{DS} Siriema (a hybrid of C. arabica x C. racemosa) ^{DT}	6 months	Dias et al. (2007)	
				-1.45b^{NI} – -0.54a*^{I} -2.66a^{NI} – -0.66a*^{I}	Robusta, clone 120 ^{DT} Robusta, clone 46 ^{DS}	2 years	DaMatta et al. (2003)	
				-3a^{NI} – -0.2a*^{I} -3a^{NI} – 0.2a*^{I}	Robusta, clone 120 ^{DT} Robusta, clone 109A ^{DS}	10 months	Lima et al. (2002)	
				EDS= -3.75*^{NI} – <-0.3^{I} DS= [-3.5 – -3]*^{NI} – [<-0.3]^{I}	Robusta, clone 02 ^{MDT} Robusta, clone 03 ^{MDT}	1 year	Silva et al. (2013)	

Variable	Abbreviation	Unit	Our range	Range in the coffee literature	Coffee cultivar literature	Age after planting	Coffee literature sources $^{\alpha}$	Comments to literature sources
				MDT= [-4.25 – -2.5]*^{NI} – [<-0.3]^{I} DT= [-3.5 – -1.75]*^{NI} – [<-0.3]^{I}	Robusta, clone 14 ^{DT} Robusta, clone 16 ^{MDT} Robusta, clone 22 ^{MDT} Robusta, clone 48 ^{DT} Robusta, clone 109 ^{DS} Robusta, clone 120 ^{DT} Robusta, clone 201 ^{DS} Robusta, Apoatã ^{EDS}			
Sap flow^{WS}	SF	kg$_{H2O}$ plant^{-1} day^{-1}	0.1 ^{I59*NI} – 8.4 ^{Rubi*I}	6 ^{NI} – 11 ^{I} 2 ^{NI} – 4 ^{I} 2 ^{NI} – 7 ^{I}	Arabica, cv. Typica^{DS} Arabica, cv. San Ramon^{DT} Arabica, cv. Yellow Caturra^{DT}	10 years	Tausend et al. (2000a)	
				4.9 1.7 4.3	Arabica, cv. Typica^{DS} Arabica, cv. San Ramon^{DT} Arabica, cv. Yellow Caturra^{DT}	10 years	Tausend et al. (2000b)	
				3.8*^{dry} – 8.3^{wet} 6.1^{dry} – 4.3^{wet} 1^{dry} – 1.2^{wet} 0.2*^{dry} – 1.7^{wet} 2^{dry} – 2.8^{wet} 1.3^{dry} – 2.2^{wet} 1.5^{dry} – 3.9^{wet} 4.3^{dry} – 5.9^{wet}	Blepharocalyx salicifolius Caryocar brasiliense Erythroxylum suberosum Kielmeyera coriaceae Ouratea hexasperma Qualea parviJora Scheflera macrocarpa Stvrax ferrupineus	---	Bucci et al. (2005)	A field experimental station located south of the center of Brasilia, Brazil. Includes extensive areas of all major physiognomic forms of Cerrado vegetation from very open to closed savannas. Same climatic region of our experimental area (Ratter et al., 1997). Whole-plant sap flow was measured during 2-3 consecutive days in each of three to five individuals per species during dry and wet seasons.
Canopy conductance^{WS}	g_C	cm s^{-1}	0.01 ^{I59*NI} – 0.41 ^{Rubi*I}	41a *^{NI} – 70a ^{I} 25a *^{NI} – 48b ^{I} 20b *^{NI} – 51b ^{I}	Arabica, cv. Typica^{DS} Arabica, cv. San Ramon^{DT} Arabica, cv. Yellow Caturra^{DT}	10 years	Tausend et al. (2000a)	g_C (mmol$_{H2O}$ m^{-2}$_{LA}$ s^{-1})= (E*P)/(V_a *TLA), where E is transpiration rate, P is atmospheric pressure, and V_a is the vapor pressure difference between the leaf interior and bulk air.
Soil-to-leaf total hydraulic conductance^{WS}	g_L	kg$_{H2O}$ MPa^{-1} plant^{-1} h^{-1}	0.012 ^{I59*NI} – 0.81 ^{Rubi*I}	DS, K_L= 4.57*^{NI} – 10^{I} DT, K_L= 0.35*^{NI} – 1.05^{I}	Catuacaí 785-15 (a hybrid between Arabica, cv. Catucaí and the hybrid Icatu (C. arabica x C. canephora) ^{DS} Siriema (a hybrid of C. arabica x C. racemosa) ^{DT}	6 months	Dias et al. (2007)	(3) Apparent leaf-to-soil hydraulic conductance (K_L, mmol$_{H2O}$ MPa^{-1} m^{-2} s^{-1}). K_L were expressed as the ratios of the total transpiration (estimated gravimetrically) from predawn to midday and the differences in the leaf water potential measured during this interval.
				EDS, K_L= 0.5*^{NI} – 6^{I} DS, K_L= [0.5 – 1]*^{NI} – [3– 3.5]^{I} MDS, K_L= [0.1 – 1]*^{NI} – [1.5 – 3.75]^{I} DT, K_L= [0.5 – 1]*^{NI} – [1.8 – 2]^{I}	Robusta, clone 02 ^{MDT} Robusta, clone 03 ^{MDT} Robusta, clone 14 ^{DT} Robusta, clone 16 ^{MDT} Robusta, clone 22 ^{MDT} Robusta, clone 48 ^{DT} Robusta, clone 109 ^{DS} Robusta, clone 120 ^{DT} Robusta, clone 201 ^{DS}	1 year	Silva et al. (2013)	(3)

Variable	Abbreviation	Unit	Our range	Range in the coffee literature	Coffee cultivar literature	Age after planting	Coffee literature sources $^{\alpha}$	Comments to literature sources
					Robusta, Apoatã ^{EDS}			
				$K_L = 0.72*^{NI} – 1.12^{I}$	Arabica, cv. Catuaí Vermelho IAC 44 ^{DS}	1 year	Cavatte et al. (2012a)	(3) (3)
Relative growth rate^{WS}	RGR	$g_{TDM}\ g^{-1}_{TDM}\ d^{-1}$	0.03 ^{mean}	$0.013a*^{NI} – 0.016b^{I}$	Catuacaí 785-15 (a hybrid between Arabica, cv. Catucaí and the hybrid Icatu (C. arabica x C. canephora) ^{DS}	6 months	Dias et al. (2007)	
				$0.014a*^{NI} – 0.020a^{I}$	Siriema (a hybrid of C. arabica x C. racemosa) ^{DT}			
				$0.0069*^{NI} – 0.0105^{I}$	Arabica, cv. Catuaí Vermelho IAC 44 ^{DS}	1 year	Cavatte et al. (2012b); Cavatte et al. (2012a)	
Net assimilation rate^{WS}	NAR	$g_{TDM}\ m^{-2}_{TLA}\ d^{-1}$	0.00025 ^{mean}	$1.52a*^{NI} – 2.11a^{I}$	Catuacaí 785-15 (a hybrid between Arabica, cv. Catucaí and the hybrid Icatu (C. arabica x C. canephora) ^{DS}	6 months	Dias et al. (2007)	
				$1.76b*^{NI} – 2.34a^{I}$	Siriema (a hybrid of C. arabica x C. racemosa) ^{DT}			
				$3.92*^{NI} – 7.98^{I}$	Arabica, cv. Catuaí Vermelho IAC 44 ^{DS}	1 year	Cavatte et al. (2012b); Cavatte et al. (2012a)	
Phenotypic plasticity index based on maximum and minimum means	PPI_m (SF, g_C, and g_L)		$SF = 0.79^{Rubi} – 0.93^{I59}$ $g_C = 0.78^{Rubi} – 0.94^{I59}$ $g_L = 0.74^{Rubi} – 0.95^{I59}$					
	PPI_m (Ψ_{pd} and Ψ_{pm})		$\Psi_{pd} = 0.67^{I59} – 0.86^{Rubi}$ $\Psi_{pm} = 0.44^{I59} – 0.60^{Rubi}$	$\Psi_{pd} = 0.93$ $\Psi_{pm} = 0.55$	Arabica, cv. Catuaí Vermelho IAC 44 ^{DS}	1 year	Cavatte et al. (2012a)	

Our range for all CV*IRR with ca. 2.2-older-year after planting (S6), with exception of hydraulic traits with ca. 1.8-older-year after planting (S5) into water stress season (^{WS}); ^{I}: irrigated during the dry season our study and for literature sources; $^{NI\_I}$: non-irrigated year 1 and irrigated during the dry season year 2, only for our study; ^{NI}: non-irrigated during the dry season our study and for literature sources; ^{DT}: drought-tolerant; ^{MDT}: moderately drought-tolerant; ^{DS}: drought-sensitive; ^{EDS}: extremely drought-sensitive; ^{UD}: unknown hydric strategy; *: $p<0.05$, indicate significant differences over irrigated treatments for a given coffee cultivars; lowercase letters: indicate significant differences between coffee cultivars for a given irrigated treatment (^{I} or ^{NI}); $^{\alpha}$: coffee literature sources in bibliography of supplementary materials

Supplementary Figures

Fig. S1. Coffee crop of 7 years old of I59 (left, drought-tolerant) and Rubi (right, drought-sensitive) cultivated in field condition the experimental field of Embrapa Cerrados-Brasilia, without irrigation and subjected to more than 200 days of drought. Note that under these conditions, leaves are still present for I59 but not for Rubi.

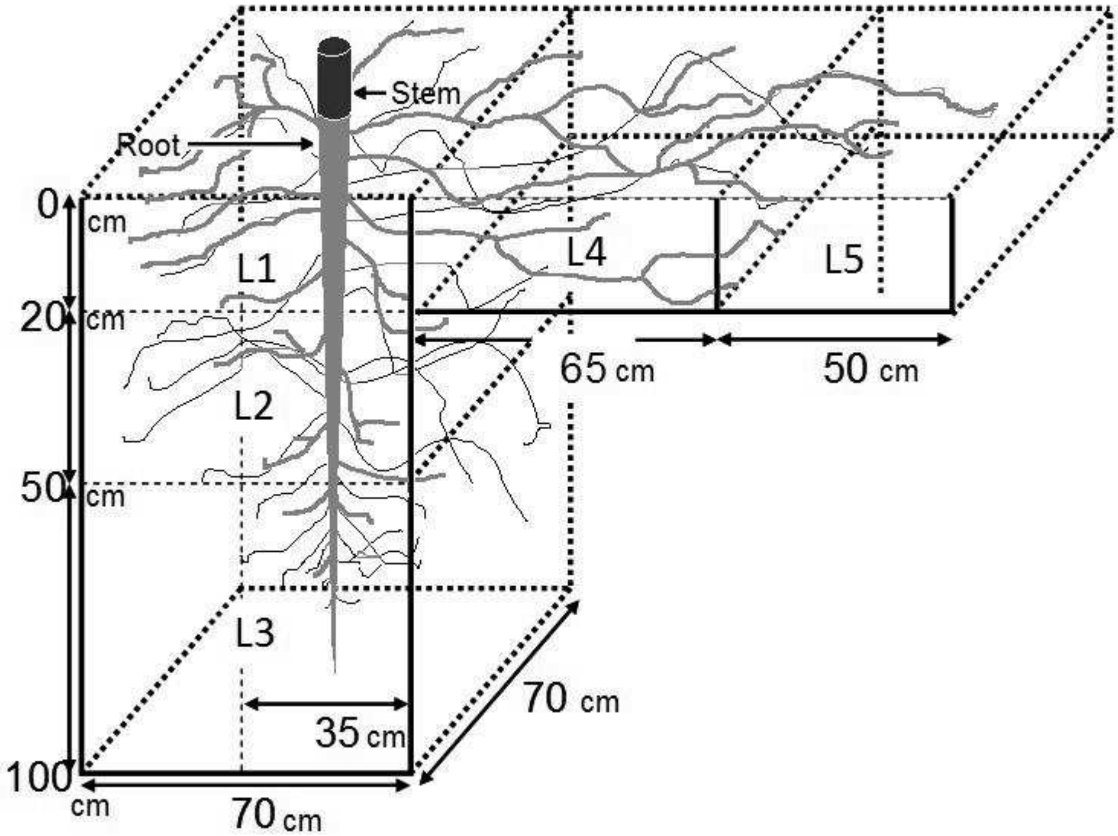

Fig. S2. Sketch of layers explored during root harvesting (H1 to H5). S1 and S2: sampling only in H1-H2; S3 to S6: sampling in H1-H3 +H4-H5, where H4 and H5 contained lateral roots in-between plantation lines. The distal end of L5 corresponded to the centre of the inter-row. Preliminary test, it was observed that more 90% of the roots were distributed in H1 to H3.

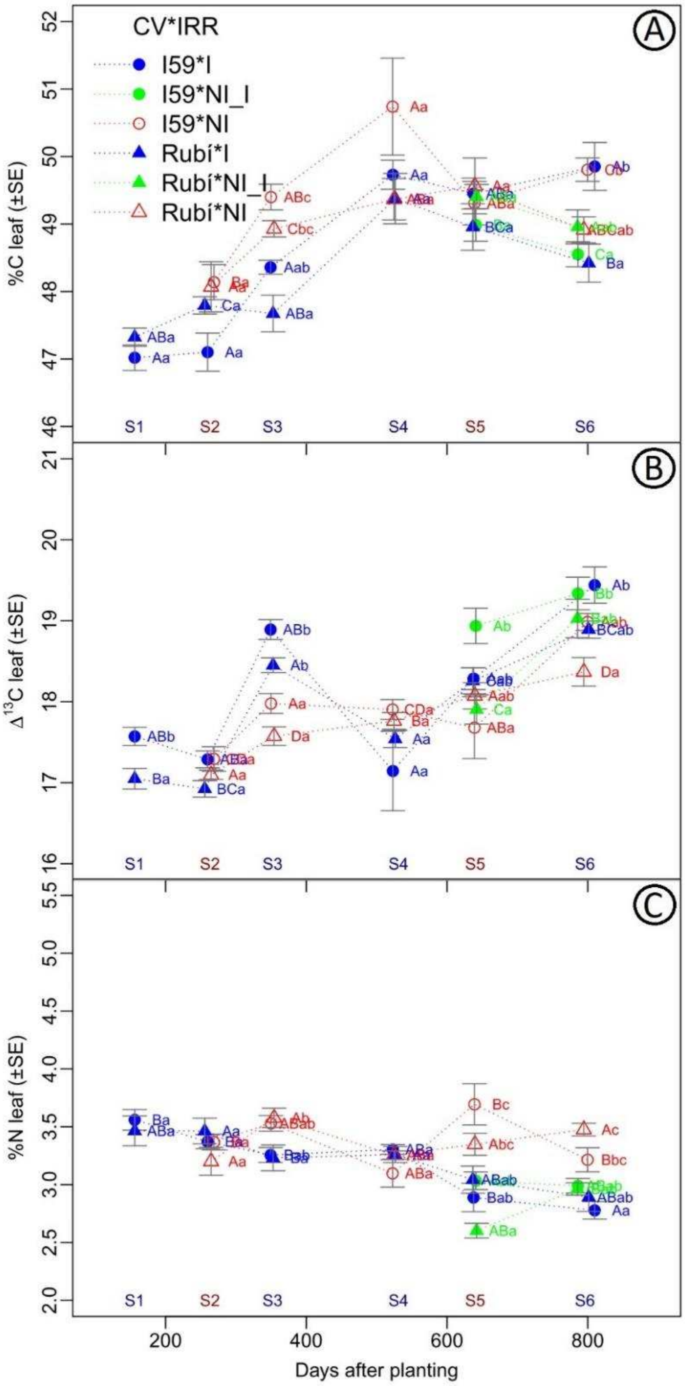

Fig. S3. Leaf composition (carbon: A; carbon isotope discrimination: B; and nitrogen: C), from S1 to S6, for cultivars I59 and Rubi (filled and empty circles, respectively), irrigated during the dry season (I, in blue), non-irrigated year 1 and irrigated during the dry season year 2 (NI_I, in green), or non-irrigated during the dry season (NI, in red). Uppercase letters indicate significant differences over time for a given CV*IRR combination, whereas lowercase letters indicate significant differences between CV*IRR combinations at a given sampling date, according to the Tukey's HSD test, p<0.05.

CHAPTER 2

Canopy architecture adjustments of two coffee cultivars contrasting in hydric functioning under moderate drought

RESEARCH PAPER

Canopy architecture adjustments of two coffee cultivars contrasting in hydric functioning under moderate drought

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Highlight

Canopy architecture adjustments proved countervailing effects that explain similar vegetative growth and yield despite differences in hydric functioning of two contrasting coffee cultivars under moderate drought.

Abstract

Plant architecture and its plasticity to drought are by far much less studied than physiological features. This study focused on the dynamics of canopy architecture traits of two coffee cultivars, cv. RUBI MG1192 (Rubi: drought sensitive) and cv. IAPAR59 (I59: drought tolerant). The trials were conducted over two years; three irrigation treatments were applied (irrigated and non-irrigated during the dry seasons, and irrigated during the second dry season only). Samplings and measurements were performed at six times (7-10 plants per treatment combination, totalling 211 plants). The following parameters were evaluated: branch setting (number and length), number of phytomers, leaf shedding and renewal, dynamics of leaf area and internode length; in addition, the patterns of light intercepted by the canopy was modelled. All canopy architectural data were analysed using the AMAPstudio-Xplo-Simeo software. Overall, drought had effects on all of the studied variables but no architectural trait appeared to be specifically responsive to water stress. Rubi expresses a greater proportion of higher order branches allowing its fast recovery from drought. This was associated with a high number of phytomers that in turn supported faster development of axillary buds (leaves and/or floral buds). These are important elements to account for selecting cultivars adapted to a given climate or for guiding breeding programs. The fitness of coffee plants submitted to climatic events depends on the adequacy of physiological and organo-morphogenetic features and, consequently, breeding programs must account for both aspects.

Key words: water stress / modelling the light intercepted / phytomer / plant canopy architecture / AMAPstudio.

Abbreviations

A: net carbon assimilation (μmol_{CO2} m^{-2} s^{-1});

B1: first order branch;

B2: second order branch;

B3: third order branch;

CV: Coffee variety (I59 vs. Rubi);

DAP: days after planting;

ET_0: potential evapotranspiration (mm_{H2O} d^{-1});

g_s: stomatal conductance ($mmol_{H2O}$ m^{-2} s^{-1});

I: irrigated;

I59: IAPAR59 coffee cultivar, drought-tolerant, and crossed with Robusta (C. arabica cv. Villa Sarchi x HT 832/2 introgression of Canephora);

IRR: irrigation factor (I, NI or NI-I);

MS: main stem;

NI: non-irrigated;

NI-I: non-irrigated during the first dry season and irrigated during the second dry season;

PAR: photosynthetically active incident radiation (MJ m^{-2} d^{-1});

R: rainfall (mm_{H2O} d^{-1});

Rh: relative humidity of the air (%);

Rubi: RUBI-MG1192 coffee cultivar, sensitive-drought, and Arabica (C. arabica cv. Mundo Novo x C. arabica cv. Catuai);

S: sampling date (S1, S2, S3, S4, S5 and S6);

SLA: specific leaf area (m^2_{TLA} kg^{-1}_{LDM});

Ta: air temperature (°C);

TB: total branches, including the first, second and third order branches;

TIL: total daily intercepted light by leaves (MJ $plant^{-1}$);

TLA: total leaf area (m^2);

VPD: vapour pressure deficit of the air (hPa);

WUE: water-use efficiency ($g_{\text{Dry mass}}$ kg_{H2O}^{-1} $plant^{-1}$).

Introduction

Coffee, a widely marked worldwide commodity, is the source of income for approximately 80 developing countries in the tropics (Pay, 2009). Among more than 100 species of the Coffea genus, Coffea arabica L. (arabica coffee) and Coffea canephora Pierre ex. A. Froehner (robusta coffee) economically dominate the world coffee trade, and represent ca. 70% and 30% of the world's commercial production, respectively. Coffee crop involves some 500 million people to manage the product, from cultivation to final consumption (Rezende and Rosado, 2004), and livelihoods of about 25 million small producers globally depend on arabica coffee (Pendergrast, 2010). Although coffee production is strongly affected by drought events, most of world's coffee has been cropped by smallholders in drought-prone regions where irrigation is an exception (DaMatta and Ramalho, 2006). Indeed, limited water supply is the major environmental stress affecting coffee production not only in Brazil but also in several other coffee growing countries (DaMatta, 2004). Selecting cultivars that could withstand severe drought spells with acceptable yields under drought conditions is therefore of utmost importance (DaMatta and Ramalho, 2006).

Several studies addressed the effects of drought on coffee physiology (DaMatta and Ramalho, 2006). They pointed out that the physiological mechanisms underlying coffee tolerance to drought are largely related to the strong sensitivity of coffee stomata regulation (Pinheiro et al., 2005). On the other hand, the role of plant structure remains poorly explored. Studies of morphological changes when plants are facing drought are commonly confined to some global variables such as plant height, leaf area per plant, number of branches or biomass (Dias et al., 2007; Matos et al., 2009) whereas the parameters of the plant structure are ignored.

Plant structure plays an important role concerning the plant interaction with environment: light capture, photosynthesis, transpiration, water and nutrient uptake, etc. The functional-structural plant modelling (FSPM) approach is dedicated to the modelling of such interactions. For instance, plants deploy photosynthetic surfaces in order to optimize light interception and produce carbohydrates which, in turn, will be allocated to all plant structures for ensuring their growth and maintenance (Guo et al., 2011). In this respect, 3D plant structure is a key piece to integrate and understand the relationships between the functions of different organs at the level of the entire plant (Guo et al., 2011). This has become a major challenge in the last decade to model and simulate the architecture of plants within different climatic scenarios (Fourcaud et al., 2008; Guo et al., 2011; Matsunaga et al., 2016).

However, using 3D structure of plants for simulating biophysical processes is only one aspect of FSPMs. Indeed, the concept of plant architecture goes beyond of the plant structure at a given time but deals with the dynamics of plants along their ontological and phenological stages (Barthélémy and Caraglio, 2007). Description of structure at a given stage does not give proper information for analysing the effects of drought events if the trajectory of plant development is not accounted for. Actually, one has to address the organogenetic (e.g. phyllochrone and branching) and morphogenetic (e.g. leaf expansion) responses to drought to really understand what are the effects of physiological stress at a given time. The emphasis is therefore put in this study on the elementary growth processes that build the plant architecture and, namely, the setting rate of new metamers and ramifications.

The present study was conducted on two cultivars of C. arabica, one deemed to be drought-tolerant (I59, which retains its leaves under severe drought) and the other deemed to be drought-sensitive (Rubi, which sheds its leaves under moderate drought). It was shown in a previous study (J. Pérez-Molina et al., in submission to J. Exp. Bot.) that these cultivars (cv. I59 classified as isohydric and cv. Rubi as anisohydric) markedly differed in their responses to drought stress, I59 exhibiting early adjustments in hydraulic behaviour leading to significant reductions in whole-plant transpiration, while Rubi exhibited better adjustments in late reactions to drought (e.g. an increased root dry mass-to-leaf area ratio). Despite these differences in hydric strategies, both cultivars displayed similar vegetative growth, yield and ability to recover after drought events. Besides, narrow differences of overall dry mass allocation patterns (shoot, root, leaf, and fruit) were found between these cultivars when submitted to different irrigation treatments. Conversely, large differences were found on the leaf area-related variables during or after drought events, the drought-sensitive cv. Rubi exhibiting a higher propensity to drop its leaves during the dry season but also a higher capacity to produce new leaves afterwards.

To our knowledge, there has been no comparative study of canopy architectural adjustments over time of coffee cultivars under real field conditions with different irrigation treatments. The organogenetic and morphogenetic responses may have slight effects on architecture on the short term but large effects on the medium and long terms. For instance setting-up axillary ramifications is a highly effective way for a plant to leverage its leaf area. The fitness of coffee plants submitted to climatic events depends on the adequacy of physiological and organo-morphogenetic features and, consequently, breeding programs must account for both aspects.

Here our central question was: to what extent do droughts reduce the growth rate of branches, their number, the size of leaves and internodes, leaf fall and the number of fruiting nodes? Answering these questions is essential to assess how a cultivar can face climatic events and can recover after a possible defoliation. To respond to these questions we performed comprehensive architectural descriptions, and explored the effect of seasons and drought events on organogenetic and morphogenetic processes in different locations of plant canopies, i.e. different branching order levels and position in the main axis. Then, we evaluated the interception of light by 3D mock-ups of observed plants as a first step towards linking physiological and architectural features. Cultivar strategies to overcome drought stresses are compared and discussed in the context of breeding programs.

Materials and Methods

Site and microclimate

The experiment of Embrapa Cerrados (15°35'S, 45°43'W), located 30 km from Brasilia, lasted from January 2008 to March 2010. A Davis Weather type station (Davis Instruments Ltd., Hayward, USA), situated near the experimental plot, was used to register data for rain, photosynthetically active radiation (PAR), air temperature and relative humidity (averaged every 30 min). The site is characterized by a wet season (from October to April) that concentrates more than 90 % of annual precipitation (800-2000 mm) and a very strong dry season (from May to September), being extremely dry in June and July; average annual minimum and maximum temperatures are 18 and 28 °C, respectively (Ratter et al., 1997). The minimum and maximum temperatures measured during dry seasons were on average 15°C and 30°C and relative humidity oscillated between 40% and 60%, with a maximum daily VPD reaching 25 hPa (Fig. 1A). The total annual precipitation and the potential evapotranspiration ($ET_{0;}$ estimated by the method described in Allen et al. (1998)) were respectively 1844 mm and 1774 mm in 2008, and 2208 mm and 1643 mm in 2009 (Fig. 1A, B). The number of consecutive days without rain during the dry seasons of 2008 and 2009 were 85 and 70, respectively. Accordingly, we noted increasing vapour pressure deficit (VPD) and ET_0 following the accumulated number of days without rain, the maximum daily value were respectively 25 hPa and 8 mm_{H2O} d^{-1} into first dry season, and 17.5 hPa and 7 mm_{H2O} d^{-1} into second dry season (Fig. 1B).

Plant material, experimental design, and plant sampling

We compared two cultivars of Coffea arabica, cv. IAPAR59 (deemed as drought tolerant) and cv. RUBI MG1192 (deemed as drought sensitive), hereafter referred to as I59 and Rubi, respectively. cv. Rubi (Mundo Novo x Catuaí) did not present recent introgression with C. canephora genomic DNA, in contrast to I59, which is the result of a cross between the Timor hybrid HT832/2 and the Villa Sarchi cultivar (Carvalho et al., 2008). Previous trials conducted in Central Brazil showed that cv. I59 has a much better capacity than cv. Rubi to maintain its leaf area over prolonged droughts. Physiological analyses of these cultivars in the present experiment further showed that I59 is the drought-tolerant cultivar (more isohydric and more plastic for hydric functioning with significant reductions during drought of transpiration) in contrast with cv. Rubi (more anisohydric, but also the more productive cultivar and more prone to drought stress) (J. Pérez-Molina et al., in submission).

In December 2007, five-month-old seedlings of both cultivars were planted (3.0 x 0.7 m spaced) in the experimental plot under full-sunlight conditions. This plot measured approximately 0.4 ha (21 m x 155 m) with SE/NW row direction, with 17 subplots, each containing 78 plants (i.e. 39 plants for each genotype), distributed on three rows, with 13 plants per row (Fig. S1). At planting, the soil was fertilized and limed according to routine agronomic practices for the coffee crop in Brazil. Weeds were manually controlled.

Irrigation was supplied by sprinklers (1.5 m high), monthly during the wet season and weekly during the dry season in order to maintain the soil moisture close to field capacity, as monitored using PR2 profile probes (Delta-T Devices Ltd., Burwell, UK). Three irrigation treatments (IRR) were applied (Fig. 1C): (i) irrigated during both dry seasons 2008 and 2009 (I); (ii) non-irrigated during dry seasons (NI); (iii) non-irrigated during the first dry season (2008) but irrigated during the second dry season (2009) (NI-I). This latter treatment was applied to examine plant recovery after the first dry season.

We harvested 7 to 10 plants per cultivar (CV) for each IRR treatment at six sampling dates (S: S1 to S6). S2 and S5 represent samplings after the dry seasons (see Fig. 1C). At S1, there was no irrigation difference irrespective of treatments and we just compared the two CV. The NI-I treatment was established only after 352 days after planting (DAP). We assumed that NI-I was the same as NI during the first year; hence, plants from NI-I were sampled only from S4 onward.

Coffee tree architecture

Definitions and concepts related to plant architecture and its analysis are summarized in Table 1. Coffee tree architecture is classified as a Roux model, characterized by a continuous growth and dimorphic axes (Hallé et al., 1978). Coffee plants exhibit an orthotropic trunk with an opposite-decussate leaf arrangement (Fig. S2; Cannell (1985)) bearing sylleptic plagiotropic branches at the axil of each leaf. These plagiotropic branches may as well axillate higher order plagiotropic branches at the axil of leaves. However, unlike ramifications borne by the trunk, these ramifications are proleptic and ‘opportunistically’ develop on already lignified nodes. Most of axillary buds on plagiotropic branches stay dormant. Plagiotropic nodes follow an orthogonal-decussate pattern of leaf initiation, similarly to orthotropic axes, but an internode torsion and a petiole reorientation lead to an apparent dorsi-ventral phyllotaxy (Dengler, 1999).

Additional “series” buds are present on trunk nodes. These orthotropic series nodes can generate orthotropic suckers (which are pruned in coffee orchards). Similarly several series buds are present at the axil of plagiotropic nodes. These buds develop into inflorescences able to produce flowers during generally one or two consecutive years.

Architectural and morphological data collection

All of the harvested coffee trees were used for the description of their aerial architecture (Fig. 1C).

At the organ scale, we measured the length of every internode and every leaf. The area of individual leaves was measured for a subsample of leaves with a leaf area meter (Laser Area Meter model CI-203, CID Inc., USA) in order to derive allometric relationships relating the area of a leaf (LA, cm^2) to its length (l, cm). This lead to slightly different relationships for I59 and Rubi leaves:

$$LA_{Rubi} = 0.4616\ l + 0.3067\ l^2; R^2 = 0.994 \quad \text{Eq. 1}$$

$$LA_{I59} = -0.1661 + 0.3909\ l + 0.3345\ l^2; R^2 = 0.993 \quad \text{Eq. 2}$$

We additionally measured the leaf area borne by each primary branch using an area-meter (model AAC 400, Hayashi Denkoh, Tokyo, Japan). Given the good adequacy between these measurements and the corresponding values obtained with the above relationships, these measurements were not pursued after the S3 campaign.

The basal diameter of the main stem (MS) and every branch was measured. Then, at the plant scale, we measured separately the dry mass of the MS, the total dry mass of all ramifications, the total dry mass of leaves and the total dry mass of coarse and fine roots.

In regards to geometry, we measured the branching angle of first order plagiotropic branches relatively to the MS. The branching angle of secondary and tertiary axes relatively to their bearer axis was only sampled on few axes. The orientation of primary branches was roughly characterized by their azimuthal orientation (North, South, East or West). For higher order branches, we just noted on which side (“right” or “left”) the branch is positioned on its bearer axis.

Reconstruction of 3D plant mock-ups

All of the collected data were coded in a spread sheet in a custom way, each plant axis being given a unique code indicating its topological position relatively to its bearer axis. A dedicated Java program “*CoffeeContext”* was then run for checking the data consistency and, ultimately, reconstructing a comprehensive description of plant topology. The topological description of coffee plants was organized as follows: each axis is decomposed as a succession of metamers and each metamer can bear axillary structures (leaves and/or axes). This organization, compliant with the principles of a Multiscale-Tree-Graph format (MTG, Godin and Caraglio (1998)), allowed to access plant structures at different scales and to derive pooled variables such as, for instance, the length of an axis, its number of ramifications or the total leaf area borne by the branch.

The geometry of internodes was represented by truncated cones and the geometry of leaves by a mesh comprising 12 triangles. The dimension of this mesh was adjusted for each leaf in order fit both its measured length and its calculated area.

A 3D mock-up was generated for each plant described at each given harvesting date and exported in an “opf” file format (Griffon and De Coligny, 2014) for visual checking, calculations of light interception and data extractions for further statistical analyses.

Data extractions were achieved by scripting under the Xplo software (Griffon and De Coligny, 2014). Taking profit of the topological information associated with plant mock-ups we thus had access to all biometrical variables (e.g. number of elements or leaf area) integrated at different plant scales (e.g. axis, branch or plant scales) and at different locations within the plant architecture (e.g. depending on branch position on the MS). All of the these extracted data were then exported to be analysed using the R programming language.

Simulation of light interception

The light intercepted by plant components was calculated using the Mapping Intercepted Radiation model (MIR) as described in Dauzat (1994), Dauzat and Eroy (1997), and Dauzat et al. (2001). Basically, the model calculates images of 3D scenes from discrete directions i distributed within the sky hemisphere according to the TURTLE model (den Dulk, 1989). Counting of the visible pixels in an image reveals the fraction of incident radiation intercepted by each plant component in the corresponding direction. The results are then weighted by the quantity of radiation coming from that direction (R_i) in order to get the quantity of light intercepted by each plant organ. Finally, the organ irradiance was obtained by dividing the quantity of intercepted light by the organ area. The calculated irradiance was set as an attribute associated with each organ, thus enabling subsequent analyses of light interception for each branch order (first, second, third, and total).

Simulations were achieved on small plots generated by the Simeo software (Griffon and De Coligny, 2014). The virtual plants are set up in the model space in such a way as to reconstitute a representative scene of the canopy being studied. In that way, it is possible to simulate the radiative balance of a plant taking into account its environment and, in particular, the shade cast by neighbouring plants.

Statistical analysis

Canopy architecture variables (number of metamers, ramifications, length of ramifications, number and area of leaves, and light intercepted for leaves) by branching order were evaluated through three-way analysis of variance (ANOVA) for the following factors: CV (I59 vs. Rubi), IRR (I vs. NI-I and NI), and sample date (S: S1 to S6); and interactions: CVxIRR and CVxIRRxS; with a posteriori comparison means with Tukey's HSD test (α=0.05). The effect of the first and second drought in terms of percentage of reduction ($\%R_{1^{st}}$ and $\%R_{2^{nd}}$, respectively) for all variables of canopy architecture by branching order for cultivars I59 and Rubi from S2 to S6, were calculated. $\%R_{1^{st}}$ was between I vs. NI-I: $\%R_{1^{st}} = -[(I - NI\_I)/I] \cdot 100)$; and $\%R_{2^{nd}}$ was between NI-I vs. NI: $\%R_{2^{nd}} = -[(NI\_I - NI)/NI\_I] \cdot 100)$. Relationship between the number of metamers on first order axillary axes and the number of metamers on MS above the axillating node for all S for each CVxIRR were made with adjustment of second order polynomial regression. In addition, the relationships between the defoliation rate of metamers (at sampling dates S4, S5, and

S6; a metamer usually contains from 0 to 2 leaves, defoliation was calculated dividing the average number of leaves per metamer by 2: from 0 to 1 scale), average area of leaves and length of internodes (at sampling dates S4 and S6) according to their position metamer on first branches from tip for each CVxIRR, these were performed with comparison means of Tukey's HSD test (α=0.05) between NI vs. I and NI-I for each position in axis. Finally, Pearson`s coefficient (ρ) by CVxIRR was done at the relationship between average areas of leaves according to their length of internodes in axis of first order branches (data combination of S4 and S6, α=0.05). All of the statistical analyses were performed using R programming language, version 3.4.0 (Crawley, 2002; RCoreTeam, 2017).

Results

Number of metamers

Overall, the number of metamers on the main stem (MS), on the first (B1) and second (B2) order branches, and on total branches (TB; the sum of first, second and third order branches) increased almost linearly over time for all CVxIRR combinations (Table 2), in contrast to what happened with the number of metamers on the third order branches (B3) which was erratic for all CVxIRR combinations. Overall, the number of metamers was higher in Rubi than in I59 under I conditions, being specifically and significantly higher in S3 (only B2), S4 (B1 and B2), and S5 (only B3) ($p<0.05$, Fig. 2 A1, A4). Under NI conditions, the above described genotype differences disappeared (Fig. 2 A2, A5), and new differences emerged: Rubi displayed higher number of metamers on MS, B1 and TB, as well as higher number of total metamers, in S2 and S3 (with the exception of B1) than I59, but these differences disappeared on S4 onwards. Finally, the number of metamers of B1 in S5 was similar when comparing NI-I and I plants of Rubi ($p>0.05$, Fig. 2 A6), in contrast to what happened with I59 which showed a lower number of metamers of B1 for NI-I than for I plants ($p<0.05$, Fig. 2 A3).

The number of metamers on B1 axillary axes increased linearly with increasing number of metamers on the MS above the axillating node regardless of CVxIRR combinations (Fig. 3). At a first glance, the number of metamers of B1 was nearly the same as the number of metamers on the MS above the node where the branch is inserted. However, the growth rate of the oldest (i.e. oldest branches) branches progressively slowed down after reaching approximately 20 metamers. As for the upper branches of B2 and B3, it was not possible to fit any type of adjustment between the number of metamers of branches and position of metamers on the MS (data not shown).

Branch setting

Overall, the number of B1 (but not that for higher orders) increased linearly over time in both cultivars. Under I, Rubi produced a greater percentage of B2 and B3 branches than did I59 ($p<0.05$, Fig. 2 B1, B4). Along the entire experiment Rubi under NI had a linear increase for the number of B1 (Fig. 2 B2, B5), unlike I59 between S4 and S5 (drought) where the emergence of new branches was almost nil

(Table 2). The emergence of B2 was unaffected by drought under NI in both cultivars (it increased over time), and Rubi presented a proportionally greater number of B2 than I59 in S3 and S5 ($p<0.05$, Fig. 2 B2, B5). With respect to the recovery treatment (NI-I), both cultivars showed similar, significant increases in the number B1 in S5 and S6 (Fig. 2 B3, B6), although Rubi markedly displayed more B2 (significant increases in S5, particularly in Rubi) than I59. The number of B3 was proportionally much lower and seemingly erratic in both coffee cultivars.

Shoot dry mass (SDM) was unresponsive to the applied treatments, and increased over the entire experiment (Fig. 2 F1 to F6).

Leaf shedding and leaf area

Irrespective of CVxIRR combinations, the number of leaves per plant increased steadily from S2 to S4 irrespective of branch orders (Table 2). However, after the second drought period (S5) in both cultivars under NI, leaf shedding was particularly noticeable on B1 ($p<0.05$) and nil on higher branch orders ($p>0.05$, Fig. 2 C2, C5). It is noteworthy that, in cv. Rubi, leaf shedding was apparently unrelated to water stress given that irrigated plants of Rubi also shed its leaves; indeed the leaf number was held in check during the dry season (between S4 and S5) due to a balance between leaf fall (older) and emergence of new leaves ($p>0.05$, Fig. 2 C4). In sharp contrast, the number of leaves increased significantly for all order of branches in I59*I ($p<0.05$, Fig. 2 C1). Regarding NI-I, both cultivars displayed increased number of leaves for all order of branches (Fig. 2 C3, C6). Notably, Rubi showed better recovery in the number of leaves for B2 (similar results between NI-I and I, $p>0.05$).

Overall, I59 outperformed Rubi for total leaf area (TLA) whatever the irrigation treatment (Table 2). Under I treatment, leaf area for B1 and B2, and TB (Fig. 2), in I59 remained steady during the second dry season (no significant increase), but decreased dramatically in Rubi ($p<0.05$, with exception B2). For all NI plants, TLA decreased significantly between S4 and S5 (Fig. 2 D2, D5), particularly in Rubi.

When analysing B1 (which is older than branches of higher orders) only, it was found that the second drought (S5) mainly affected the fall of older leaves regardless of cultivar, as inferred from the significant differences between NI and I in terms of defoliation rate of nodes from the 5^{th} metamer onwards (old metamers, Fig.

4 B, E), a result that was sustained until S6 (Fig. 4 C, F). Interestingly, only Rubi showed significant differences between NI and I in defoliation rate for the oldest leaves (from the 15th metamer onwards, Fig. 4 A, D) during the rainy season that precedes the second drought period (S4). Regardless of cultivar and NI and I conditions, the climatic effect (high VPD and temperature) of the first dry season led to decreased defoliation rate of metamers from 13th to 15th metamer in S4 (Fig. 4 A, D); climatic effects during the second drought were clearly noticeable when comparing S5 and S6 profiles.

Size of leaves and internodes

Irrespective of CVxIRR, averaged leaf area and length of internode per position metamer in B1 (Fig. 5) showed two patterns in S4 and S6. The first one was characterized by a linear increase of both averaged leaf area per metamer and length of internode from the 1st to the 5 th-7th metamer. The second pattern, in turn, was related to the older metamers: there were decreases in averaged leaf area and length of internode from the 5th-7th until the 13th metamer, with the exception of length of internode for I59 in S6 for all irrigated treatment (IRR: I, NI, and NI-I; remained invariant, Fig. 5 B2). Finally, we found significant correlations between averaged leaf area and length of internodes in axis in B1 for each CVxIRR (each CVxIRR with $\rho > 0.71$ and $p < 0.001$, Fig. 5C).

Simulation of light interception

The total daily intercepted light (TIL) increased over time in both CV under I (Fig. 2 E1, E4) and NI-I (Fig. 2 E3, E6) , but under NI the TIL did not increase from S4 to S5 (Fig. 2 E2, E5). Regardless of IRR at each sample date (S: S1 to S6), TIL did not differ significantly between CV and branch orders, except for I in S3 (B1 and TIL), S4 and S5 (B2); and for NI-I in S5 (B2), all of them were higher in Rubi (Table 2).

Finally, young plants (from S1 to S3), independently of CVxIRR combinations, showed lower TIL in the upper part of the canopy and higher TIL in the lower-middle part of the canopy (Fig. 6 B1 to B6). In contrast, adult plants (from S4 to S6) reached maximum TIL in the middle part of the canopy (i.e. from 10th to 15th position metamer on MS), with a reduction of TIL when moving from the middle to the top or to the bottom of the canopy.

Plasticity of architectural traits

For B1, the only significant effect of the first drought (%$R_{1^{st}}$, evaluated as percentage of reduction, i.e. comparison between NI-I vs. I) was noted in the number of ramifications in S2 (first drought) for I59 (Table 3). In S3 (90 days after the first dry season), all canopy architecture variables were significantly affected by drought irrespective of CV, with the exception of the number of ramifications in Rubi. In S4, %$R_{1^{st}}$ remained significant for all variables (except TIL) but only in Rubi, whereas in S5 only I59 was significantly affected (number of metamers, and number and area of leaves). In S6, the number of metamers decreased significantly due to drought regardless of cultivar; the number of ramifications decreased, but only in I59. Finally, for B2, %$R_{1^{st}}$ decreased significantly for all canopy architecture variables, but only in S3 independently of CV.

For B1 in the second drought, all of the canopy architecture variables were significantly affected in S5 (%$R_{2^{nd}}$, i.e. comparison between NI vs. NI-I, Table 3) independently of CV. In S6, %$R_{2^{nd}}$ remained significant in Rubi for all variables (with the exception of TIL) whereas for I59 only the number and area of leaves and TIL were significantly affected. Finally, for B2, %$R_{2^{nd}}$ was significant for the number de leaves but only in Rubi.

Discussion

Plant architecture and its plasticity to drought are by far much less studied than physiological features. Analyses of plant architecture enable to gain detailed information dealing on how plants can deploy photosynthetic surfaces and intercept light over time. The dynamics of plant architecture is synthetized below and the cultivars' strategies for developing photosynthetic structures, for accumulating biomass and, finally, for setting and sustaining fruit production are discussed.

Branch setting and plasticity

The core architecture of young C. arabica is composed of one orthotropic MS axillating two plagiotropic branches on each node (except for the very basal nodes which are missing, dead or broken branches). Given that these B1 are sylleptic (Cannell, 1985), and that they have the same phyllochron as their bearing MS during most of their life (Cilas et al., 2006; Matsunaga et al., 2016), the potential number of metamers on B1 (NM_{B1}) can be evaluated by a simple function of the number of metamers on MS (NM_{MS}): $\sum NM_{B1} = NM_{MS} + {NM_{MS}}^2$. However, the growth rate of the oldest branches declined when reaching about 20 nodes for all CVxIRR. Given that branches having more than 20 nodes are located at the bottom of the canopy, we may assume that shading plays a role in this decline. The development of B2 on old branches may be an additional factor. Whatever the reason of the observed growth decline, the sum of NM_{B1} per plant is comparable for the two cultivars when irrigated. However, when subjected to drought stress, both cultivars exhibited reduced growth rates: the water stress during the first drought induced a maximal reduction of ΣNM_{B1} of about 29% for both cultivars in S3 (I59) or in S4 (Rubi). The delayed effects of drought persisted until S6, with a similar reduction of ΣNM_{B1} (approximately 13%) for both cultivars. The reduction factor of the second water stress in S6 was approximately 20% for both cultivars. Also, water deficit during first drought (S2) had an effect on the growth rate of the MS (increasing of its phyllochron between S1 and S3 for I59 more than in Rubi, 32 and 22 days, respectively). Although this effect is not drastic, it has important impacts on the plant structure since it results in less B1 that have themselves a decreased growth rate. It has been shown that growth is synchronized among MS and B1. This finding is consistent with other studies showing that the growth rate of MS and branches varies together with plant age, planting density and arrangement (Matsunaga et al., 2016) and that the production of metamers in B1 accompany the oscillations in the growth of the MS (DaMatta, 2018).

On the contrary, the total number of metamers on B2 is proportionally higher for Rubi than for I59 whatever IRR, and B3 is proportionally much lower and seemingly erratic in both coffee cultivars. Contrarily to B1, B2 and B3 are proleptic ramifications (sensu Barthélémy and Caraglio (2007)) and appear occasionally on already lignified nodes (except in rare cases, e.g. when the bearer axis is broken). If we assume that the phyllochone of B2 and B3 is also similar to the MS phyllochrone, it follows that the number of metamers on B2 and B3 depends on the number of B1 and B2 and their age. The metamer number of an axillary axis is supposed to be equal to the “rank from tip” of its bearer above the axillary insertion node if (i) the ramification is not delayed and (ii) the phyllochrone is the same for the axillary axis and its bearer axis.

Regarding the number of branches, a first general effect of drought was a decrease of the growth rate during the dry season. This effect, higher for I59 than for Rubi, concerned similarly the MS and the branches of different ramification orders. Another important response concerned the setting of B2 and B3 during the second year, being a faster emergence for Rubi. Rubi proportionally produces more B2 and B3 than I59 under irrigation as also under drought stress. The overall effects at plant scale are a reduction of both the number and the size of vegetative axes (see length of ramifications in Table S1). This effect was proportionally more important in I59 than in Rubi. Shoot growth in Arabica coffee was slow during the dry season and rapid during the rainy season, as also reported elsewhere (Barros et al., 1999; DaMatta et al., 1999), and these fluctuations are probably not related to soil moisture, because irrigation does not alter the general pattern of growth, although it may affect the growth rates of the outbreaks (Ferreira et al., 2013; Silva et al., 1997). Finally, plants irrigated only during the second year (NI-I) did not make up from their first year growth loss but they nevertheless recovered their regular growth pattern with apparently no delayed effects other than the ones induced by a reduced plant structure.

When analysing the effect of drought, it can be seen that the first drought reduced comparably the number of B2 for the two cultivars in S4 (-55.2% for I59 and -57.4% for Rubi) but that the second drought had more different and complex effects (-22.9% and -38.3% in S5; and -5.5% and -33.3% in S6, for I59 and Rubi respectively). Such observation stresses important features of plant development that are related to ontogenic stages. In young stages, plants can only develop B1 with nearly no degree of freedom (i.e. changes of their canopy architecture is limited to only about MS and B1). Then, approximately at 300 DAP, plant began developing secondary ramifications and, later on, tertiary ramifications. These ramifications enable a plant to rapidly set-up new leaves, especially after defoliation. However, the number of ramifications would rapidly lead to an excessive foliage density in the absence of self-regulation of the ramification process. We can hypothesize that such a self-regulation is effective for Rubi after S5. However plants in S5 are reaching the ontogenic stage when they can express flowering and fruiting. The competition for carbohydrates between vegetative and reproductive organs thereby plays a major role as was illustrated by the number of ramifications and partitioning of the dry mass per plant.

On brief, the number of branches is doubly important since setting branches is a way for a plant: i) to rapidly increase its leaf area, and ii) to multiply the potential number of fruiting nodes. This may have important implications in the subsequent drought recovery, because the branches in coffee (shoot-structure) can be a carbohydrate storage source (DaMatta, 2018) that could help the follow-up of new photosynthetic structures (leaf renewal) and/or flowering structures depending on the reproductive or vegetative period the plant is found. The number of fruiting sites primarily depends on the number of nodes mature enough but not too old. To this respect, Rubi had higher potentialities to develop flowers because of its higher number of B1 and B2 axes. However, some newest ramifications may have been too young during the second dry season for fully expressing these potentialities. In all cases, the climatic conditions must be considered conducive for a cohort flowering.

Leaf shedding and leaf renewal

As highlighted above, the potential number of leaves strictly depends on the number of metamers and, hence, on the number of ramifications. Leaf renewal is strictly related to the setting of new metamers that systematically bear two leaves and this is highly dependent on the setting of new axes. Following this reasoning, Rubi was more prone to the growth of new leaves due to its higher number of metameres and new ramifications of higher orders. However leaves have a limited lifespan. According to our observations, the maximal lifespan of leaves in the absence of water stress corresponds to about 20 phyllochrones, i.e. about 28 days. Additionally, a leaf is generally rapidly dropped when a ramification appears at its axil. Irrespective of the time of establishment, water stress stimulates earlier leaf senescence, particularly in physiologically older leaves (DaMatta et al., 2007), which often coincides with the harvest and post-harvest periods (DaMatta, 2018). Leaf shedding during drought was particularly noticeable on B1 (older leaf) and less on higher order branches (younger leaf, data not shown; in Correia et al. (2016) was showed lowest lifespan for leaves born on B1, and highest in higher orders).

When comparing the defoliation rates between treatments, it clearly appears that water deficit had a drastic effect on the node defoliation rate. As a result, the leaf area per plant is strongly decreased during droughts for NI plants (Fig. 2D). Globally, the decrease of the number of leaves is proportionally more important for Rubi than for I59 (respectively -41.4% and -23.8% consecutively to the first water stress and -43.0% and -26.8% consecutively to the second water stress). One important feature to notice is that climatic variables (temperature and air VPD) had a marked effect on the number of leaves for Rubi in the NI treatment during the second dry season (S5), i.e. after a period characterized by high air temperature and VPD. But, paradoxically, the number of leaves increased about linearly during the same period in the NI-I treatment. This observation suggests a self-adjustment of the TLA related to the plant ontogenic stage: plants that not irrigated during the first drought had fewer branches and a lower TLA in S4. Subsequently they had to face a lower transpiration flow during the dry season and the plants in the NI-I treatment tended to catch up the plants of the I treatment.

We hypothesize that leaf shedding breaks bud inhibition in Rubi. A general consequence of this hypothesis is that Rubi exhibited a higher ability to rapidly develop photosynthetic surfaces than I59. However, Rubi also exhibited a greater propensity to drop leaves under hot and dry air conditions even if irrigated (S5). In irrigated plants the abscission of the leaf is less than in NI plants (as was observed in the Conilon coffee in Ronchi and DaMatta (2007)). Leaf drop is comparable for plants with and without irrigation when considering absolute values, but it is proportionally much higher for NI plants. It is noteworthy that soil moisture during the drought is not the only one factor leading to leaf dropping since irrigated plants also dropped leaves during the dry season (especially for Rubi). This can be linked to microclimatic conditions characterized by high temperatures and low air humidity in the canopy, leading to a high evaporative demand, which consequently stimulates senescence of older leaves (DaMatta et al., 2007).

The leaf growth rate as area final per plant varies seasonally, and the leaves reach larger sizes and grow faster if the expansion starts at the beginning of the rainy season (DaMatta et al., 2007; Ronchi and DaMatta, 2007). Like the dynamics of specific leaf area (SLA) reflect the proportion of young leaves: high SLA during rainy season and lower SLA consecutively to drought (whole plant, J. Pérez-Molina et al., in submission). The dynamics in the leaf area of the coffee trees is the result of synchronization in phyllochron, the duration of leaf expansion and the useful life of the plant branching structure (Correia et al., 2016), and according to Silva et al. (2004), the length of B1 has a seasonal synchronization (vegetative growth of 78% and 22% in the rainy and dry seasons, respectively). Our results indicate that the two patterns of the average leaf area per metamers and internode length for position in axis from tip were associated effectively with the emergence of new phytomers between the S (linear increase until the 5th-9th metamer), and with the oldest nodes (linear reduction after the 5th-9th metamer), both patterns are possibly synchronization with the rainy and dry seasonal effect that can affect the phyllochron, the duration of the leaf expansion, and lifespan of the branching structure of adult coffee plants. Regardless of IRR and S, when comparing CV for the number of leaves for by leaf-size with difference intervals every 10 cm^2, Rubi showed smaller leaves, especially in NI plants` (Fig. S4). The results suggest that the phyllochron in Arabica coffee plants changes within the branching hierarchy and is seasonally modified (likewise as in Correia et al. (2016)). But, it must be noted that the apparent effect on the leaf size can be biased because the age of leaves varied among cultivars and treatments.

On brief, our results showed that dynamics on time-course of leaf area are much more variable than the number of leaves. This appears particularly obvious when comparing the dynamics on time-course of the area and number of leaf of B1 between S4 and S5, it was observed how the leaf area falls mostly for Rubi while the number of leaves was maintained. Rubi (sensitive-drought) had a low hydraulic regulation during the drought in contrast to I59 (i.e. accumulated water losses for transpiration greater than I59). Here, it could to tell that Rubi faces a moderate drought through of leaf abscission as mechanism to limit whole-plant transpiration. Then, Rubi compensate the loss of leaf area with a rapid renewal of leaves during dry and beginning of the rainy season, which would fulfil as a form of compensation to loss of photosynthetic surface. However, some studies indicate that leaf abscission might represent a much more direct consequence of hydraulic failure during water stress (DaMatta, 2003; Tesfaye et al., 2013). In fact, it has been suggested that drought-tolerant coffee cultivars postpone or decrease drought-induced leaf fall (DaMatta, 2003; DaMatta, 2018), as in I59.

Feedbacks of plant architecture on physiological processes

This study highlighted major architectural traits differing between the two cultivars and their plasticity vs. water deficit. The observed differences are consistent with the results of a previous study targeting physiological differences (Perez-Molina et al., in submitted). However, the multiple feedbacks between architecture and physiology represent a large field to be investigated. The primary feedback of plant architecture on physiological processes concerns the interception of photosynthetically active radiation. Our simulations on individual mock-ups bring such information at the scale of individual leaves (Fig. 6A) and for short time steps (not shown). New features of Archimed software furthermore enable to assess the photosynthesis of leaves, their transpiration and their temperature provided their stomatal conductance is known. However, at this time, we are only able to reconstruct plants as they were described at harvest dates. A way to overcome this problem is to reconstruct mock-ups of plants at different dates prior to their harvesting date. This can be achieved by applying the observed growth rates in reverse way (J. Dauzat et al., in preparation).

Performance of cultivars depend greatly on their capacity to fix carbon under seasonal conditions (DaMatta et al., 2003; DaMatta et al., 1997; Silva et al., 2004), which also involves reproduction and/or vegetative growth (Chaves et al., 2012; DaMatta et al., 2008). We took into account that an average solar radiation intensity is not enough to evaluate the possible assimilation of carbon insofar as the potential photosynthesis of a leaf cannot be inferred from its average radiation during a day (Fig. S3): but the most efficient architecture for carbon fixation is the one that allows a more uniform radiation throughout the plant over the course of the day (Perez et al., 2017). The same distribution patterns of TIL in vertical profile (position metamer in MS) were found between CV for the same IRR and S. The distribution of interception of light and leaf area (data not shown) in the vertical profile of plants was no uniform and they had same patterns (S4 to S6: 70% and 30% approximately into upper and lower canopy, respectively), indicating no scattered foliage with efficient occupation of space (similar result of Rakocevic and Androcioli (2010)).

Several environmental factors vary with the depth in a canopy, but the most important with regard to photosynthesis is light, both in quantity and quality (Kull, 2002). A comprehensive net carbon assimilation (A) data of leaves in the vertical and horizontal profile of the plagiotropic axis is required for the estimation of A, because the age of the leaves could throw a different perspective when integrating the A for whole plant (younger B2 and B3). In addition, morphological and physiological response capacity should be considered in light of individual leaves within the crown (Niinemets, 2007; Valladares et al., 2000), because upper canopy leaves are generally thicker, with less chlorophyll, higher concentration of N, and lower susceptibility to photoinhibition of photosynthesis (Evans and Poorter, 2001; Kull, 2002; Niinemets, 2007). Whatever the difference between the CV at the level of photosynthetic traits of the leaf as mentioned above, the total light intercepted for a leaf was comparable between Rubi and I59 cultivar for the same IRR and S. In the same way, the two cultivars exhibited roughly comparable vegetative growth and biomass partitioning at the end of the study despite of marked differences in canopy architecture in respect to their growth rate of branches, their number, and the size of leaves.

Conclusion and perspectives

The physiological functioning of plants is most of the time analysed without considering the feedbacks of physiological processes on plant architecture, thus preventing conclusive evaluation of their behaviour on the mid and long term, e.g. after a short or longer drought event. As a matter of rule, environmental changes trigger rapid responses of most physiological processes such as stomatal regulation while the response of growth processes is progressive and has delayed but nevertheless important effects on plant structure.

A key message from this research resides on the fact that the organogenetic and morphogenetic responses have slight effects on architecture on the short term but large effects on the medium and long terms, i.e. setting-up axillary ramifications is a highly effective way for a plant to leverage its leaf area, since it contributes to the fastest leaf renewal. Overall, drought had effects on all of the studied variables but no architectural trait appeared to be specifically responsive to water stress. We stressed that the propensity of the anisohydric cultivar to set-up ramifications is an important lever for recovering foliage after drought. A canopy architecture with a high proportion of higher order branches would help the subsequent recovery of the drought provided that: i) a high number of phytomers has a potential of development axillary buds (leaves and / or floral buds), ii) conserved a satisfactory amount of foliar area with carbon assimilation capacity, iii) enough reserves to maintain the growth demands of new structures (axillary buds, leaves, metamers, and flower buds), and iv) without severe damage to hydraulic integrity of the whole plant after drought. The fitness of coffee plants submitted to climatic events depends on the adequacy of physiological and organo-morphogenetic features and, consequently, these aspects should be accounted in breeding programs.

In perspectives, given the well-differentiated behaviours of the cultivars with respect to their physiology (and namely their level of isohydricity, Pérez-Molina et al., in submission), the next step will be to assess more precisely the consequences of the combined canopy architectural and physiological features from functional-structural plant model (FSPM) approach. The data collected in this study provided countless information that could be used for building a functional-structural plant coffee model coupling architectural rules and ecophysiological processes such as carbon acquisition. Our research efforts will focus in the near future on the development of a FSPM approach to simulate the dynamic growth of coffee, in interaction with its environment.

Supplementary data

Table S1. ANOVA results for length of ramifications

Figure S1. Experimental plot

Figure S2. Design shoot morphology of Arabica Coffee

Figure S3. Daily leaves irradiation

Figure S4. Distribution size-leaf per plant

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Tables

Table 1. Definition of concepts for the design of plant architecture

Concept	Definition
Axis	The trunk or a branch without their eventual ramifications.
Order (ramification)	1st order ramifications (or primary branches) are axillated on trunk; 2nd order branches are axillated on primary branches, etc.
Metamer (or phytomer)	Botanical unit including a node and its subtending internode plus the leaves and axillary buds present on the node.
Phyllochron	Intervening period between the sequential emergences of leaves on the main stem, also rendered as leaf appearance^{-1}. One phytomer unit is added over the course of one phyllochron (days).
Orthotropic (axis)	Vertical axis. Trunk and suckers of coffee trees are opposite-decussate orthotropic axes.
Plagiotropic (axis)	More or less horizontal axis. Coffee tree ramifications are plagiotropic.
Rank from tip or reverse rank (metamer or axis)	The metamer position on the axis (counted from its tip) or the metamer position on which the current axis is axillated.

Table 2. ANOVA results for number of ramifications, number of metamer, number of leaves, leaf area, and daily light intercepted for leaf per plant, for two cultivars (CV: I59 and Rubi), under three irrigation treatments (IRR: irrigated during the dry season= I, non-irrigated= NI, or non-irrigated year 1 and irrigated year 2= NI_I), from six sampling date (S: S1 to S6)

Variable (abbr.)	S	I59*I	I59*NI	I59*NI_I	RU*I	RU*NI	RU*NI_I	CV		IRR			S	CV* IRR	CV* IRR*S	F	R^2	P
								I59	Rubi	I	NI	NI_I						
Number of metamer per plant																		
Main stem (MS)	S1	12.1(0.3) Aa			12.9(0.3) Aa				***	***			***	**	***	**147.9**	**0.95**	***
	S2	16.3(0.2) Bab	15.7(0.3) Aa		16.6(0.2) Bab	16.9(0.2) Ab												
	S3	20.9(0.6) Cb	18.3(0.6) Ba		22.8(0.6) Cb	21.9(0.5) Bb												
	S4	28.3(0.6) Dab	27.1(0.6) Ca		30.7(0.6) Db	26.9(0.9) Ca												
	S5	34(0.5) Ebc	30.1(1) Da	32.5(0.7) Aabc	35.7(0.5) Ec	31.7(0.9) Dab	33.6(0.6) Abc											
	S6	41(0.9) Fcd	36.7(0.6) Eab	38.3(0.5) Bbc	42(0.9) Fd	34.4(0.6) Ea	39.9(0.6) Bcd											
Branch order 1st (MB1)	S1	22.3(1.5) Aa			27.3(1.5) Aa				***	***			***	*	***	**417**	**0.98**	***
	S2	88.8(1.9) Bab	79.5(4) Aa		89.2(1.9) Bab	94.1(4.1) Ab												
	S3	240.1(10.1) Cbc	171.7(10.6) Ba		242.4(10.1) Cc	204.2(9.3) Bab												
	S4	509.4(16.3) Da	457(21.1) Ca		630.8(16.3) Db	443.9(37.8) Ca												
	S5	778.7(7.7) Ed	528.4(28.1) Ca	664.5(36.6) Abc	797.4(7.7) Ed	613.7(31) Dab	736.9(27.3) Acd											
	S6	1154.4(26.5) Fcd	902.1(30.1) Da	997(44.1) Bab	1248.7(26.5) Fd	876.1(31.5) Ea	1091.9(22.6) Bbc											
Branch order 2nd (MB2)	S3	15.3(5.6) Aa	18.8(10.7) Aa		53.8(5.6) Ab	47.9(9.3) Aab			***	***			***	***	***	**36.6**	**0.83**	***
	S4	155.4(10.6) Bb	78.7(8.1) ABa		298.2(10.6) Bc	125.4(23.3) ABab												
	S5	283.1(32.5) Bab	228.6(35.8) Ba	222.2(44.5) Aa	451.1(32.5) Bb	229.1(59.2) Ba	392(35.7) Aab											
	S6	519.4(65.4) Cab	376.7(55.1) Ca	305.1(52.9) Aa	753.4(65.4) Cb	405.3(67) Ca	502.9(36.6) Aab											
Branch order 3rd (MB3)	S4	0(0) ABa	0(0) Aa		2.3(0) ABa	0(0) Aa			*	**			***	**n.s.**	*	**3.4**	**0.31**	***
	S5	2(2) ABa	0.3(0.3) ABa	0.3(0.3) Aa	13.6(2) ABb	1.4(1.4) ABa	3.7(1.9) Aab											
	S6	5(3.6) Ba	7(4.3) Ba	4.9(2) Aa	20.1(3.6) Ba	23.7(13.6) Ba	2(1) Aa											
Total branch (TMB)	S1	22.3(1.5) Aa			27.3(1.5) Aa				***	***			***	**	***	**145.1**	**0.95**	***
	S2	88.8(1.9) Aab	79.5(4) Aa		89.2(1.9) Aab	95(4.5) Ab												
	S3	255.4(12.8) Bb	190.5(9.7) Aa		296.2(12.8) Bb	252.1(16.4) Ab												
	S4	664.9(19.1) Ca	535.7(24.8) Ba		931.3(19.1) Cb	569.3(58) Ba												
	S5	1063.9(36.4) Dbcd	757.3(58.8) Ca	887(72.6) Aabc	1262.1(36.4) Dd	844.3(88.2) Cab	1132.6(53.8) Acd											
	S6	1678.9(87.6) Eab	1285.9(80) Da	1307(91.9) Ba	2022.3(87.6) Eb	1305.1(108.3) Da	1596.7(55.2) Ba											
Total metamer (TM)	S1	34.4(1.7) Aa			40.2(1.7) Ab				***	***			***	**	***	**147.9**	**0.95**	***
	S2	105.1(2) Aab	95.2(4.2) Aa		105.8(2) Aab	111.9(4.5) Ab												
	S3	276.3(13.1) Bb	208.8(9.7) Aa		319(13.1) Bb	274(16.6) Ab												
	S4	693.1(19.7) Ca	562.9(25.3) Ba		962(19.7) Cb	596.1(58.8) Ba												
	S5	1097.9(36.5) Dbcd	787.4(59.5) Ca	919.5(73.1) Aabc	1297.9(36.5) Dd	876(88.8) Cab	1166.1(54.1) Acd											
	S6	1719.9(88.1) Eab	1322.6(80.5) Da	1345.3(92) Ba	2064.3(88.1) Eb	1339.6(108.8) Da	1636.6(55.5) Ba											
Number of ramifications per plant																		
Branch order 1st (NR1)	S1	8(0.3) Aa			8.5(0.3) Aa				***	***			***	*	***	**474.2**	**0.98**	***
	S2	16.7(0.3) Bb	14.8(0.4) Aa		16.1(0.5) Bab	17.5(0.4) Ab												
	S3	27.4(0.8) Cb	22.5(0.9) Ba		27.8(0.7) Cb	25.4(0.6) Bab												
	S4	41.9(0.6) Dab	39(1.3) Ca		45.5(1.1) Db	38(2.1) Ca												
	S5	52.4(0.8) Ecd	42.1(1.2) Ca	48.7(1.5) Abc	54.3(0.5) Ed	46(1.3) Dab	50.7(1.2) Acd											
	S6	68.9(1.1) Fc	58.6(1.2) Dab	60.7(1.3) Bb	69.9(0.9) Fc	55.3(1.1) Ea	65.9(0.9) Bc											
Branch order 2nd (NR2)	S3	3.9(1.1) Aa	5.7(3.7) ABa		16.7(3.3) Ab	14.2(2.7) Aab			***	***			***	**	***	**27.4**	**0.79**	***
	S4	52.3(3.9) Bb	23.4(2.4) Ba		63.3(7.4) Bb	27(5.2) ABa												
	S5	59.9(8) Bab	44.6(6.8) Ca	57.8(11.3) Aab	85.7(7.2) BCab	58.3(16.7) Bab	94.4(14.7) Ab											
	S6	88.6(10.9) Cab	51.4(8.9) Ca	54.4(8) Aa	103.9(17) Cb	57.6(7.7) Ba	86.3(6.4) Aab											

Variable (abbr.)	S	I59*I		I59*NI		I59*NI_I		RU*I		RU*NI		RU*NI_I		CV		IRR			S	CV* IRR	CV* IRR*S	F	R^2	P
														I59	Rubi	I	NI	NI_I						
Branch order 3rd (NR3)	S4	0(0)	Aa	0(0)	Ba			0.8(0.8)	Aa	0(0)	Aa				**	*			***	n.s.	*	3.5	0.32	***
	S5	0.6(0.6)	Aab	0.1(0.1)	Aa	0.2(0.2)	ABa	3.7(1.5)	Bb	0.3(0.3)	Aa	1.6(0.9)	Aab											
	S6	1.4(1.1)	Aa	1.3(0.6)	Aa	1.7(0.6)	Ba	5.3(2.9)	Aa	4.7(2.4)	Aa	0.6(0.3)	Ba											
Total number ramification	S1	8(0.3)	Aa					8.5(0.3)	Aa						***	***			***	**	***	56.7	0.88	***
	S2	16.7(0.3)	ABb	14.8(0.4)	Aa			16.1(0.5)	Aab	17.8(0.6)	Ab													
	S3	31.3(1.6)	Bab	28.2(3.2)	Aa			44.5(3.7)	Bc	39.6(3)	ABbc													
	S4	94.1(4.1)	Cb	62.4(3.3)	Ba			109.7(7.8)	Cb	65(7)	Ba													
	S5	112.9(8)	Cab	86.9(7.1)	Ca	106.7(12.7)	Aab	143.7(6.4)	Cb	104.6(17.8)	Cab	146.7(14.9)	Ab											
	S6	158.9(12.5)	Dab	111.3(9.8)	Da	116.9(8.9)	Aa	179(18.9)	Db	117.6(10.8)	Ca	152.7(6.7)	Aab											
Number of leaf per plant																								
Branch order 1st (NL1)	S1	43.3(2.9)	Aa					52.8(3.4)	Ab						n.s.	***			***	n.s.	***	194.9	0.96	***
	S2	171.6(5.3)	Aa	156(7.4)	Aa			173.2(9.6)	Ba	178.3(9.3)	Aa													
	S3	475.5(21.2)	Bbc	343.4(21.2)	Ba			484.8(19.3)	Cc	405.9(18.5)	Bab													
	S4	784(62.7)	Ca	736.3(27.5)	Ca			1055.8(28.5)	Db	723.6(62.8)	Ca													
	S5	1136(41.1)	Dc	616.4(51.2)	Ca	906.7(48.3)	Ab	1057(14.3)	Dbc	605.7(37.1)	Ca	975.1(33.3)	Abc											
	S6	1445.6(74.3)	Eb	1042.6(30.4)	Da	1288.9(61.6)	Bb	1344.4(31.9)	Eb	1029.6(45.7)	Da	1360.3(35.1)	Bb											
Branch order 2nd (NL2)	S3	30.6(11.3)	Aa	37.6(21.5)	ABa			107.6(20.2)	Ab	92.2(18.2)	ABab				***	***			***	**	***	33.2	0.82	***
	S4	294.6(20.2)	Bb	148.6(16.6)	Ba			571(42.1)	Bc	227(41.8)	Bab													
	S5	496.4(55.2)	Cabc	333(61.2)	Cab	394.7(83.1)	Aab	747.1(60.6)	BCc	278.7(82.6)	Ba	581.6(57.4)	Abc											
	S6	739.3(109.7)	Dab	456.1(63.8)	Ca	431.1(71.6)	Aa	849.6(145.2)	Cb	544(81.7)	Cab	688.6(44.1)	Aab											
Branch order 3rd (NL3)	S4	0(0)	Aa	0(0)	Ba			4.3(4.3)	ABa	0(0)	Aa				*	*			***	n.s.	*	3.3	0.31	***
	S5	3.6(3.6)	Aa	0.6(0.6)	Aa	0.7(0.7)	ABa	25.3(9)	Bb	2.6(2.6)	Aa	6.6(3.2)	ABa											
	S6	9.1(6.6)	ABa	9.3(5.4)	Aa	7.3(2.9)	Ba	29.9(16)	Aa	43(25.7)	Aa	3.6(1.8)	Ba											
Total number leaf	S1	54.6(2.9)	Aa					64.8(3.3)	Ab						***	***			***	*	***	103.4	0.93	***
	S2	183.4(5.8)	Aa	167(7.2)	Aa			187.7(10.1)	Aa	191.7(9.5)	Aa													
	S3	547.9(27.1)	Bb	417.6(19.5)	Ba			638(34.4)	Bb	541.8(32.8)	Bb													
	S4	1100.4(77.2)	Ca	903.1(34.9)	Ca			1650.2(68.3)	Cb	967.7(99.9)	Ca													
	S5	1657.4(78.1)	Dbc	964.4(106.8)	Ca	1317.7(120.6)	Aab	1850.3(70.5)	Cc	901.1(120)	Ca	1581.6(67.5)	Abc											
	S6	2216.6(177.4)	Eb	1529.9(75.7)	Da	1749(115.4)	Bab	2250(143.7)	Db	1637.6(148.5)	Da	2075.4(77)	Bab											
Leaf area per plant (m2)																								
Branch order 1st (LA1)	S1	0.17(0.02)	Aa					0.16(0.02)	Aa					***		***			***	*	***	133	0.95	***
	S2	0.57(0.03)	Aa	0.5(0.02)	Aa			0.52(0.04)	Ba	0.51(0.06)	Aa													
	S3	1.97(0.1)	Bc	0.85(0.07)	Aa			1.34(0.08)	Cb	0.75(0.05)	Aa													
	S4	5.17(0.44)	Cb	4.44(0.15)	Cab			5.24(0.18)	Eb	3.36(0.31)	Ca													
	S5	6.06(0.39)	Cd	2.72(0.27)	Bab	4.69(0.4)	Ac	4.46(0.06)	Dc	1.97(0.14)	Ba	3.64(0.16)	Abc											
	S6	7.57(0.5)	Dc	5.28(0.22)	Dab	7.16(0.46)	Bc	5.06(0.17)	Eab	3.92(0.22)	Ca	5.61(0.31)	Bb											
Branch order 2nd (LA2)	S3	0.08(0.04)	Aa	0.06(0.03)	Aa			0.17(0.04)	Aa	0.11(0.03)	Aa				*	***			***	*	***	33.5	0.82	***
	S4	1.46(0.08)	Bb	0.75(0.12)	Ba			2.45(0.18)	Bc	0.96(0.19)	Bab													
	S5	1.92(0.26)	Bab	1.23(0.23)	Ba	1.52(0.42)	Aa	2.84(0.29)	Bb	0.83(0.22)	Ba	1.96(0.19)	Aab											
	S6	3.18(0.42)	Ca	1.99(0.24)	Ca	2.17(0.39)	Aa	3.01(0.51)	Ba	1.97(0.34)	Ca	2.81(0.26)	Ba											
Branch order 3rd (LA3)	S4	0(0)	Aa	0(0)	Aa			0.01(0.01)	Aa	0(0)	Aa				*	*			***	n.s.	n.s.	2.6	0.26	***
	S5	0.01(0.01)	Aab	0(0)	Aa	0(0)	ABa	0.06(0.02)	Ab	0.01(0.01)	Aa	0.01(0)	Aa											
	S6	0.03(0.02)	Aa	0.03(0.02)	Aa	0.02(0.01)	Ba	0.1(0.06)	Aa	0.17(0.11)	Aa	0.01(0.01)	Aa											
Total leaf area (TLA)	S1	0.23(0.02)	Aa					0.22(0.02)	Aa					***		***			***	n.s.	***	102.5	0.93	***
	S2	0.61(0.03)	Aa	0.54(0.02)	Aa			0.58(0.04)	Aa	0.56(0.06)	Aa													
	S3	2.11(0.12)	Bc	0.93(0.06)	Aa			1.56(0.1)	Bb	0.89(0.07)	Aa													
	S4	6.72(0.44)	Cb	5.25(0.18)	Ca			7.78(0.32)	Cb	4.39(0.48)	Ca													
	S5	8.08(0.58)	Cd	4(0.42)	Bab	6.28(0.76)	Acd	7.44(0.33)	Ccd	2.85(0.34)	Ba	5.67(0.27)	Abc											
	S6	10.87(0.8)	Dc	7.39(0.3)	Dab	9.45(0.71)	Bbc	8.25(0.53)	Cab	6.11(0.66)	Da	8.52(0.56)	Babc											

Variable (abbr.)	S	I59*I	I59*NI	I59*NI_I	RU*I	RU*NI	RU*NI_I	CV		IRR			S	CV* IRR	CV* IRR*S	F	R^2	P
								I59	Rubi	I	NI	NI_I						
Daily light intercepted per plant (MJ)																		
Branch order 1st (IL1)	S1	1.19(0.09) Aa			1.13(0.09) Aa	()			***	***			***	n.s.	***	84.1	0.87	***
	S2	3.07(0.1) Aa	2.91(0.12) Aa		3.08(0.21) Ba	3.1(0.27) Aa												
	S3	9.81(0.41) Bc	4.93(0.33) Ba		6.9(0.35) Cb	4.5(0.26) Aa												
	S4	11.47(0.78) Ba	11.02(0.47) Ca		11.9(0.28) Da	10.12(0.72) Ba												
	S5	15.38(0.54) Cd	10.3(0.57) Cab	13.29(0.66) Acd	13.53(0.43) Ecd	9.24(0.51) Ba	12.33(0.59) Abc											
	S6	20.94(2.02) Da	17.77(0.88) Da	20.11(2.45) Ba	18.8(0.22) Fa	15.92(0.84) Ca	18.04(1.47) Ba											
Branch order 2nd (IL2)	S3	0.37(0.13) Aa	0.23(0.11) Aa		0.66(0.11) Aa	0.51(0.11) Aa			***	***			***	***	*	22.1	0.66	***
	S4	1.76(0.07) Bb	1.16(0.12) Ba		2.94(0.18) Bc	1.58(0.12) Bab												
	S5	2.22(0.14) Bab	2.76(0.26) Cab	1.98(0.3) Aa	4.19(0.31) BCc	2.36(0.39) Bab	3.25(0.22) Abc											
	S6	3.82(0.53) Cab	3.26(0.39) Cab	2.46(0.34) Aa	5.4(1.01) Cb	3.89(0.36) Cab	4.4(0.41) Bab											
Total intercepted light (TIL)	S1	1.19(0.09) Aa			1.13(0.09) Aa			n.s.		***			***	n.s.	***	37.5	0.85	***
	S2	3.07(0.1) Aa	2.91(0.12) Aa		3.08(0.21) Ba	3.1(0.27) Aa												
	S3	10.13(0.47) Bc	5.06(0.34) Ba		7.57(0.37) Cb	4.93(0.34) Aa												
	S4	13.24(0.79) Cab	12.18(0.44) Ca		14.85(0.41) Db	11.48(0.86) Ba												
	S5	17.61(0.63) Dc	13.06(0.75) Cab	15.27(0.91) Abc	17.78(0.62) Ec	11.61(0.87) Ba	15.59(0.68) Abc											
	S6	24.78(2.34) Ea	21.05(1.16) Da	22.58(2.72) Ba	24.42(1.17) Fa	20.04(1.09) Ca	22.46(1.85) Ba											

Three-way ANOVA for number of ramifications, number of metamer, number of leaves, leaf area, and intercepted light for leaf (factor: CV, IRR, S, and interaction CVxIRR, CVxIRRxS);

n.s.: not significant; *: $p<0.05$.; **: $p<0.01$; ***: $p<0.001$; asterisk's position inside columns CV and IRR marks greater trend; F: Fisher´s value; R^2: determination coefficient; P: probability model; mean;

Letters at the right of the mean show comparison using Tukey's HSD test, same uppercase letters indicate no significant differences between sampling date for each CVxIRR, same lowercase letters indicate no significant differences between CVxIRR into same sampling date, $p<0.05$;

For all CVxIRR, IL3 was negligible less than <0.4 MJ $plant^{-1}$ (data not shown).

Table 3. The effect of the first and second drought in terms of percentage of reduction ($\%R_{1^{st}}$ and $\%R_{2^{nd}}$, respectively) for all variables de canopy architecture (metamer, ramification, leaves, and light intercept for leaf) by branches order for cultivars I59 and Rubi from S2 to S6.

$\%R_{1^{st}}$ was calculated between irrigated plant`s during both dry seasons 2008 and 2009 (I) vs. non-irrigated plant`s during the first dry season but irrigated during the second dry season (NI-I; $\%R_{1^{st}} = -[(I - NI\_I)/I] \cdot 100$).

$\%R_{2^{nd}}$ was calculated between NI-I vs. non-irrigated plant`s during dry seasons (NI; $\%R_{2^{nd}} = -[(NI\_I - NI)/NI\_I] \cdot 100$)

Variable	**S**	**Branch 1^st^ order**				**Branch 2^nd^ order**				**Total branch**			
		$\%R_{1^{st}}$		$\%R_{2^{nd}}$		$\%R_{1^{st}}$		$\%R_{2^{nd}}$		$\%R_{1^{st}}$		$\%R_{2^{nd}}$	
		I59	**Rubi**	**I59**	**Rubi**	**I59**	**Rubi**	**I59**	**Rubi**	**I59**	**Rubi**	**I59**	**Rubi**
Number of metamer	**S2**	-10.5	5.5							-9.4	5.8		
	S3	**-28.5**	**-15.8**			22.9	-11.0			**-24.4**	-14.1		
	S4	-10.3	**-29.6**			**-49.4**	**-57.9**			-18.8	**-38.0**		
	S5	**-14.7**	-7.6	**-20.5**	**-16.7**	-21.5	-13.1	2.9	-41.5	-16.2	-10.1	-14.4	**-24.9**
	S6	**-13.6**	**-12.6**	-9.5	**-19.8**	-41.3	-33.3	23.5	-19.4	-21.8	**-20.7**	-1.7	-18.1
Number of ramification	**S2**	**-11.4**	8.7							**-11.4**	10.6		
	S3	**-17.9**	-8.6			46.2	-15.0			-9.9	-11.0		
	S4	-6.8	**-16.5**			**-55.2**	**-57.4**			**-33.7**	**-40.7**		
	S5	-7.2	-6.6	**-13.4**	**-9.3**	-3.4	10.2	-22.9	-38.3	-5.5	2.1	-18.6	-28.7
	S6	**-11.8**	-5.7	-3.5	**-16.1**	-38.5	-16.9	-5.5	-33.3	-26.4	-14.7	-4.8	-23.0
Number of leaves	**S2**	-9.1	2.9							-8.9	2.1		
	S3	**-27.8**	**-16.3**			22.9	-14.3			**-23.8**	-15.1		
	S4	-6.1	**-31.5**			**-49.6**	**-60.2**			-17.9	**-41.4**		
	S5	**-20.2**	-7.7	**-32.0**	**-37.9**	-20.5	-22.2	-15.6	**-52.1**	-20.5	-14.5	-26.8	**-43.0**
	S6	-10.8	1.2	**-19.1**	**-24.3**	-41.7	-19.0	5.8	-21.0	-21.1	-7.8	-12.5	-21.1
Leaf area	**S2**	-11.9	-1.8							-11.8	-4.1		
	S3	**-57.0**	**-43.6**			-27.5	-37.5			**-56.1**	**-42.9**		
	S4	-14.1	**-35.9**			**-49.0**	**-60.6**			**-21.8**	**-43.5**		
	S5	**-22.5**	-18.4	**-42.0**	**-45.8**	-20.8	-30.9	-19.0	-57.8	-22.2	-23.8	**-36.2**	**-49.8**
	S6	-5.3	10.8	**-26.2**	**-30.3**	-31.7	-6.4	-8.2	-30.1	-13.1	3.3	-21.8	-28.2
Daily light intercepted	**S2**	-5.2	0.6							-5.2	0.6		
	S3	**-49.7**	**-34.8**			-37.8	-22.7			**-50.0**	**-34.9**		
	S4	-3.9	-15.0			**-34.1**	**-46.3**			-8.0	**-22.7**		
	S5	-13.6	-8.9	**-22.5**	**-25.1**	-10.8	-22.4	39.4	-27.4	-13.3	-12.3	-14.5	**-25.5**
	S6	-4.0	-4.0	-11.6	-11.8	-35.6	-18.5	32.5	-11.6	-8.9	-8.0	-6.8	-10.8

Branch 3rd order was negligible, this one was discarded from the analysis;

$\%R_{1^{st}}$ in S2 to S3 were same “NI vs. I”.

Values highlighted in bold and grey relief indicates significant effect, using Tukey's HSD test, p<0.05.

Figures

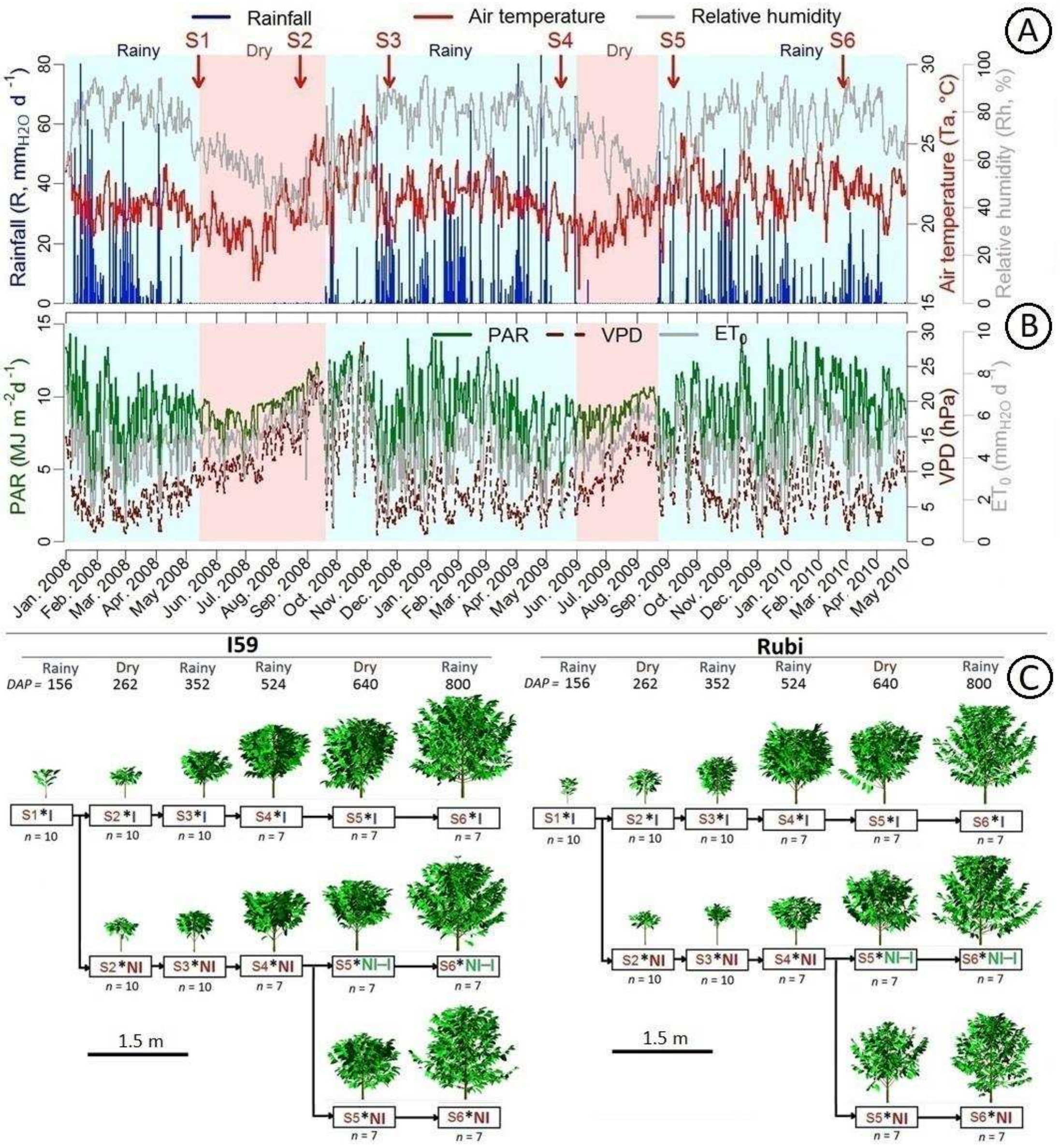

Fig. 1. Microclimate and irrigation treatments applied during the experiment:

A-B) Daily rainfall, air temperature, relative humidity, PAR (photosynthetically active radiation), VPD (vapour pressure deficit) and ET$_0$ (potential evapotranspiration). Arrows indicate the dates (S1 to S6) at which coffee plant where harvested for biomass and architectural measurements; blue area: wet season; pink area: dry season;

C) 3D mock-ups plant reconstructed from architectural descriptions from S1 to S6 for cultivars I59 (left) and Rubi (right) subjected to different irrigation treatments applied during the experiment (I: irrigation during dry seasons; NI-I: irrigated only during the 2nd dry season; and NI: never irrigated). DAP: days after planting; n indicates the number of described plants for each cultivar.

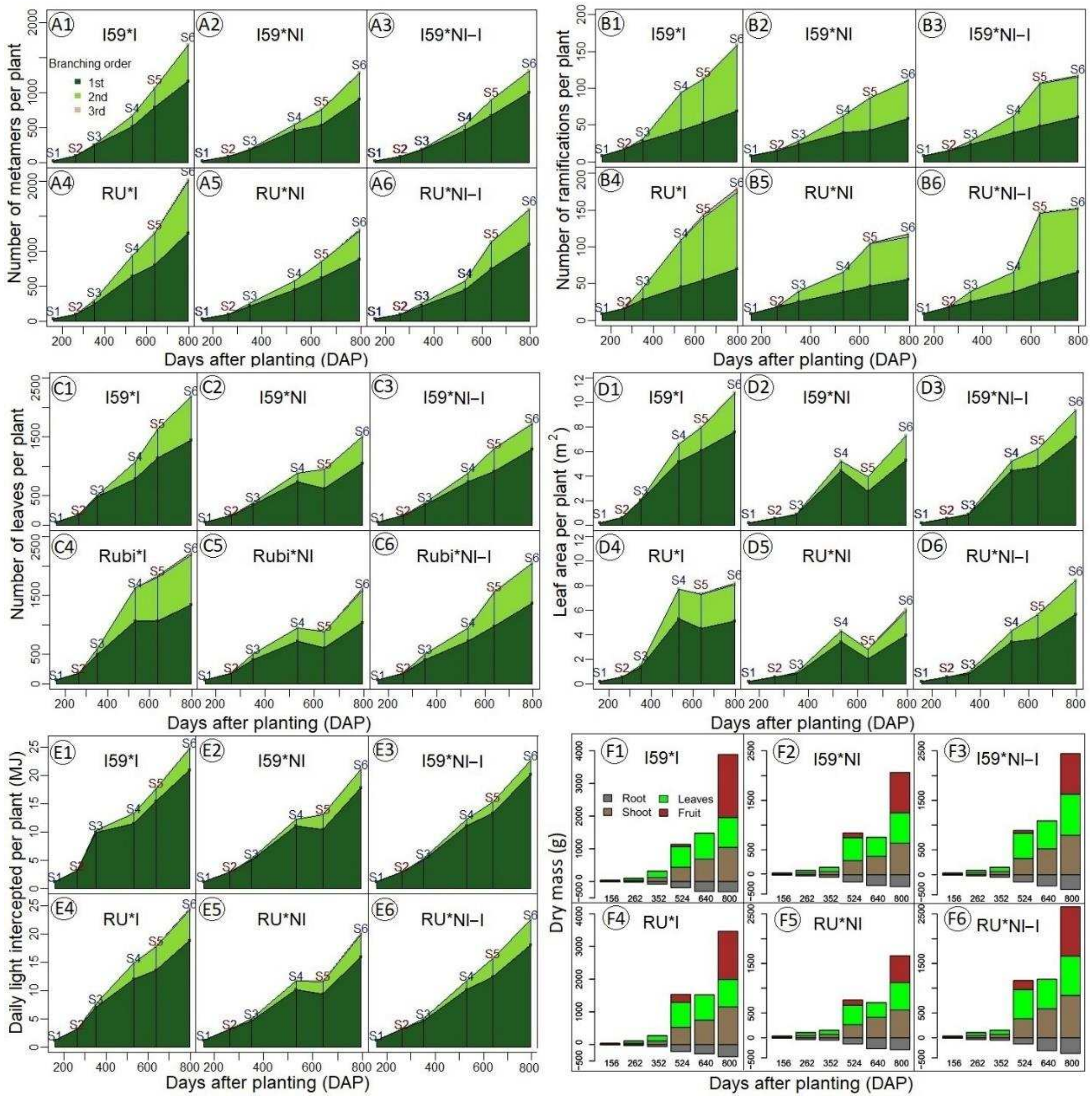

Fig. 2. Evolution over time of plants structural and biometrical variables for each cultivar (I59 and Rubi) and each irrigation treatment (I, NI and NI-I). A1 to A6: total number of metamers per plant; B1 to B6: total number of ramifications per plant; C1 to C6: total number of leaves per plant; D1 to D6: total leaf area per plant; E1 to E6: daily light intercepted per plant; and F1 to F6: Partitioning of the dry mass per plant (root, shoot, leaves, and fruit; there are no fruit dry mass measurements in S5). Dark green and light green areas represent the values obtained respectively for 1st order axes and higher order axes. Corresponding statistical analyses are given in Table 2.

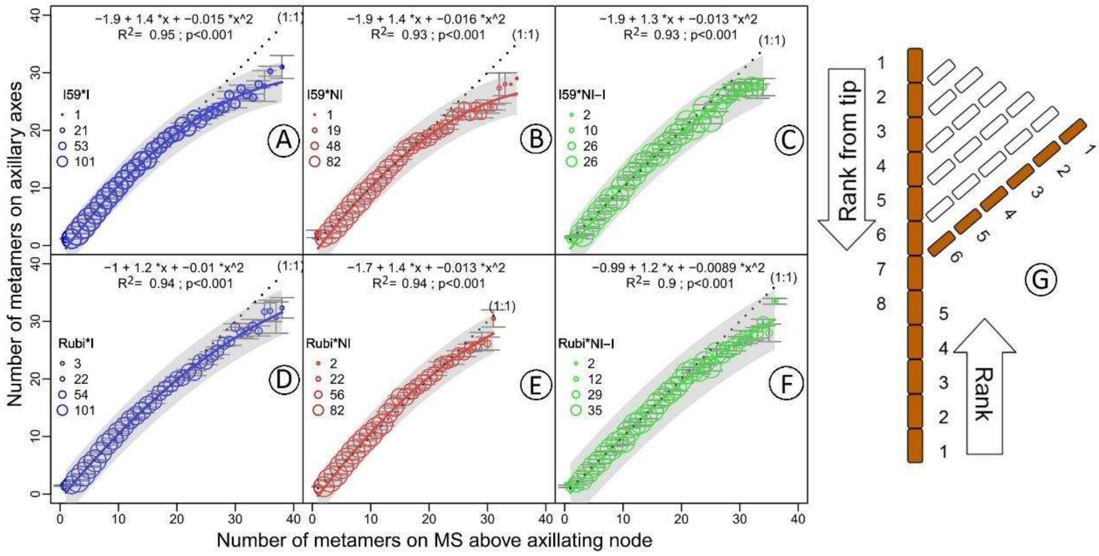

Fig. 3. Relationship between the number of metamers on 1st order axillary axes and the number of metamers on main stem (MS) above the axillating node (A to F). The sketch on the right illustrates the case when these numbers are the same for main stem and axillary axes (G). R^2: determination coefficient.

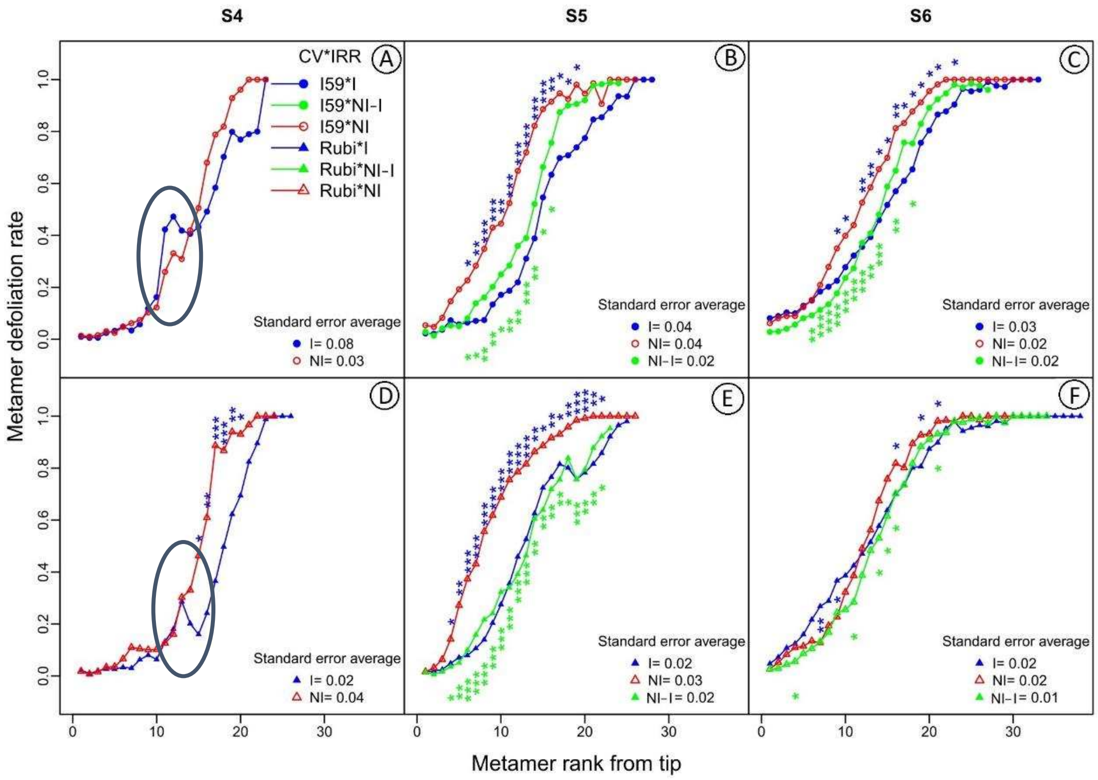

Fig. 4. Defoliation rate of metamers according to their position in 1st branches (see Table 1 for the definition of "rank from tip") for each cultivar (I59 and Rubi) and treatment (I, NI, and NI-I) at sampling dates S4 (DAP 524), S5 (DAP 640) and S6 (DAP 800). Asterisks indicate significant differences (Tukey's HSD test with α=0.05; *: $p<0.05$, **: $p<0.01$, and ***: $p<0.001$) for NI vs. I (blue) and NI vs. NI-I (green). Blue circle in S4 mark the effect of first dry season.

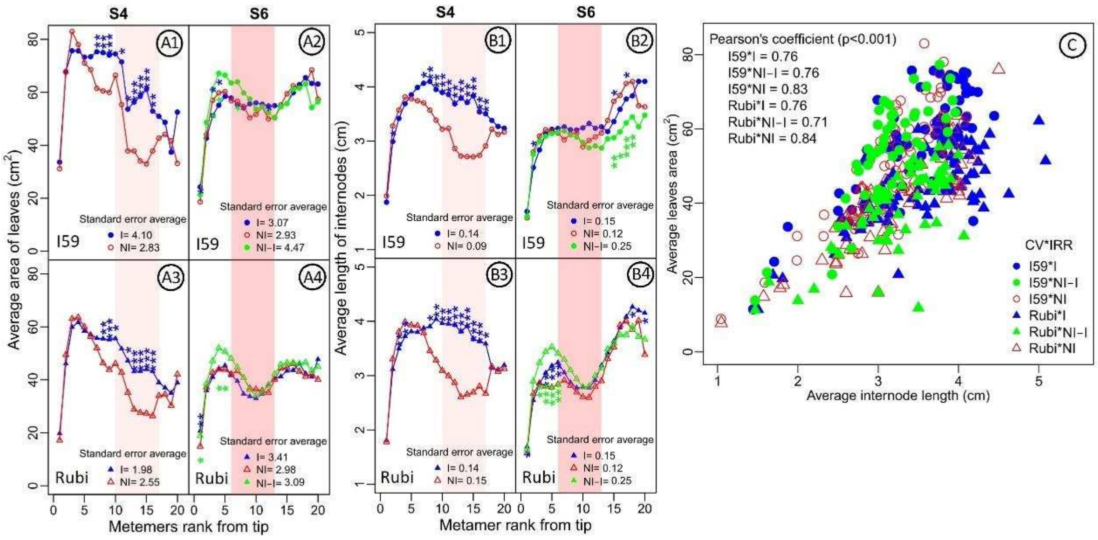

Fig. 5. Organ size in 1st order branches consecutively to drought events: (A1 to A4) Average area of leaves and (B1 to B4) average length of internodes according to their metamer position (see Table 1 for the definition of "rank from tip") at two sampling dates (S4 and S6) for each cultivar (CV: I59 and Rubi) and each treatment (IRR: I, NI and NI). The red bands approximately delimit the metamers that were set-up during the 1st (light red) and the 2nd (dark red) dry seasons; Asterisks indicate significant differences (Tukey's HSD test with α=0.05; *: $p<0.05$, **: $p<0.01$, and ***: $p<0.001$) for NI vs. I (blue) and NI vs. NI-I (green). (C) Relationship between average areas of leaves according to their length of internodes in branches 1st order (data combination of S4 and S6), with Pearson`s coefficient ($p<0.001$) for each CVxIRR.

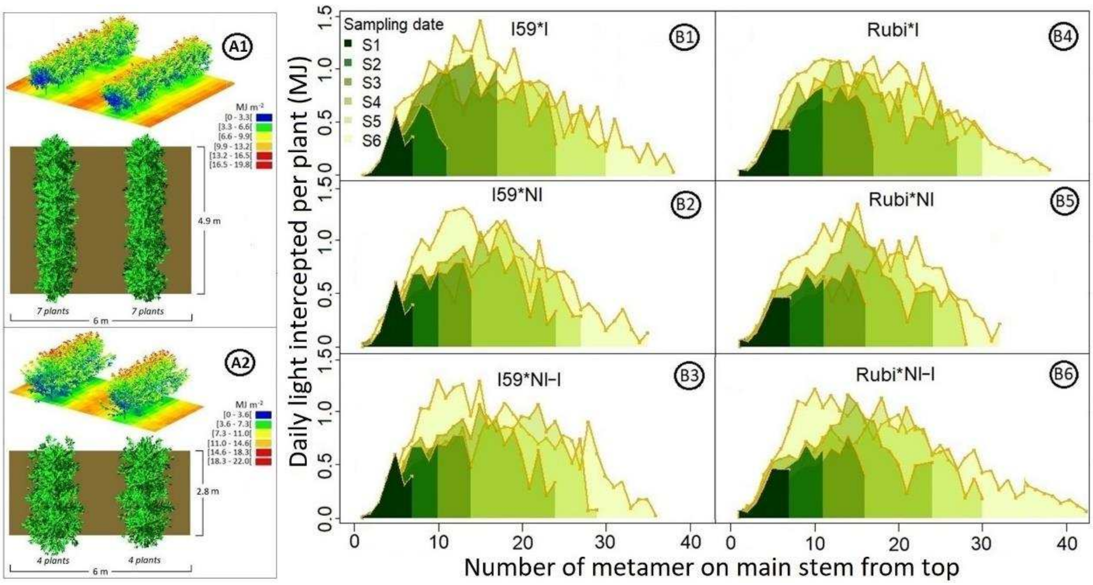

Fig. 6. Sketch of scene plot for light intercepted by the leaves for S1 to S5 (A1) and S6 (A2); color gradient indicates daily irradiation (MJ m^{-2}), from less (blue) to higher (red). Daily light intercepted (B1 to B6) according to their metamer position on main stem from top for each cultivar (I59 and Rubi) and irrigated treatment (I, NI, and NI-I) at sampling dates (S1 to S6).

SUPPLEMENTARY DATA

Supplementary tables

Table S1. ANOVA results for length of ramifications, for two cultivars (CV: I59 and Rubi), under three irrigation treatments (IRR: irrigated during the dry season= I, non-irrigated= NI, or non-irrigated year 1 and irrigated year 2= NI_I), from six sampling date (S: S1 to S6)

Variable (abbreviation)	S	I59*I	I59*NI	I59*NI_I	RU*I	RU*NI	RU*NI_I	CV		IRR			S	CV* IRR	CV* IRR*S	F	R^2	P
								I59	Rubi	I	NI	NI_I						
Length of ramifications (m)																		
Branch order 1st (LR1)	S1	0.86(0.07) Aa			1.05(0.09) Aa				***	***			***	**	***	**226.7**	**0.97**	***
	S2	2.46(0.05) Aa	2.17(0.1) Aa		2.6(0.19) Aa	2.6(0.13) Aa												
	S3	7.91(0.43) Bb	4.45(0.29) Ba		7.6(0.38) Bb	5.53(0.32) Ba												
	S4	17.88(0.76) Ca	14.87(0.73) Ca		22.29(0.82) Cb	14.41(1.25) Ca												
	S5	25.42(0.31) Dde	15.03(0.96) Ca	20.68(1.37) Abc	26.87(0.54) De	18.07(1.09) Dab	22.75(0.81) Acd											
	S6	36.95(1.87) Ec	27.46(1) Da	29.27(2.6) Bab	40.08(0.76) Ec	24.97(0.86) Ea	34.54(1.31) Bbc											
Branch order 2nd (LR2)	S3	0.37(0.17) Aa	0.35(0.18) Aa		1.37(0.29) Ab	0.85(0.18) ABab			***	***			***	**	***	**34.1**	**0.82**	***
	S4	4.99(0.29) Bb	2.54(0.32) Aa		9.66(0.74) Bc	3.93(0.77) BCab												
	S5	8.11(0.99) Ba	6.14(1.01) Ba	6.43(1.48) Aa	13.3(1.22) Bb	5.65(1.49) Ca	10.17(1) Aab											
	S6	15.43(2.07) Cab	10.8(1.37) Ca	9.06(1.93) Aa	21.75(3.42) Cb	9.95(1.83) Da	14.25(1.28) Bab											
Branch order 3rd (LR3)	S4	0(0) Aa	0(0) Ba		0.07(0.07) ABa	0(0) Aa			*	*			***	n.s.	n.s.	**2.9**	**0.28**	***
	S5	0.06(0.06) Aab	0(0) Aa	0.01(0.01) ABa	0.3(0.11) Bb	0.04(0.04) Aa	0.07(0.03) ABab											
	S6	0.14(0.1) ABa	0.17(0.1) Aa	0.13(0.06) Ba	0.56(0.33) Aa	0.67(0.41) Aa	0.05(0.03) Ba											
Total length ramification (TLR)	S1	0.86(0.07) Aa			1.05(0.09) Aa				***	***			***	**	***	**120.2**	**0.94**	***
	S2	2.46(0.05) Aa	2.17(0.1) Aa		2.6(0.19) Aa	2.61(0.14) Aa												
	S3	8.28(0.54) Bb	4.8(0.28) Aa		8.98(0.52) Bb	6.38(0.45) Aa												
	S4	22.86(0.73) Cb	17.41(0.85) Ba		32.02(1.47) Cc	18.34(1.86) Bab												
	S5	33.59(1.16) Dbc	21.17(1.65) Ba	27.12(2.65) Aab	40.46(1.53) Dc	23.76(2.47) Ba	32.99(1.62) Abc											
	S6	52.52(3.65) Ebc	38.43(2.1) Cab	38.46(4.37) Aab	62.39(4.11) Ec	35.59(2.97) Ca	48.84(2.34) Babc											

Three-way ANOVA for length of ramifications (factor: CV, IRR, S, and interaction CVxIRR, CVxIRRxS);
n.s.: not significant; *: $p<0.05$.; **: $p<0.01$; ***: $p<0.001$; asterisk’s position inside columns CV and IRR marks greater trend; F: Fisher´s value; R^2: determination coefficient; P: probability model; mean;
Letters at the right of the mean show comparison using Tukey's HSD test, same uppercase letters indicate no significant differences between sampling date for each CVxIRR, same lowercase letters indicate no significant differences between CVxIRR into same sampling date, $p<0.05$.

Supplementary figures

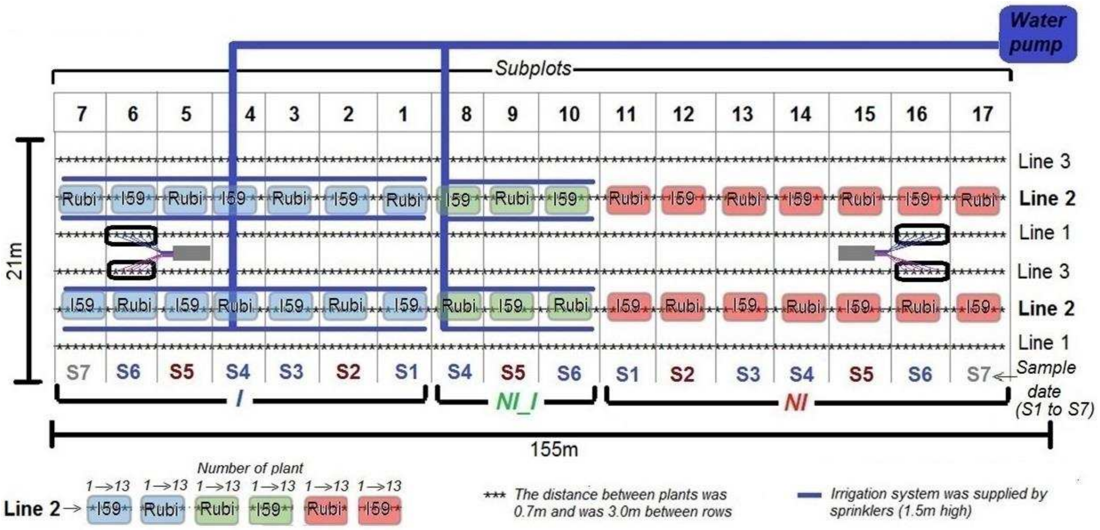

Fig. S1. Experimental plot, comprising 17 subplots, each defined as the area formed by the two cultivars (CV: I59 and Rubi), under one given irrigation treatment IRR (I, NI_I, or NI): and for one given sampling date (S: S1 to S7). Subplots 1 to 7 were irrigated during the dry seasons (I, in blue), subplots 8 to 10 were non-irrigated during dry season of year 1 and irrigated during dry season of year 2 (NI-I, in green), and subplots 11 to 17 were non-irrigated during the dry seasons (NI, in red). Each subplot contains 78 plants, i.e. 39 plants for each CV, each distributed on 3 lines (13 plants per line). Line 1 and 3 were meant for borders only. Lines 2 include 10 plants that were used for destructive dry mass partitioning. S7 was for reserve only (not used here).

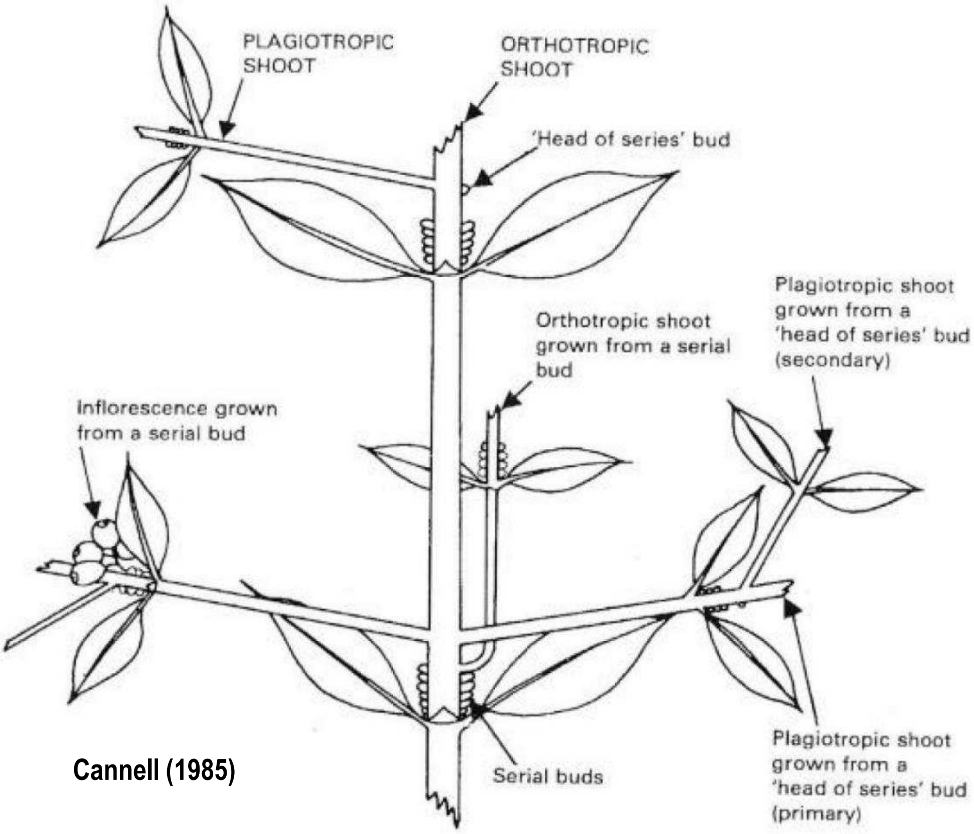

Fig. S2. Design shoot morphology of Arabica Coffee.

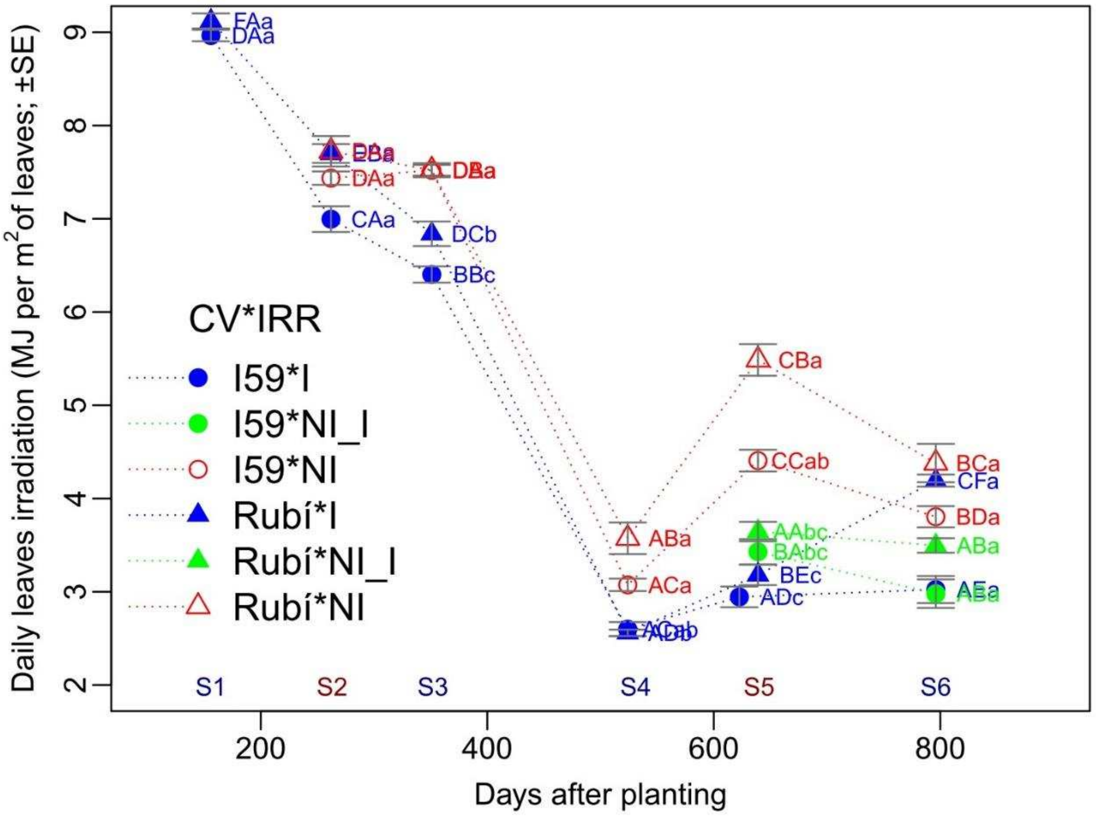

Fig. S3. Daily leaves irradiation from S1 to S6 for CVxIRR. Letters at the right of the mean show comparison using Tukey's HSD test, same uppercase letters indicate no significant differences between sampling date for each CVxIRR, same lowercase letters indicate no significant differences between CVxIRR into same sampling date, p<0.05.

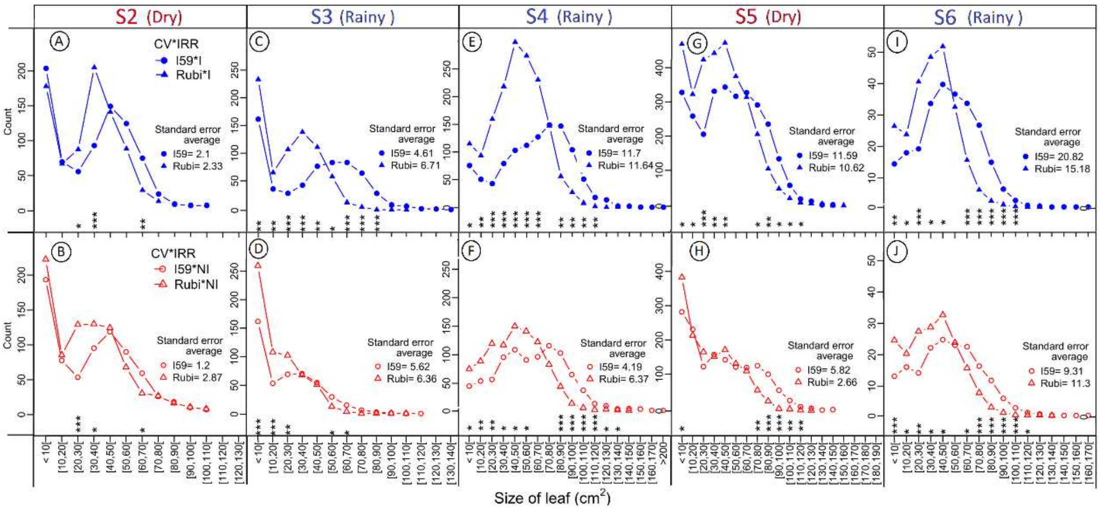

Fig. S4. Distribution size-leaf per plant for cultivars I59 and Rubi. Blue= I, and red= NI, NI-I not show, it has the same result as I treatment. Asterisks are comparison means with Tukey's HSD test (α=0.05) between Rubi and I59 for each size-leaf range and irrigated treatment (NI or I), *: $p<0.05$, **: $p<0.01$; and ***: $p<0.001$.

GENERAL CONCLUSION

This study highlighted some links between drought tolerance, plasticity (physiological and architectural), iso/anisohydric behaviour in Arabica coffee cultivars. The drought-tolerant cultivar (cv. I59) could be classified as isohydric and plastic for canopy conductance (exhibiting a precocious reaction to drought) whereas the drought-sensitive cultivar (cv. Rubi) was revealed as anisohydric and more plastic for late reactions to drought (e.g., allocation growth to roots in particular and leaf shedding with faster leaf renewal due to greater number of second/third order branches). Notably, the drought-sensitive cultivar also displayed a faster ability to recover from drought stress; indeed this cultivar had similar partitioning of dry mass in irrigated and not-irrigated plants at the end of two years of evaluations. The cultivars herein examined also differ in their strategies to cope with drought in terms of their abilities to set-up second order ramifications, i.e. Rubi was quicker to establish a greater number of branches of 2nd order than I59. Setting ramifications seems to be a most efficient way for increasing/restoring leaf area, particularly because setting ramifications can multiply the number of potential fruiting nodes.

A key message from this research resides on the fact that evaluation of crop performance under drought conditions should combine analyses of both physiological and organo-morphogenetic processes. The most important difference between cultivars concerns the stomatal regulation which has immediate effects on photosynthesis and transpiration. The organogenetic and morphogenetic responses have slight effects on architecture on the short term but large effects on the medium and long terms, i.e. setting-up axillary ramifications is a highly effective way for a plant to leverage its leaf area, since it contributes to a faster leaf renewal. The data collected in this study provided countless information that could be used for building a functional structural coffee model coupling architectural rules and ecophysiological processes such as carbon acquisition. The fitness of coffee plants submitted to climatic events depends on the adequacy of physiological and organo-morphogenetic features and, consequently, these aspects should be accounted for in breeding programs aimed at improving drought tolerance in coffee.