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Effect of Magnesium on Gas Exchange and Photosynthetic Efficiency of Coffee Plants Grown under Different Light Levels

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Abstract: The aim of the present study was to investigate the effects of magnesium on the gas exchange and photosynthetic efficiency of Coffee seedlings grown in nutrient solution under different light levels. The experiment was conducted under controlled conditions in growth chambers and nutrient solution at the Department of Plant Pathology of the Federal University of Lavras. The treatments consisted of five different Mg concentrations (0, 48, 96, 192 and 384 mg·L^{-1}) and four light levels (80, 160, 240 and 320 µmol photon m^{-2}·s^{-1}). Both the Mg concentration and light levels affected gas exchange in the coffee plants. Photosynthesis increased linearly with the increasing light, indicating that the light levels tested were low for this crop. The highest CO_2 assimilation rate, lowest transpiration, and highest water use efficiency were observed with 250 mg·Mg·L^{-1}, indicating that this concentration was the optimal Mg supply for the tested light levels.

Keywords: coffee plant nutrition; photoinhibition; photoprotection; leaf scald

1. Introduction

Coffee was originally an understory plant, however, it is now mostly grown under full sunshine conditions in Brazil [1]. This crop presents the lowest net CO_2 assimilation rates reported for C_3 woody plants grown in tropical climates [2]. The low photosynthetic capacity of coffee plants is a physiological trait characteristic of shade-adapted plants grown under full sunshine conditions [3].

Coffee leaves are saturated at relatively low light levels (between 300 and 700 µmol·m^{-2}·s^{-1}) due to the induction of strong stomatal control of photosynthesis [4]. On a clear day (without clouds), the photon flux may reach approximately 2000 µmol·m^{-2}·s^{-1} during the afternoon [2,3]. Therefore, irradiance levels higher than the coffee photosynthesis saturation point are common.

When leaves are exposed to more light than they can use, the photosystem II (PSII) reaction center is inactivated and frequently damaged. Chlorophylls in their excited state may react with molecular oxygen due to the absorption of excess light, resulting in the production of reactive oxygen species (ROS), which damage the photosynthetic apparatus [5,6]. This stress resulting from excess light is known as photoinhibition and in more serious cases may result in photooxidation, with visible damage to leaf tissues [7]. Photooxidation is most likely responsible for leaf scald symptoms in coffee

plants, which are increasingly more common, especially in the frontal face of planting rows (facing the afternoon sun) [8].

The expansion of coffee plantations towards Cerrado areas and climate changes such as long periods of dry weather with heat waves and increased irradiance peaks [9] have worsened this problem. Crop shading is not a good option in large-scale cultivation. Although this approach decreases photoinhibition, it also typically decreases coffee plant productivity [1] due to a lower CO_2 assimilation rate, and causes greater stimulation of vegetative growth with negative effects on floral bud emission, a reduced number of nodes, and lower development of flowers per node [10]. Additionally, shading restricts mechanization and increases production costs.

In chloroplasts, the light triggers activation of ribulose-1,5-bisphosphate (RuBP) carboxylase, the main enzyme responsible for the photosynthesis process. On the other hand, magnesium (Mg) deficiency negatively affects many fundamental physiological and biochemical processes that are required for plant growth and development. Suitable Mg concentrations increase the activity of RuBP carboxylase and also of other stromal enzymes. Recent studies showed that Mg-deficient plants were more susceptible to photooxidation damage, indicating that plants growing under high light conditions have higher Mg requirements [11,12]. Thus, Mg availability in the environment could lead to better photosynthetic capacity, especially at high light levels.

The aim of the present study was to investigate the effects of Mg on the gas exchange and photosynthetic efficiency of *Coffea arabica* L. seedlings grown in nutrient solution under different light levels.

2. Materials and Methods

The experiments were conducted under controlled conditions in growth chambers at the Department of Plant Pathology (Departamento de Fitopatologia) of the Federal University of Lavras (Universidade Federal de Lavras—UFLA). The plants were grown in nutrient solution. Five different Mg concentrations and four light levels were tested. The Mg concentrations tested were 0, 48 (the Mg concentration in Hoagland solution; [13]), 96, 192 and 384 mg·Mg·L^{-1}. The light levels tested were 80, 160, 240 and 320 µmol·m^{-2}·s^{-1}. The lowest light level was chosen to resemble the low lighting conditions experienced by coffee plants grown in understories under shaded conditions or under a high planting density. The highest light level (320 µmol·m^{-2}·s^{-1}) simulated the light level in which coffee leaves should be saturated [4]. Two intermediate light levels (160 and 240 µmol·m^{-2}·s^{-1}) were also tested to establish a gradient of light incidence on plants and enable the fitting of regression equations.

Three-liter pots were used in these experiments. A randomized block experimental design was applied with a 5 × 4 factorial scheme, with 6 replicates and one plant per experimental unit in a total of 120 plots.

Seedlings of the coffee cultivar Mundo Novo IAC 379/19 were used. The seedlings had 4 pairs of true leaves and were grown in soil not subjected to liming at the Experimental Farm of the Agricultural Research Company of Minas Gerais (Fazenda Experimental da Empresa de Pesquisa Agropecuária de Minas Gerais (EPAMIG)) in Machado. The seedlings were removed from the soil and placed in trays containing deionized water for 10 days until new roots emerged. Then, the seedlings were transferred to 3 L pots containing half-strength Hoagland and Arnon nutrient solution [13] from which Mg was omitted. The seedlings remained in the pots for 15 days with constant aeration.

Following this period, the seedlings were transferred to full-strength Hoagland solution with one of the following Mg concentrations: 0, 48, 96, 192 or 384 mg·Mg·L^{-1}. The nutrient solution was constantly aerated. The solution volume was refilled daily with deionized water, and the pH was corrected to 5.0–5.5 using 0.1 mol·L^{-1} HCl or 0.1 mol·L^{-1} NaOH. When Mg depletion reached 70% of the initial concentration, all solutions were exchanged for corresponding solutions to maintain approximately constant Mg availability during the experimental period.

Light was provided by daylight tubular fluorescent lamps (Osram 20 W). Different light levels were achieved by varying the distance between the plants and the light source using different shelf

heights. The plants were grown under a 12 hour light: 12 hour dark photoperiod. The light levels at the different plant heights were measured using a quantum sensor (Licor LI-190SA; Li-Cor Biosciences, Inc., Lincoln, NE, USA).

Ninety days following the beginning of the treatments, ecophysiological measurements were performed in fully expanded leaves using an infrared gas analyzer (IRGA) (LI-6400XT Portable Photosynthesis System, LI-COR, Lincoln, NE, USA). The following parameters were directly measured: delta CO_2 and delta H_2O, leaf temperature, light intensity in the chamber and gas flux; while the following were indirectly assessed, based on the algorithms, by the software of the system: CO_2 internal concentration (Ci; $\mu mol \cdot m^{-2} \cdot s^{-1}$), transpiration (E; mmol H_2O $m^{-2} \cdot s^{-1}$), stomatal conductance (Gs; mol H_2O $m^{-2} \cdot s^{-1}$), vapor pressure deficit (VPD; kPa), and CO_2 assimilation rate (photosynthesis, A; $\mu mol \cdot m^{-2} \cdot s^{-1}$), water use efficiency (WUE; A/E; μmol CO_2 mol^{-1} H_2O) and instantaneous carboxylation efficiency (A/Ci) [14,15].

Measurements were performed one hour after the onset of illumination in the growth chamber. The measurements were performed within a closed chamber (Blue + Red LED LI-6400-02B, LI-COR, Lincoln, NE, USA) using an artificial source of photosynthetically active radiation (PAR) at the same light intensity under which the plants were grown. The CO_2 assimilation rate in the chamber was measured using the environment CO_2 concentration (453.1 $\pm$ 40 μmol CO_2 mol^{-1}).

After photosynthetic evaluation, the leaves were washed and packaged separately in paper bags and oven dried at 60 ° C until reaching constant weight. The coffee leaves were ground for chemical analysis.

A variance analysis using the F test was applied to test for significant differences between treatments. When significant differences were found, the effect of Mg concentrations and light level were analyzed using regression analysis. Non-significant interactions were not shown, thus in those cases, each factor was analyzed using the mean of another. All analyses were performed using the Sisvar software [16], and graphs were built using the SigmaPlot 11.0 software souced by Systat Software Inc. Chicago, USA. The maximum and minimum points for the quadratic equations were calculated by equaling the first derivative to zero.

3. Results and Discussion

3.1. Stomatal Conductance and Leaf Temperature

A significant interaction between the Mg concentration and light level was observed for stomatal conductance (Gs) (Figure 1A). The Gs decreased with the increasing Mg concentration at all light levels, with a tendency to stabilize from 192 $mg \cdot Mg \cdot L^{-1}$. This result was related to the decrease in potassium (K) availability with the increasing Mg concentration (Figure 2). K plays an important role in stomatal conductance. Its accumulation and release by stomatal guard cells leads to changes in cell turgor, resulting in stomatal opening and closing [6,17].

The reduction in leaf K contents as a function of the increase in Mg doses is due to the antagonistic effect among these nutrients. In general, increasing the amount absorbed from one cation can result in the reduction of the absorption of another cation [18]. This inhibition between these nutrients is competitive, that is, there is competition by the same site of the "carriers" in the membrane [19]. The antagonistic relationship between Mg and K was observed in experiments with several cultures [20–22].

Another factor that decreased stomatal conductance was the vapor pressure deficit (VPD) (Figure 1B). The difference between vapor pressure inside the leaves and in the air induces stomatal movement; this difference depends on the total leaf transpiration rate and water potential gradient between guard cells and other epidermal cells [23]. High VPD values may cause stomatal closing to prevent excessive water loss through transpiration [6]. Marenco et al. [24] observed a pronounced decrease in Gs and photosynthesis with the increasing VPD.

Chaves et al. [25] studied coffee plants under field conditions in 2007 and observed low Gs values (approximately 0.06 mol H_2O $m^{-2}{\cdot}s^{-1}$) with high VPDs. Therefore, VPD and Gs were negatively correlated.

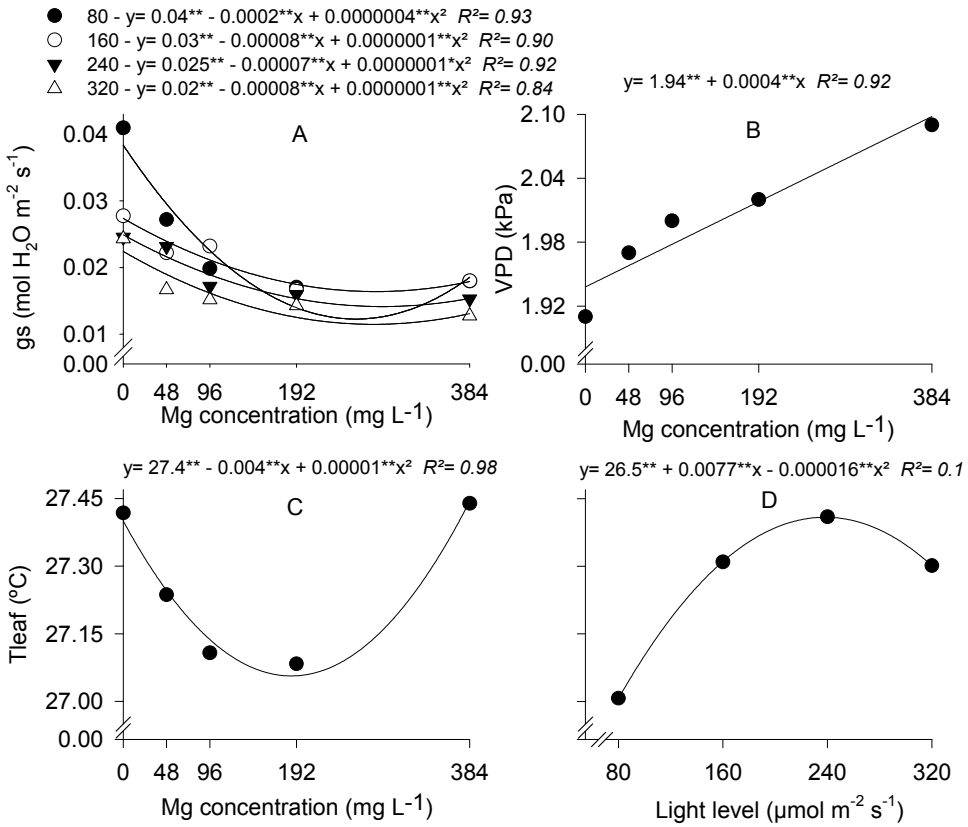

Figure 1. (**A**) Stomatal conductance (Gs; mol H_2O $m^{-2}{\cdot}s^{-1}$), (**B**) vapor pressure deficit (VPD; kPa), and (**C**,**D**) leaf temperature (Tleaf; °C) in coffee seedlings grown with different Mg concentrations and under different light levels. (*) Significant according to the *t* test at $p < 0.05$. (**) Significant according to the *t* test at $p < 0.01$.

The average Gs for coffee plants is 0.108 mol H_2O $m^{-2}{\cdot}s^{-1}$ [26]. The low Gs values observed in the present study (even for the control treatment 0 mg·Mg·L^{-1}, which presented a lower VPD) were probably due to the low light levels.

The Gs value was highest with the lowest light level tested (80 µmol·$m^{-2}{\cdot}s^{-1}$), which was related to the lower leaf temperatures observed for this light level (Figure 1D). This finding was especially true for the treatment lacking Mg (0 mg·Mg·L^{-1}) that did not have competition between Mg and K. So the K uptake had no negative effect. Leaf temperatures higher than the air temperature may cause stomatal closing and decrease the Gs [27].

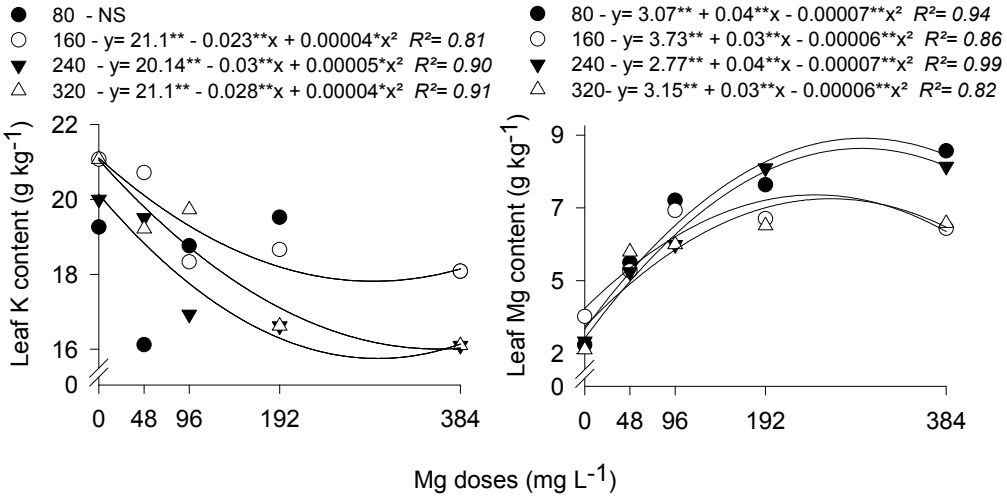

Figure 2. Contents of Mg and K in leaves of coffee seedlings grown with different Mg concentrations and under different light levels. (*) Significant according to the *t* test at $p < 0.05$. (**) Significant according to the *t* test at $p < 0.01$.

3.2. Gas Exchange

No significant interactions were observed between the Mg concentration and light level for the CO_2 internal concentration (Ci), transpiration (E) and photosynthesis (A) (Figure 3).

The Ci decreased linearly with the increasing Mg supply; its variation depending on the light level was best fitted by a positive quadratic equation (Figure 3A, B). The decrease in Ci with the increasing Mg supply was a result of the improved CO_2 use, due to the higher efficiency of the photosynthetic apparatus (Figure 3E). CO_2 concentrations tend to be lower with higher photosynthetic rates and Ci has a negative linear correlation with the photosynthetic rate [28]. Mg binding increases the affinity of Rubisco for CO_2 and doubles its maximum reaction velocity [11].

The lower Ci observed with the intermediate light levels might be related to the higher leaf temperatures observed for these light levels (Figure 1D). Increased leaf temperatures in coffee plants may cause a gradual increase in photorespiration and the internal CO_2 concentration [1].

The variation observed in the transpiration (E) with the increasing Mg supply was best fitted by a positive quadratic equation (Figure 3C). The leaf transpiration rate is primarily determined by the light level, VDP, and Gs [29]. The decrease in transpiration observed with 250 mg·Mg·L^{-1} down to 0.324 mmol H_2O m^{-2}·s^{-1} might have been related to the Gs, which presented variation with the increasing Mg, best fitted by a positive quadratic equation (Figure 1A). This result was in accordance with Assad et al. (2004), who observed a decrease in transpiration due to stomatal closing as a result of the increasing VPD. In a field study, Gutiérrez and Meinzer [30] attributed the decrease in transpiration of coffee plants to the stomatal closing induced by high temperatures and VPDs.

E decreased with increasing light levels starting from 125 μmol·m^{-2}·s^{-1} (Figure 3D). Coffee plants tend to decrease their transpiration and increase their photosynthetic capacity at high light levels by increasing their specific leaf mass (ratio between the leaf mass and area) [31]. In contrast, decreasing transpiration with decreasing irradiance has been observed in shaded coffee plants [4,32]. However, the light levels in the field are higher than those tested in the present study.

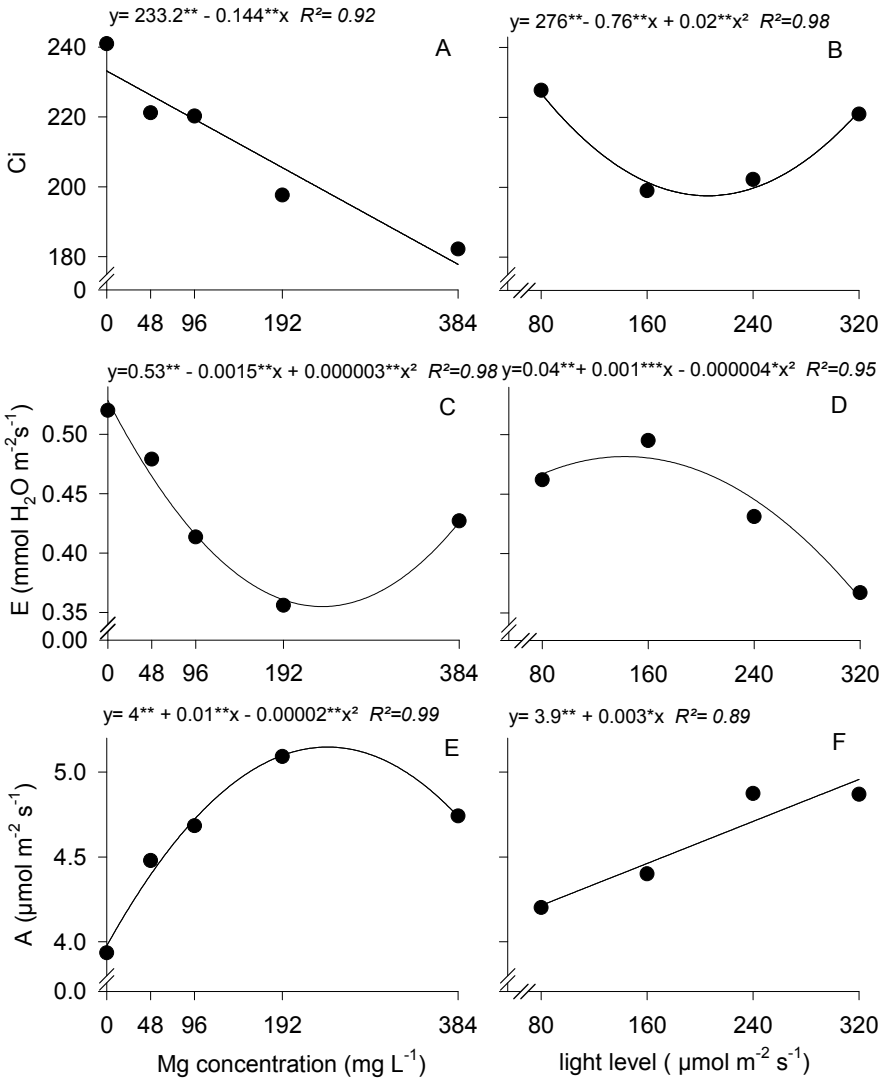

Figure 3. (**A**,**B**) CO_2 internal concentration (Ci; µmol·mol^{-1}), (**C**,**D**) transpiration (E; mmol H_2O m^{-2}·s^{-1}), and (**E**,**F**) CO_2 assimilation rate (photosynthesis, A; µmol·m^{-2}·s^{-1}) in coffee seedlings grown with different Mg concentrations and under different light levels. (*) Significant according to the *t* test at $p < 0.05$. (**) Significant according to the *t* test at $p < 0.01$.

Similar to the VPD, the high temperatures that usually accompany high light levels have a high impact on C assimilation and transpiration [1]. Additionally, the increase in VPD under higher temperatures results in stomatal closing and decreased transpiration [33], thereby preventing the evaporative cooling of leaves and the maintenance of leaf temperatures at higher light levels (Figure 3D).

The variation in photosynthesis (A) with the increasing Mg supply was best fitted by a negative quadratic equation, with a maximum value of 5.25 µmol·m^{-2}·s^{-1} observed with 250 mg Mg·L^{-1}. Photosynthesis exhibited a positive linear correlation with the light level (Figure 3E,F).

The increase in photosynthesis with the increasing Mg supply is related to several key roles of Mg in plant functions, including the regulation of photophosphorylation (adenosine triphosphate formation in chloroplasts), CO_2 photosynthetic fixation, protein synthesis, chlorophyll formation, phloem loading, the partitioning and utilization of photoassimilates, the generation of reactive oxygen species (ROSs), photooxidation in leaf tissues, and enzyme activation. Mg is the nutrient that activates most enzymes in plants (i.e. ATPases and Rubisco) [11]. Mg deficiency causes carbohydrate

accumulation in leaves [11,17,34], which may affect the photosynthetic metabolism and decrease the use of absorbed light for photosynthesis.

The decrease in photosynthesis from 250 mg $Mg \cdot L^{-1}$ may be related to the imbalance caused by excess Mg, especially due to the decreased K uptake (Figure 2). K is extremely important for the activation of the carboxylase function of Rubisco [35], which has been proposed to explain the increased photosynthetic rates observed with an adequate K supply [36,37].

The photosynthesis rates in C_3 plants generally vary between 10 and 20 $\mu mol \cdot m^{-2} \cdot s^{-1}$ [6]. However, due to the limiting CO_2 supply coffee plants present low net CO_2 assimilation rates (between 4 and 11 $\mu mol \cdot m^{-2} \cdot s^{-1}$) [1]. Therefore, the net CO_2 assimilation rates of 4 to 6 $\mu mol \cdot m^{-2} \cdot s^{-1}$ observed in the present study can be considered normal for coffee plants, even with the low tested light levels and the low observed Gs (Figure 1A).

Chaves et al. [20] observed photosynthesis rates of approximately 2.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in the field. According to these authors, coffee plant leaves present plasticity and are able to adapt to environments with different light levels. However, higher light than the level needed for photosynthesis may results in an energy imbalance, often resulting in photoinhibition. Photoinhibition is a complex set of molecular processes that leads to the inhibition of photosynthesis due to excess light [25].

Prolonged exposure of plants or organelles to excess light may result in photodestruction of photosynthetic pigments as a result of light- and oxygen-dependent bleaching. This process is usually called photooxidation and may lead to cell or organism death. In most cases, photooxidation is a secondary phenomenon that occurs following a distinct lag phase. During this lag phase, there is a decline in photosynthesis that is dependent on the light intensity and exposure time (photoinhibition) and a lack of change in the composition of the pigment reserves [7]. Photoinhibition is not a consequence of pigment destruction; instead, pigment bleaching occurs following a certain degree of photoinhibition. Thus, these processes represent two different phenomena [7].

Photooxidation is most likely responsible for leaf scald symptoms in coffee plants. ROS are produced during photoinhibition and can result in oxidative stress (photooxidation) if the plant antioxidant complex is not capable of removing the generated ROS [38].

Leaf scald symptoms have been observed in several coffee producing regions. Photoinhibition preceding photooxidation should be even more common because the photon flux from early morning until midday generally varies between 800 and 1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$, and may reach 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ during the afternoon [2,3] and coffee leaves are saturated by relatively low irradiances between 300 and 700 $\mu mol \cdot m^{-2} \cdot s^{-1}$ [1]. Photorespiration is an effective mechanism for protection against photoinhibition and Mg plays a direct role in photorespiration. During photorespiration, excess energy stored as ATP and NADPH during the photochemical phase of photosynthesis is dissipated [6]. Energy transference from chlorophylls to carotenoids formed during the xanthophyll cycle leads to energy dissipation as heat at the PSII light-harvesting complex [39].

Although the photosynthesis rate increased with the increasing light level (Figure 3F), an increase in the superoxide dismutase (SOD) and ascorbate peroxidase (APX) activities was also observed [17]. Prior to the appearance of the visual symptoms of Mg deficiency, enzyme activities from the plant antioxidant complex delay the photooxidative damages caused by ROS and the inactivation of photosynthetic enzymes. Photosynthesis is only decreased during the more advanced phases of Mg deficiency [40].

3.3. Water Use Efficiency and Instantaneous Carboxylation Efficiency

The variation in the water use efficiency (WUE)—the ratio between photosynthesis and transpiration—with the increasing Mg supply was best fitted by a negative quadratic equation, with a maximum value observed with 245 mg $Mg \cdot L^{-1}$ (Figure 4A). The WUE increased due to higher photosynthetic efficiency and decreased transpiration with the increasing Mg supply. The lower WUEs observed with the higher Mg concentrations were related to the imbalance caused by excess Mg, which had a negative effect on the photosynthetic rates.

The WUE increased linearly with the increasing light level (Figure 4B) due to the increased photosynthetic rate (Figure 3F) and decreased transpiration (Figure 3D). In field experiments with shaded coffee plants, the WUE was higher with 0% and 50% shading [32].

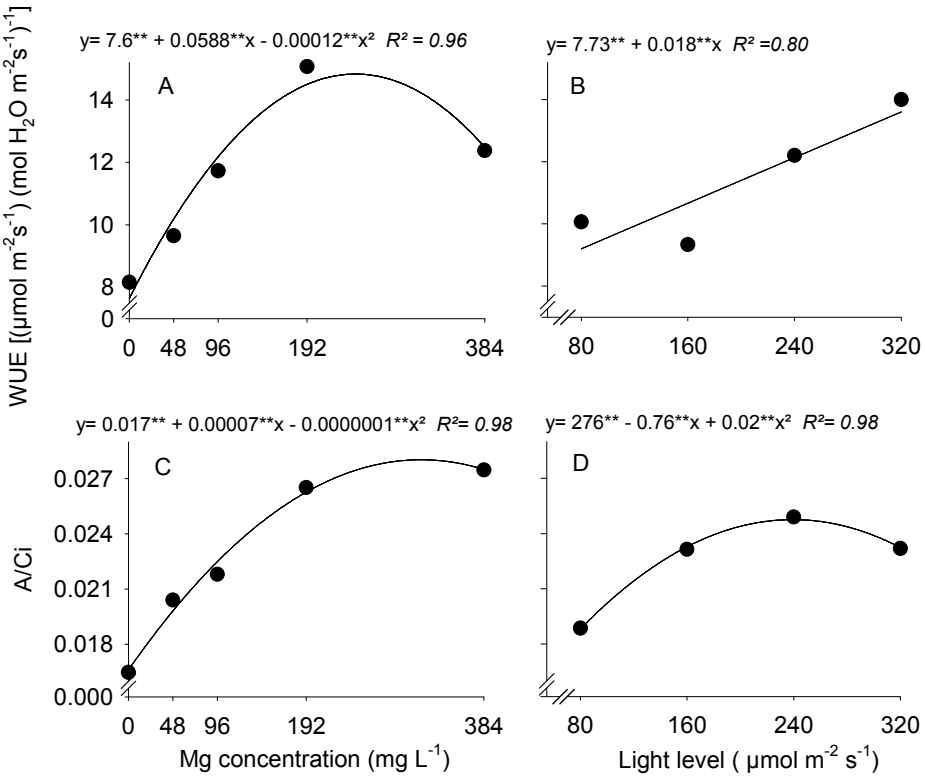

Figure 4. (**A**,**B**) Water use efficiency (WUE) and (**C**,**D**) instantaneous carboxylation efficiency (A/Ci) in coffee seedlings grown with different Mg concentrations and under different light levels. (*) Significant according to the *t* test at $p < 0.05$. (**) Significant according to the *t* test at $p < 0.01$.

The instantaneous carboxylation efficiency (A/Ci) calculated as the ratio between photosynthesis and the CO_2 internal concentration are closely related to the intracellular CO_2 concentration and CO_2 assimilation rate [41]. The variations in the A/Ci with the increasing Mg supply and light levels were best fitted by negative quadratic equations (Figure 4A, B). An increased A/Ci with an increasing Mg supply and light level is related to an increase in the photosynthesis rate (Figure 3E, F) and a decrease in the internal C concentration (Figure 3A,B).

The highest CO_2 assimilation rate, lowest transpiration, and highest water use efficiency were observed with 250 mg·Mg·L^{-1}, indicating that this concentration was the optimal Mg supply for the tested light levels. The critical Mg supply for coffee plants most likely varies with the light level. For example, coffee plants grown in the west region of Bahia may need more Mg than those grown in the south of Minas or in regions with lower light levels.

4. Conclusions

Both the Mg supply and the light level affected gas exchange in coffee plants. The positive linear correlation between photosynthesis and the light level showed that the tested light levels were low for coffee plants. The highest CO_2 assimilation rate, lowest transpiration, and highest water use efficiency were observed with approximately 250 mg Mg·L^{-1}, indicating that this concentration represented the optimal Mg supply for the tested light levels.

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Conflicts of Interest: The authors declare no conflicts of interest.

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