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AVALIAÇÕES MORFOFISIOLÓGICAS EM TRÊS CULTIVARES DE CAFÉ
CRESCENDO EM DUAS CONDIÇÕES DE LUMINOSIDADE

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**AVALIAÇÕES MORFOFISIOLÓGICAS EM TRÊS VARIEDADES DE CAFÉ
CRESCENDO SOB DIFERENTES CONDIÇÕES DE LUMINOSIDADE**

Versão Final

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Abstract

Coffee is one of the main agricultural products traded in the world and species *Coffea arabica* L. and *Coffea canephora* Pierre ex A. Froehner are the most cultivated. They are plants that can be grown in environments of different shading conditions, but with productivity and morphophysiological characteristics that can be altered. The objective of the present study was to evaluate the effect of shading on growth, gas exchange and heat tolerance of photosystem II (PSII) in three coffee cultivars, Mundo Novo and Catuaí Amarelo (*C. arabica*) and Conilon (*C. canephora*). We hope that: I - the varieties are capable of acclimatization to the different shading conditions, with important morphophysiological alterations for photosynthesis; II - plants in sun-exposed environments showed higher tolerance of photosynthetic apparatus to heat; III - Conilon variety will have the most heat tolerant photosynthetic apparatus, as *C. canephora* originates from warm habitat. To test these hypotheses, plants of the three varieties were grown in containers with 3 liters of soil under two light conditions (Sun and Shade), with climate monitoring, constant hydration and nutrient replacement. Plant growth parameters (leaf number, plant growth and stem diameter), gas exchange (from light response curves), stomatal traits, pigment content and PSII heat tolerance were evaluated. Temperature and humidity varied significantly between growing conditions. In general, coffee trees growing in sun-exposed environmental conditions presented higher leaf number, higher density and stomatal index, higher gas exchange rates and other parameters evaluated by light response curves. In Shade condition the plant size, stomata size and chlorophyll content were higher. About the thermotolerance of PSII, Conilon was the most heat tolerant variety, and plants in Shade condition plants were more thermotolerant. Growing in a brighter environment may be beneficial to plant growth and photosynthetic rates of Mundo Novo and Catuaí Amarelo, varieties of *C. arabica*. However, for Conilon (*C. canephora*), the microclimate variation in Sun condition can be detrimental to PSII growth and thermotolerance in this variety. According to the morphophysiological responses found, coffee varieties generally exhibit similar adaptations for each growing condition, but each variety has distinct responses even if they belong to the same species. Thus, the cultivation of varieties must respect their

adaptive limitations to ensure a good physiological status of the plants and consequently good productivity.

Key-words: *Coffea arabica*. *Coffea canephora*. Temperature. Gas exchange. Shading. Microclim. Thermotolerance.

Resumo

O café é um dos principais produtos agrícolas comercializados no mundo sendo as espécies *Coffea arabica* L. e *Coffea canephora* Pierre ex A. Froehner as mais cultivadas. São plantas que podem ser cultivadas em ambientes com distintas condições de sombreamento, porém com produtividade e características morfofisiológicas podendo ser alteradas em cada condição de luminosidade. O objetivo do presente estudo foi avaliar o efeito do sombreamento no crescimento, trocas gasosas e tolerância do fotossistema II (PSII) ao calor em três cultivares de café, Mundo Novo e Catuaí Amarelo (*C. arabica*) e Conilon (*C. canephora*). Esperamos que: I - as variedades são capazes de aclimação às distintas condições de sombreamento, com alterações morfofisiológicas importantes para fotossíntese; II - plantas em ambientes mais ensolarados apresentaram maior tolerância do aparato fotossintético ao calor; III – a variedade Conilon terá o aparato fotossintético mais tolerante ao calor, pois *C. canephora* é originária de habitat quente. Para testar essas hipóteses, plantas das três variedades foram crescidas em recipientes com 3 litros de terra sob duas condições de luminosidade (Sol e Sombra), havendo monitoramento climático, constante hidratação e reposição de nutrientes. Foram avaliados parâmetros de crescimento das plantas (número de folhas, crescimento e diâmetro do caule), trocas gasosas (a partir de curvas de resposta a luz), características estomáticas, teor de pigmentos e termotolerância do PSII. Temperatura e umidade variaram significativamente entre as condições de crescimento. No geral, cafeeiros crescendo em condição ambiental mais ensolarada apresentaram, maior número de folhas, maior densidade e índice estomático, maiores taxas de trocas gasosas e demais parâmetros avaliados pelas curvas de resposta a luz. Em condição sombreada o tamanho da planta, tamanho dos estômatos e o teor de clorofila foram maiores. Acerca da termotolerância do PSII, Conilon foi a variedade mais tolerante ao calor, sendo que nessa variedade plantas de ambiente mais sombreados foram mais termotolerantes. Crescer em ambiente mais luminoso pode ser benéfico ao crescimento das plantas e taxas fotossintéticas de Mundo Novo e Catuaí Amarelo, variedades de *C. arabica*. Porém para Conilon (*C. canephora*),

a variação microclimática existente no ambiente mais ensolarado pode ser prejudicial ao crescimento e termotolerância do PSII nessa variedade. De acordo com as respostas morfofisiológicas encontradas, as variedades de café exibem no geral adaptações semelhantes para cada condição de crescimento, porém cada variedade tem respostas distintas mesmo pertencendo a mesma espécie. Sendo assim, o cultivo das variedades deve respeitar suas limitações adaptativas para garantir um bom status fisiológico as plantas e consequentemente boa produtividade.

Palavras-chave: *Coffea arabica*. *Coffea canephora*. Temperatura. Trocas Gasosas. Sombreamento. Microclima. Termotolerância.

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Table 1. Growing of aerial part and stomatal traits in coffee plants that were subjected to two growing conditions. Means $\pm$ SE followed by the same letter do not differ significantly from one another. For the results about plant growth, the $n = 10$; for stomatal characteristics see n in material and methods ($P < 0.05$, ANOVA and Tukey test for all parameters, and Kruskal-Wallis and Dunn's test for stomatal size). The data of total number of leaves, stomatal density and stomatal size presented in the table are the original data, and the uppercase letters placed in front of the values refer to statistical analysis done with the data of the logarithmic transformation.

Table 2. Photosynthetic parameters derived from the photosynthetic light-response curves (P_N / I curve): light compensation point (**LCP**; $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$), light saturation point (**LSP**; $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$), dark respiration (**R_d**; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), photosynthetic assimilation rate in LSP (**P_{Nmax}**; $\mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$), maximum apparent photosynthetic quantum yield at $I = 0$ (**$\Phi_{(I_0)}$** ; $\mu\text{mol (CO}_2\text{) } \mu\text{mol (photon)}^{-1}$), stomatal conductance in LSP (**g_s**; $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$), transpiration in LSP (**E**; $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) and internal CO₂ concentration in LSP (**C_i**; $\text{mmol CO}_2 \text{ mol}^{-1} \text{ air}$), Water use efficiency in LSP (**WUE**), intrinsic Water Use Efficiency in LSP (**iWUE**) and instantaneous carboxylation efficiency (**Φ_c**) in coffee plants that were subjected to shading conditions. Means $\pm$ SE followed by the same uppercase letter do not differ significantly from one another for sun and shade treatments within varieties. Uppercase letters indicate difference between treatments. ($n = 8$, $p < 0.05$, Two-way ANOVA and Tukey test).

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Figure 1. Photosynthetically photon flux density (PPFD) in January 28 (a) and February 04 (b), the days with more and less PPFD, respectively. The continuous line represents the Sun and the dotted line the Shade growth condition.

Figure 2. Temperature, air relative humidity and precipitation during January to March in Sun, Shade and local weather station. Minimal, mean and maximum temperature registered, in Sun (a), Shade (b) and for weather station (c). Air relative humidity for Sun (d), Shade (e) and for weather station.

Figure 3. Example of stomatal structure and epidermis cells in abaxial surface of the coffee varieties growth in the sun (left column) and shade (right column) conditions. Catuaí Amarelo is represented by (a) and (b); Mundo Novo is represented by (c) and (d); Conilon is represented by (e) and (f). Letters inside the structures mean: ST, stomatal; EP, epidermis cells. Scale bars = 200 μ m.

Figure 4. Result of SPAD index and DMSO pigments quantification are shown in the following graphs: SPAD readings (a), Total Chlorophylls content (b), Chlorophyll a/b ratio (c), Chlorophyll/Carotenoid ratio (d) and Carotenoids content (e) in coffee varieties in each shading condition (sun and shade). Vertical bars are mean $\pm$ SE. Different letters in columns indicate statistically significant differences in that variety ($n = 10$, $p < 0.05$, Two-way ANOVA and Tukey test).

Figure 5. Relationship between stomatal traits and gas exchange. Significant relationships are shown for P_{Nmax} and SD (A), and P_{Nmax} and SI (B), E and SD (C) and g_s and SD (D). Filled symbols represent the varieties in the shade and open symbols the varieties in the sun. Each symbol represents a variety, square (Conilon), triangle (Mundo

Novo) and circle (Catuaí Amarelo).

Figure 6. PSII thermotolerance of coffee varieties under different shading conditions, using two methodologies, ramping assay with results of T_{50} **(a)** and in static assay with results of H_{50} **(b)**. Means $\pm$ SE followed by the same uppercase letter do not differ significantly from one another for sun and shade treatments within varieties. ($n = 5$, $p < 0.05$, Two-way ANOVA and Tukey test).

Summary

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REFERENCES

- Allakhverdiev SI, Kreslavski VD, Klimov V V., Los DA, Carpentier R, Mohanty P.** 2008. Heat stress: an overview of molecular responses in photosynthesis. *Photosynthesis Research* **98**, 541–550.
- Alves V, Goulart FF, Jacobson TKB, Filho RJ de M, Ribas CEDC.** 2016. Shade's Benefit: Coffee Production under Shade and Full Sun. *Journal of Agricultural Science* **8**, 11.
- Apel K, Hirt H.** 2004. Reactive oxygen species: metabolism, oxidative stress, and signal transduction. *Annual review of plant biology* **55**, 373–99.
- Assad ED, Pinto HS, Zullo Junior J, Ávila AMH.** 2004. Climatic changes impact in agroclimatic zoning of coffee in Brazil. *Pesquisa Agropecuária Brasileira* **39**, 1057–1064.
- Baliza DP, Cunha RL, Guimarães RJ, Barbosa JPRAD, Ávila FW, Passos AMA.** 2012. Physiological characteristics and development of coffee plants under different shading levels. *Revista Brasileira de Ciencias Agrarias* **7**, 37–43.
- Barradas VL, Fanjul L.** 1986. Microclimatic characterization of shaded and open-grown coffee (*Coffea arabica* L .) plantations in Mexico. *Agricultural and Forest Meteorology* **38**, 101–112.
- Beer J.** 1987. Advantages, disadvantages and desirable characteristics of shade trees for coffee, cacao and tea. *Agroforestry Systems* **5**, 3–13.
- Berry J, Bjorkman O.** 1980. Photosynthetic Response and Adaptation to Temperature in Higher Plants. *Annual Review of Plant Physiology* **31**, 491–543.
- Bita CE, Gerats T.** 2013. Plant tolerance to high temperature in a changing environment: scientific fundamentals and production of heat stress-tolerant crops. *Frontiers in Plant Science* **4**, 1–18.
- Bote AD, Struik PC.** 2015. A study of the effects of shade on growth , production and quality of coffee (*COFFEA ARABICA*) in Ethiopia. *International Journal of Agricultural Sciences* **5**, 748–752.
- Bunn C, Läderach P, Ovalle Rivera O, Kirschke D.** 2015. A bitter cup: climate

change profile of global production of Arabica and Robusta coffee. *Climatic Change* **129**, 89–101.

De Camargo MBP. 2010. The impact of climatic variability and climate change on arabic coffee crop in Brazil. *Bragantia* **69**, 239–247.

Chaves CJN, Leal BSS, de Lemos-Filho JP. 2015. Temperature modulation of thermal tolerance of a CAM-tank bromeliad and the relationship with acid accumulation in different leaf regions. *Physiologia Plantarum* **154**, 500–510.

Chaves ARM, Ten-Caten A, Pinheiro HA, Ribeiro A, Damatta FM. 2008. Seasonal changes in photoprotective mechanisms of leaves from shaded and unshaded field-grown coffee (*Coffea arabica* L.) trees. *Trees - Structure and Function* **22**, 351–361.

Covre AM, Partelli FL, Bonomo R, Braun H, Ronchi CP. 2016. Vegetative growth of Conilon coffee plants under two water conditions in the Atlantic region of Bahia State, Brazil. *Acta Scientiarum. Agronomy* **38**, 535.

DaMatta FM. 2004. Ecophysiological constraints on the production of shaded and unshaded coffee: A review. *Field Crops Research* **86**, 99–114.

Damatta FM, Avila RT, Cardoso AA, Martins SCV, Ramalho JC. 2018. Physiological and Agronomic Performance of the Coffee Crop in the Context of Climate Change and Global Warming: A Review. *Journal of Agricultural and Food Chemistry* **66**, 5264–5274.

DaMatta FM, Grandis A, Arenque BC, Buckeridge MS. 2010. Impacts of climate changes on crop physiology and food quality. *Food Research International* **43**, 1814–1823.

Damatta FM, Ramalho JDC. 2006. Impacts of drought and temperature stress on coffee. *Brazilian Journal of Plant Physiology* **18**, 55–81.

DaMatta FM, Ronchi CP, Maestri M, Barros RS. 2007. Ecophysiology of coffee growth and production. *Brazilian Journal of Plant Physiology* **19**, 485–510.

Davis AP, Gole TW, Baena S, Moat J. 2012. The Impact of Climate Change on Indigenous Arabica Coffee (*Coffea arabica*): Predicting Future Trends and Identifying Priorities. *PLoS ONE* **7**, 10–14.

- Davis AP, Govaerts R, Bridson DM, Stoffelen P.** 2006. An annotated taxonomic conspectus of the genus *Coffea* (Rubiaceae). *Botanical Journal of the Linnean Society* **152**, 465–512.
- Fanjul L, Arreola-Rodriguez R, Mendez-Castrejon MP.** 1985. Stomatal responses to environmental variables in shade and sun grown coffee plants in Mexico. *Experimental Agriculture* **21**, 249–258.
- Farquhar GD, Sharkey TD.** 1982. Stomatal Conductance and Photosynthesis. *Annual Review of Plant Physiology* **33**, 317–345.
- Franck N, Vaast P.** 2009. Limitation of coffee leaf photosynthesis by stomatal conductance and light availability under different shade levels. *Trees - Structure and Function* **23**, 761–769.
- Gimeno TE, Pas B, Lemos-Filho JP, Valladares F.** 2009. Plasticity and stress tolerance override local adaptation in the responses of Mediterranean holm oak seedlings to drought and cold. *Tree Physiology* **29**, 87–98.
- Godoy O, de Lemos-Filho JP, Valladares F.** 2011. Invasive species can handle higher leaf temperature under water stress than Mediterranean natives. *Environmental and Experimental Botany* **71**, 207–214.
- Hatfield JL, Prueger JH.** 2015. Temperature extremes: Effect on plant growth and development. *Weather and Climate Extremes* **10**, 4–10.
- IPCC.** 2014. *Climate change 2014*.
- Johansen DA.** 1940. *Plant Microtechnique*. New York: McGraw-Hill Book Company.
- Jones HG.** 1998. Stomatal control of photosynthesis and transpiration. *Journal of Experimental Botany* **49**, 387–398.
- Lichtenthaler HK.** 2012. Vegetation Stress: an Introduction to the Stress Concept in Plants. *Journal of Plant Physiology* **148**, 4–14.
- Lobo F de A, de Barros MP, Dalmagro HJ, Dalmolin ÂC, Pereira WE, de Souza ÉC, Vourlitis GL, Rodríguez Ortíz CE.** 2013. Fitting net photosynthetic light-response curves with Microsoft Excel — a critical look at the models. *Photosynthetica* **51**, 445–456.

Machado EC, Schmidt PT, Medina CL, Ribeiro R V. 2005. Photosynthetic responses of three citrus species to environmental factors. *Pesquisa Agropecuaria Brasileira* **40**, 1161–1170.

Marias DE, Meinzer FC, Still C. 2017*a*. Leaf age and methodology impact assessments of thermotolerance of *Coffea arabica*. *Trees - Structure and Function* **31**, 1091–1099.

Marias DE, Meinzer FC, Still C. 2017*b*. Impacts of leaf age and heat stress duration on photosynthetic gas exchange and foliar nonstructural carbohydrates in *Coffea arabica*. *Ecology and Evolution* **7**, 1297–1310.

Martins SCV, Araújo WL, Tohge T, Fernie AR, DaMatta FM. 2014*a*. In high-light-acclimated coffee plants the metabolic machinery is adjusted to avoid oxidative stress rather than to benefit from extra light enhancement in photosynthetic yield. *PLoS ONE* **9**, 1–11.

Martins SCV, Galmés J, Cavatte PC, Pereira LF, Ventrella MC, DaMatta FM. 2014*b*. Understanding the low photosynthetic rates of sun and shade coffee leaves: Bridging the gap on the relative roles of hydraulic, diffusive and biochemical constraints to photosynthesis. *PLoS ONE* **9**, 1–10.

Martins MQ, Rodrigues WP, Fortunato AS, *et al.* 2016. Protective Response Mechanisms to Heat Stress in Interaction with High [CO₂] Conditions in *Coffea* spp. *Frontiers in Plant Science* **7**.

Mathur S, Agrawal D, Jajoo A. 2014. Photosynthesis: Response to high temperature stress. *Journal of Photochemistry and Photobiology B: Biology* **137**, 116–126.

Matos FS, Wolfgramm R, Gonçalves F V., Cavatte PC, Ventrella MC, DaMatta FM. 2009. Phenotypic plasticity in response to light in the coffee tree. *Environmental and Experimental Botany* **67**, 421–427.

Matthews JSA, Vialet-Chabrand S, Lawson T. 2018. Acclimation to Fluctuating Light Impacts the Rapidity of Response and Diurnal Rhythm of Stomatal Conductance. *Plant Physiology* **176**, 1939–1951.

Mittler R. 2002. Oxidative stress, antioxidants and stress tolerance. *Trends in Plant Science* **7**, 405–410.

Mittler R. 2006. Abiotic stress, the field environment and stress combination. Trends in Plant Science **11**, 15–19.

Moat J, O’Sullivan RJ, Gole TW, Davis AP. 2018. The IUCN Red List of Threatened Species: *Coffea arabica*. The IUCN Red List of Threatened Species **8235**.

Morais H, Caramori PH, De Arruda Ribeiro AM, Gomes JC, Koguishi MS. 2006. Microclimatic characterization and productivity of coffee plants grown under shade of pigeon pea in Southern Brazil. Pesquisa Agropecuaria Brasileira **41**, 763–770.

Morais LE, Rodríguez-López NF, Medina EF, Cavatte PC, DaMatta FM, Martins SC V., Silva PEM. 2012. Physiological and biochemical abilities of robusta coffee leaves for acclimation to cope with temporal changes in light availability. Physiologia Plantarum **149**, 45–55.

Müller L-LB, Albach DC, Zotz G. 2017. ‘Are 3 °C too much?’: thermal niche breadth in Bromeliaceae and global warming (G Matlack, Ed.). Journal of Ecology **105**, 507–516.

Mussatto SI, Machado EMS, Martins S, Teixeira JA. 2011. Production, Composition, and Application of Coffee and Its Industrial Residues. Food and Bioprocess Technology **4**, 661–672.

Naidu SL, DeLucia EH. 1998. Physiological and morphological acclimation of shade-grown tree seedlings to late-season canopy gap formation. Plant Ecology **138**, 27–40.

Niinemets Ü, Valladares F. 2004. Photosynthetic acclimation to simultaneous and interacting environmental stresses along natural light gradients: Optimality and constraints. Plant Biology **6**, 254–268.

Nobel PS. 2009. *Physicochemical and Environmental Plant Physiology*. Elsevier.

Noirot M, Charrier A, Stoffelen P, Anthony F. 2016. Reproductive isolation, gene flow and speciation in the former *Coffea* subgenus: a review. Trees - Structure and Function **30**, 597–608.

Prioul JL, Chartier P. 1977. Partitioning of Transfer and Carboxylation Components of Intracellular Resistance to Photosynthetic CO₂ Fixation: A Critical Analysis of the Methods Used. Annals of Botany **41**, 789–800.

Ramvalho JC, DaMatta FM, Rodrigues AP, Scotti-Campos P, Pais I, Batista-Santos P, Partelli FL, Ribeiro A, Lidon FC, Leitão AE. 2014. Cold impact and acclimation response of *Coffea* spp. plants. *Theoretical and Experimental Plant Physiology* **26**, 5–18.

Ramvalho JC, Rodrigues AP, Semedo JN, *et al.* 2013. Sustained photosynthetic performance of *Coffea* spp. under long-term enhanced [CO₂]. *PLoS ONE* **8**, 1–19.

Rascher U, Liebig M, Lüttge U. 2000. Evaluation of instant light-response curves of chlorophyll fluorescence parameters obtained with a portable chlorophyll fluorometer on site in the field. *Plant, Cell and Environment* **23**, 1397–1405.

Rodrigues WP, Martins MQ, Fortunato AS, *et al.* 2016. Long-term elevated air [CO₂] strengthens photosynthetic functioning and mitigates the impact of supra-optimal temperatures in tropical *Coffea arabica* and *C. canephora* species. *Global Change Biology* **22**, 415–431.

Rodríguez-López NF, Martins SC V, Cavatte PC, *et al.* 2014. Morphological and physiological acclimations of coffee seedlings to growth over a range of fixed or changing light supplies. *Environmental and Experimental Botany* **102**, 1–10.

Ronchi CP, DaMatta FM, Batista KD, Moraes GABK, Loureiro ME, Ducatti C. 2006. Growth and photosynthetic down-regulation in *Coffea arabica* in response to restricted root volume. *Functional Plant Biology* **33**, 1013–1023.

Rozendaal DMA, Hurtado VH, Poorter L. 2006. Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. *Functional Ecology* **20**, 207–216.

Suzuki N, Rivero RM, Shulaev V, Blumwald E, Mittler R. 2014. Abiotic and biotic stress combinations. *New Phytologist* **203**, 32–43.

Terashima I, Hanba YT, Tazoe Y, Vyas P, Yano S. 2006. Irradiance and phenotype: Comparative eco-development of sun and shade leaves in relation to photosynthetic CO₂ diffusion. *Journal of Experimental Botany* **57**, 343–354.

Teskey R, Wertin T, Bauweraerts I, Ameye M, McGuire MA, Steppe K. 2015. Responses of tree species to heat waves and extreme heat events. *Plant Cell and Environment* **38**, 1699–1712.

Tiwari BS, Belenghi B, Levine A. 2002. Oxidative Stress Increased Respiration and Generation of Reactive Oxygen Species, Resulting in ATP Depletion, Opening of Mitochondrial Permeability Transition, and Programmed Cell Death. *Plant Physiology* **128**, 1271–1281.

Valladares F. 2003. Light Heterogeneity and Plants: from Ecophysiology to Species Coexistence and Biodiversity. In: Esser K., In: Lüttge U., In: Beyschlag W., In: Hellwig F, eds. *Progress in Botany*. Progress in Botany. Berlin, Heidelberg: Springer Berlin Heidelberg, 439–461.

Valladares F, Niinemets Ü. 2008. Shade Tolerance, a Key Plant Feature of Complex Nature and Consequences. *Annual Review of Ecology, Evolution, and Systematics* **39**, 237–257.

Vega FE, Rosenquist E, Collins W. 2003. Global project needed to tackle coffee crisis. *Nature* **425**, 343–343.

Wahid A, Gelani S, Ashraf M, Foolad MR. 2007. Heat tolerance in plants: An overview. *Environmental and Experimental Botany* **61**, 199–223.

Wellburn AR. 1994. The Spectral Determination of Chlorophylls a and b, as well as Total Carotenoids, Using Various Solvents with Spectrophotometers of Different Resolution. *Journal of Plant Physiology* **144**, 307–313.

Yamori W, Hikosaka K, Way DA. 2014. Temperature response of photosynthesis in C3, C4, and CAM plants: Temperature acclimation and temperature adaptation. *Photosynthesis Research* **119**, 101–117.

Zandalinas SI, Mittler R, Balfagón D, Arbona V, Gómez-Cadenas A. 2018. Plant adaptations to the combination of drought and high temperatures. *Physiologia Plantarum* **162**, 2–12.