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Mini Review

Plant Responses to High-Temperature Stress

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Abstract

Temperature above optimal for the specie will reduce photosynthesis and increase dark respiration and photorespiration in part due to increased solubility of O_2 compared to CO_2 but also due to the decrease in CO_2 mesophyll conductance to the chloroplast. In addition, night temperature has a great impact on carbohydrates balance because high night temperature reduces the efficiency of the generation of ATP from respiration consuming more sugars to maintain growth. Another effect on species that have their cycle sensitive to temperature, inducing the reproductive phase soon or later depending on air temperature. The majority of plants adapted to high temperatures above their optimum synthesize small HSPs, which will maintain the integrity and reactivity of bigger enzymes and membranes. Therefore, plant adaptation to high temperatures is a multigenic characteristic depending on biochemical, physiological, and morphological traits.

Introduction

Temperatures above the optimum range for the plant cause reduced yield. This reduction is due, among other reasons, to the decrease in liquid photosynthesis [1], with increased photorespiration and mitochondrial respiration (Figure 1), the reduction of the cycle, in plants that depend on the accumulation of thermal units to initiates the reproductive phase, as well as the marked abortion of flowers and fruits due to ethylene production in shoot [2]. The reduction in CO_2 assimilation rate (A), at temperatures above optimal about is caused in part by the increase in the solubility of O_2 compared to CO_2, increasing Ribulose-1,5-Bisphosphate Oxygenase activity and decreasing the Carboxylase activity (Rubisco) of this enzyme [3, 4]. The reduction of photosynthesis under high temperatures is also a consequence of the decrease in mesophilic conductance (gm), reducing the availability of CO_2 that reaches the chloroplast, where you have the Rubisco activity [5], as seen in figures 2 and 3. However, a genotype, Diplomata, considered tolerant to high temperatures in field studies [6] showed optimal temperature, A, and gm values higher than for a sensitive genotype, Nobre (Figures 2 and 3).

Night Temperature and Yield

On the other hand, the nocturnal temperature has a marked effect on agricultural yield, because growth respiration occurs at night when plants have maximal cell turgidity to promote growth [2]. If the night temperatures are high, despite the increase in the respiration rate (Figures 1 & 2), there is a loss of efficiency in the respiration reaction, reducing the generation of ATP by oxidized glucose molecule, with more heat loss in the process [3]. This will cause a significant reduction in the starch and sucrose contents in the leaf, thus, reducing the productive potential when the night temperature is higher than the optimal temperature for the plant [3]. The optimal temperature for the specie varies in function of the temperature in the origin center of its evolution or natural adaptation [2], as for Diplomata (Figure 2).

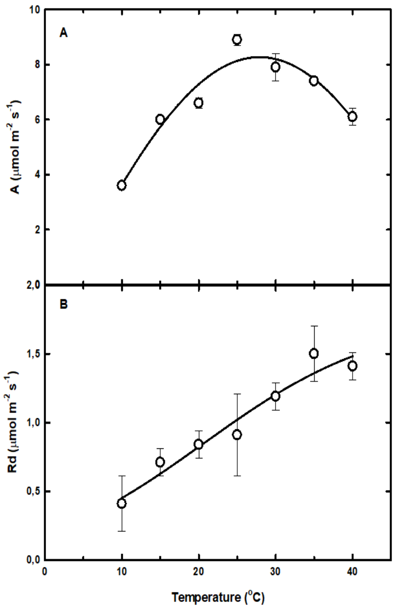

Figure 1: Temperature response of A) CO_2 assimilation rate (A); and B) dark respiration (Rd), determined from gas exchange measurements on Citrus limon.

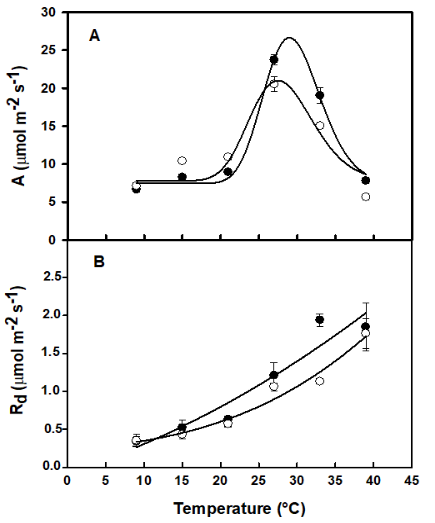

Figure 2: *In vivo* temperature response of net CO_2 assimilation rate (A) at 390 μmol CO_2 mol^{-1}; and day respiration rate in illuminated leaf tissues (Rd, in B) in Phaseolus vulgaris L. genotypes Diplomata (●), a genotype tolerant to high temperature, and Nobre (○), a genotype sensitive to high temperature. Each symbol represents the mean value of three replications (± SD).

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Thermal Unities and Yield

In addition to the effect of temperature on the carbohydrate balance, there is a reduction or increase in the vegetative phase of species sensitive to the temperatures occurring during this phase, such as cotton, common beans, corn, millet, and others. In these species, the accumulation of thermal units (or degrees. day-1) induce flowering initiation affecting the duration of the vegetative phase. Therefore, higher temperatures for the genotype will reduce the duration of the vegetative phase, reducing the number of leaves emitted, and the photosynthetic potential of plants, because when flowering begins, the vegetative growth is arrested [2].

Other Biochemical Effects on Different Genotypes

On the other hand, the abortion of flowers and fruits under temperatures above the optimum can occurs due to the increase in ethylene production in these organs, as is seen in some genotypes of common beans [2]. However, a common bean genotype more adapted to high temperatures showed a higher gm than a more sensitive genotype (Figure 3), indicating that this physiological variable may be one of the characteristics that can be used to evaluate and select more adapted genotypes. The reduction of gm seems to be associated with decreased activity of Carbonic Anhydrase and Aquaporins in photosynthesizing cells [5]. Therefore, temperature tolerance above optimal depends on several biochemical, physiological, and morphological adaptation mechanisms.

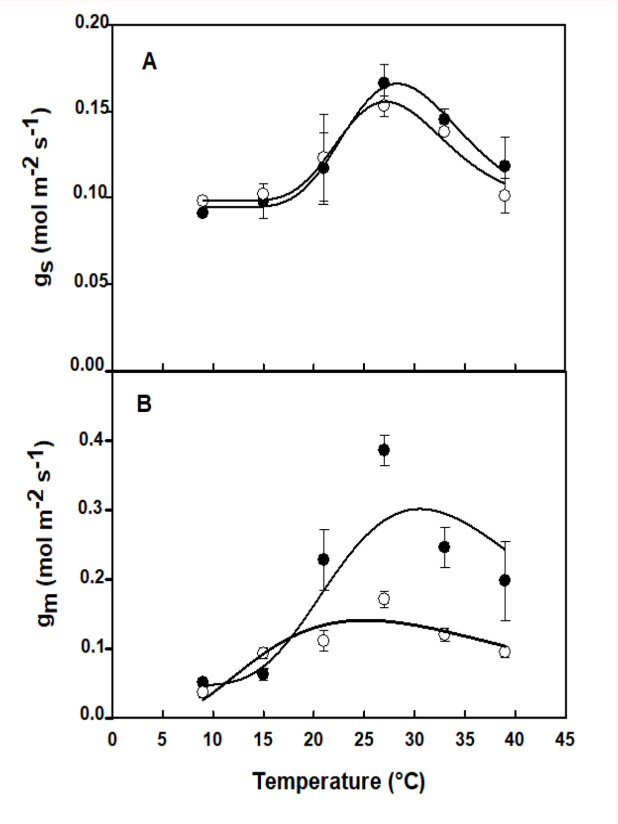

Figure 3: *In vivo* temperature response of stomatal conductance (gs, in A); and mesophyll conductance (gm, in B) in Phaseolus vulgaris L. genotypes Diplomata (●), tolerant to high temperature, and Nobre (○), sensitive to high temperature. Each symbol represents the mean value of three replications (± SD).

Genetic Control of the High-Temperature Adaptation

Heat tolerance is under polygenic control because heat adaptation depends on several traits [4,7]. Another mechanism for the adaptation of several species to high temperatures is the induction of the expression of Heat Shock Proteins (HSPs) reducing, at least in part, the synthesis of normal cellular proteins [7]. These HSPs are also involved in plant adaptation to others stresses, such as drought, and salinity [2]. The expression of HSPs is another biochemical process that can increase thermo-tolerance, by protecting structural proteins, enzymes, and membranes. The HSPs are proteins with a small molecular weight, produced in eukaryotes, and can be grouped into six different families/classes: HSP100, HSP90, HSP70, HSP60, sHSPs (small HSPs), and the Ubiquitin HSP8.5 group [7]. These proteins act as chaperones, which create ionic bonds with unstable proteins and membrane components, to prevent its denaturation by heat [5,7].

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