Alterations in chlorophyll a fluorescence, pigment concentrations and lipid peroxidation to chilling temperature in coffee seedlings

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ABSTRACT

Coffee arabica L. is considered to be sensitive to low temperatures throughout its life cycle. In some Brazilian regions, seedling production occurs under shade conditions and during the winter, with average temperatures of around 10 °C. The formation and functioning of the photosynthetic apparatus are strongly controlled by temperature. This study aimed to assess the changes that occurred in pigment contents, lipid peroxidation and variables of chlorophyll a fluorescence during the greening process of coffee seedlings submitted to chilling. Results indicate that saturation of the photosynthetic activity of coffee seedlings occurred before saturation of the accumulation of chloroplastid pigments. Pigment accumulation during the greening process is far beyond the metabolic needs for the maintenance of photosynthetic activity, more specifically of photosystem II. Coffee seedlings attained a quantum yield equivalent to that of the control with approximately half the chlorophyll a and b contents and around 40% of the carotenoid. Low temperature decreases the metabolism of seedlings, consequently reducing free radical production and lipid peroxidation. The chilling temperature (10 °C) used inhibited the accumulation of chloroplast pigments, in turn altering the capacity of the photosynthetic tissue of etiolated coffee seedlings to capture and transfer photon energy to the photosystem II reaction centre. These alterations were better demonstrated by O-J-I-P chlorophyll a fluorescence transients, rather than Fv/Fm and Fv/F0 ratios.

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1. Introduction

Coffee seedlings produced in high altitude regions acquire a tolerance factor to low temperatures, termed “hardening”. However, those seedlings that do not adapt to these conditions suffer some degree of damage. Tolerance may indicate a natural selection of individuals, since the occurrence of moderate photoinhibition under field conditions is common (Lovelock et al., 1994), particularly in young plants transferred during their growth in nurseries under full sun conditions (Fahl et al., 1994). In Brazil, coffee seedlings are produced during the winter in regions with average temperatures of approximately 10 °C. These seedlings grow in shady conditions and hardening is required before they are transferred to the field. It is known that acclimatization of plants to low temperatures requires a biochemical and physical restructuring of cell membranes in order to increase their fluidity (Bohn et al., 2007). According to Hariyadi and Parkin (1993), alterations in the membranes occur due to lipid peroxidation via the action of reactive oxygen species generated by stress factors, such as low temperature. As superoxide anions (O2−) are produced in the chloroplast environment in the presence of light (Asada, 2006), fatty acid chains of the thylakoid membranes (polyunsaturation rich) are highly vulnerable to peroxidation. These membranes are a potential site for photoinhibition at chilling temperatures (Zhang and Scheller, 2004). Chilling temperatures may also affect the transfer of energy among the electron carriers of the photosynthetic electron transport chain. The enzyme activities of the carbon reduction cycle in the stroma, as well as the photosynthetic transport mechanisms of chloroplasts, also affect photophosphorylation (Öquist, 1983).

Chlorophyll a (Chl a) fluorescence signals have been extensively used for the assessment of several environmental effects on photosynthetic metabolism (Oliveira et al., 2002; Costa et al., 2003; Calatayud et al., 2008; Flowers et al., 2008; Lage-Pinto et al., 2008; Naumann et al., 2008). Some Chl a fluorescence ratios are frequently used to evaluate stress conditions. Environmental stresses may affect photosystem II (PSII) efficiency by decreasing Fv/Fm (Krause and Weis, 1991). However, some authors have reported that Fv/F0 is a better parameter than Fv/Fm for evaluating stress conditions
were fertilized once a week with nutritive solution (Hoagland absence of light for about 20 days. During this period, the seedlings pots (500 mL) containing vermiculite and kept under complete

2. Material and methods

2.1. Plant material and chilling treatments

Coffee seeds (*Coffea arabica* L.) were germinated in plastic pots (500 mL) containing vermiculite and kept under complete absence of light for about 20 days. During this period, the seedlings were fertilized once a week with nutritive solution (Hoagland and Arnold, 1951). The temperature was controlled (25 °C/20 °C, day/night) until the application of the chilling treatment when the seedlings with one pair of completely unpigmented cotyledonary leaves were transferred to growing rooms (FORMA SCIENTIFIC Inc.; model 24) with constant photosynthetic photon flux density (PPFD) (150 µmol m−2 s−1) and controlled temperature, according to treatment.

The seedlings were submitted to the greening process under two temperature treatments: 10 and 25 °C. Chl a fluorescence analyses, pigment contents and lipid peroxidation were evaluated by sampling at 0, 1, 2, 4 and 8 days. After 8 days at 10 °C, the room temperature was raised to 25 °C and the Chl a fluorescence analyses, pigment contents and lipid peroxidation were evaluated by sampling at 2-day intervals until the 10th day, from which this interval passed to 4 days until the 26th day. For each treatment (10 and 25 °C), four seedlings were evaluated and one measurement was carried out for each seedling. Each result is the mean of four replications.

2.2. Chl a fluorescence analyses

Chl a fluorescence ($F_0$, $F_m$ and $F_p$) was determined at room temperature (25 °C) using a portable PEA fluorometer (Plant Efficiency Analyser, Hansatech Instruments Ltd.), according to the procedure and conditions described by Oliveira et al. (2002). At the beginning, and on the 1st, 10th, 18th, and 26th days during the greening process of the coffee seedlings, the Chl a fluorescence transients O-J-I-P were measured following the procedure proposed by Strasser et al. (1995). Fluorescence kinetics were used to calculate the rate of the fast fluorescence rise ($F_{300 \mu s} - F_{50 \mu s}$) and the relative rate of photochemistry ($dV/dt_0 = (F_{300 \mu s} - F_{50 \mu s})/(F_m - F_0)$) (Strasser et al., 1995).

2.3. Pigment concentrations

For the determination of Chl a, Chl b and carotenoid ($C_{x+c}$) concentrations, 50 mg of leaf tissue fresh weight (FW) was placed in a test tube containing 5 mL of 80% acetone. The sample was incubated at 70 °C for 20 min, left to cool in the dark and, afterwards, the volume was corrected to the initial 5 mL. Absorbance was measured at wavelengths of 470, 646 and 663 nm. Pigment concentrations were calculated according to the procedure described by Lichtenthaler and Wellburn (1983). The concentrations of the Chl s and carotenoids (Chl a, b and $C_{x+c}$) were expressed by µg g−1 FW relative to total pigment content (Chl a + Chl b + $C_{x+c}$). Adjusted curves were used to determine the following parameters for each treatment: concentration, time, increment rate (in relation to the beginning) at the maximum points and $T/2$ (50% of the maximum) for each pigment.

2.4. Lipid peroxidation

The membrane lipid peroxidation was estimated by measuring the malondialdehyde (MDA) content, a by-product of lipid peroxidation, in leaf tissue extracts. The MDA concentration was calculated from 150 mg of leaf fresh weight (FW) using the procedure of Dhindsa et al. (1981), adapted from Heath and Packer (1968). The extinction coefficient ($\varepsilon$) used for this assay was 155 mM−1 cm−1.

2.5. Statistical analyses

Chl a fluorescence data were submitted to analysis of variance (ANOVA) and, when significant, were compared by the Duncan test ($P<0.05$).

3. Results

The chilling temperature (10 °C) applied to the coffee seedlings affected the chloroplast pigment accumulation capacity (Fig. 1 and Table 1). Following the temperature change from 10 to 25 °C, pigment synthesis was reinitiated from the 14th day (Fig. 1A–C), while the Chl a/b ratio (Fig. 1D) reached control values from the 22nd day onwards. However, as depicted in Table 1, chilling to 10 °C did not interfere in the balance between relative pigment concent-

### Table 1

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Pigment/treatment</th>
<th>Chl a 10 °C</th>
<th>Chl b 10 °C</th>
<th>$C_{x+c}$ Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tmax (days) 10 °C</td>
<td></td>
<td>24</td>
<td>23</td>
<td>24</td>
</tr>
<tr>
<td>T1/2 (days) 10 °C</td>
<td></td>
<td>18</td>
<td>15</td>
<td>18</td>
</tr>
<tr>
<td>Pigment concentration T1/2</td>
<td>µg g−1 FW</td>
<td>178.29</td>
<td>61.77</td>
<td>28.43</td>
</tr>
<tr>
<td>Pigment concentration Tmax</td>
<td>µg g−1 FW</td>
<td>356.59</td>
<td>121.90</td>
<td>65.32</td>
</tr>
<tr>
<td>Rate of increase in T1/2</td>
<td>µg g−1 day−1</td>
<td>7.54</td>
<td>1.51</td>
<td>5.39</td>
</tr>
<tr>
<td>Relative pigment conc. (%)</td>
<td></td>
<td>66.4</td>
<td>10.6</td>
<td>100.0</td>
</tr>
</tbody>
</table>

FW—fresh weight, Chl—chlorophyll, $C_{x+c}$—carotenoids.
In contrast to observations for the chilling temperature, after 1 day beginning of the seedling greening just with O and P transients. The chilling treatment resulted in a lower MDA production. After the 18th day all transients were observed. However, in contrast to the $F_v/F_m$ and $F_{v}/F_{0}$ ratios (Fig. 2A and B), transient levels did not reach those of the seedlings that were treated at control temperature (Fig. 3C and D).

Table 2 presents the rate of fast fluorescence increase and relative variable fluorescence ($dV/dt_0$) during the greening process. On the 10th day, at 10°C, the rate of the fast fluorescence (0.041) was the lowest; while the maximum fast fluorescence rate (0.828) was observed at 25°C. The largest increase in fast fluorescence (0.936), as well as the highest $dV/dt_0$ (0.593) was observed on the 18th day for the chilling treatment. At 25°C, on the 1st day of greening (Table 2), $dV/dt_0$ (relative rate of photochemistry) increased ($P<0.05$) compared to the beginning of the greening process (0.029).

An increase in MDA (Fig. 4) was observed in the control treatment, practically throughout the entire period of the experiment. The chilling treatment resulted in a lower MDA production. After the change of temperature from 10 to 25°C (8th day, Fig. 4 arrow), slight variation was observed until the 14th day, whereas between

Table 2
Rate of the fast fluorescence rise ($\left[F_{\text{S00ms}} - F_{\text{50ms}}\right]/F_{0}$) and relative variable fluorescence ($dV/dt_0$) in coffee cotyledons during the greening process (means of four repetitions ± standard error).

<table>
<thead>
<tr>
<th>Time (days)</th>
<th>($F_{\text{S00ms}} - F_{\text{50ms}}$)/$F_{0}$</th>
<th>$dV/dt_0$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>10°C. 25°C</td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>$0.151 \pm 0.034$ c</td>
<td>$0.029 \pm 0.008$ c</td>
</tr>
<tr>
<td>1</td>
<td>$0.151 \pm 0.034$ c</td>
<td>$0.029 \pm 0.008$ b</td>
</tr>
<tr>
<td>10</td>
<td>$0.041 \pm 0.009$ c</td>
<td>$0.192 \pm 0.040$ b</td>
</tr>
<tr>
<td>18</td>
<td>$0.936 \pm 0.074$ a</td>
<td>$0.593 \pm 0.061$ a</td>
</tr>
<tr>
<td>26</td>
<td>$0.487 \pm 0.070$ b</td>
<td>$0.257 \pm 0.025$ b</td>
</tr>
</tbody>
</table>

The average with same letters in the same column were not significantly different at 5% level by Duncan’s multiple range test.

* Not measured.
temperatures. (Fig. 1) and control (25 °C, ▲) temperatures for 8 days before changing temperature to 25 °C. Points represent the beginning (□), 1st (A), 10th (B), 18th (C) and 26th (D) days. Each point represents the average of four repetitions. a.u.—arbitrary units.

Fig. 4. Alterations in the lipoperoxidative activity, expressed as MDA concentrations, in coffee seedlings during greening in response to chilling (10 °C) and control (25 °C) temperatures. (□) 10 °C and (▲) 25 °C. Arrow indicates the time when the temperature treatment was changed from 10 to 25 °C. Each point represents the average of four repetitions and bars show the standard error of mean. MDA—malondialdehyde.

The chilling temperature (10 °C) affected all parameters analyzed. The lower pigment concentrations at 10 °C (Fig. 1 and Table 1) altered the luminous energy capture and transfer into the PSII reaction centre (RC) complex in the photosynthetic tissue of the etiolated coffee seedlings. In contrast, totally green cotyledon leaves of coffee seedlings did not present differences in pigment accumulation and PSII quantum yield when grown at 10 and 25 °C (Oliveira et al., 2002). This finding suggests that the combined effect of chilling and light induces irreversible damage in the photosynthetic apparatus, as observed from the Chl a fluorescence transient O-J-I-P data presented herein (Fig. 3).

Increases in \( F_v/F_m \) and \( F_v/F_o \) ratios (Fig. 2) and pigment concentrations (Fig. 1) were observed after the temperature alteration (10 °C from 25 °C). In contrast, on the 1st day at 25 °C, the PSII quantum yield decreased dramatically (from 0.843 to 0.300), possibly due to the lower reoxidation capacity of the PSII RC. The reoxidation of the RC by the reduction of QA involves the ability of the pool of POQ to once again supply QA (oxidized), which will then be reduced. QA− then undergoes a second reduction step forming POQH2 and dissociates from the RC after protonation events to form plastid quinol (PQH2). The POQ pool was probably still low during this time, contributing to a fall in PSII quantum yield and a decrease in \( \text{ROQ}_{\text{PSII}} \) reoxidation. While the synthesis of pigments was inhibited by around 50% after chilling, \( F_v/F_m \) and \( F_v/F_o \) was re-established, indicating that the effect of chilling temperature on PSII quantum yield does not seem to have been permanent in this assay. This finding demonstrates that accumulation of pigments, particularly PSII, during the greening process is beyond the metabolic needs for the maintenance of photosynthetic activity at high levels. Godde and Dannehl (1994) observed that spinach plants (under nutritional stress) with around 50% Chl concentration presented a decrease of just 10% in the \( F_v/F_m \) ratio.

\( F_v/F_o \) and \( F_v/F_m \) ratios showed a slight decrease at both temperatures after the 18th day, indicating a reduction in photochemistry capacity of the PSII, possibly due to cotyledon leaf senescence. This finding may indicate the start of the process. At this time point, a high pigment concentration and Chl a/b ratio were observed, particularly in the control, suggesting the maintenance of the thylakoid stacking level (Lichtenthaler et al., 2006) and reflecting the absence of the senescence marker, chlorosis (Meier and Lichtenthaler, 1982).

In coffee seedlings exposed to chilling stress, Da Matta et al. (1997) and Oliveira et al. (2002) suggested the use of the \( F_o/F_m \) ratio, rather than the \( F_v/F_m \) ratio, for better discrimination of small differences in the PSII quantum yield. In the present study, the variation in \( F_o/F_m \) ratio was similar to that of the \( F_v/F_m \) ratio (Fig. 2A and B), reflecting the PSII quantum yield, but with a greater amplitude of values. However, the use of the O-J-I-P transients (Fig. 3) allows a better discrimination of small differences in the PSII activity, as observed by some authors (Force et al., 2003; Strauss et al., 2006). Before the greening process (beginning), the Chl a fluorescence kinetics are characterized by the presentation of just two transients, O and P (Fig. 3A, square). In this sampling and similarly to the observations made by Strasser et al. (1995), J and I inflections were not observed, as indicated by absence of overlapping P (I = P). As the seedling’s photosynthetic apparatus was in formation, together with the accumulation of the PSII and PQ pigments, these values demonstrated small qualitative variations. On the 10th day of seedling greening at 25 °C, the O value increased, relative to that of the chilling treatment (Fig. 3B), reflecting the increase in the capture of energy by complex antenna pigments. These data demonstrate the progression in the accumulation of pigments at 25 °C (Fig. 1). From the 18th day of greening onwards, the Chl a fluorescence transients (to chilling seedlings) presented typical kinetics (Fig. 3C and D), reflecting alterations in the photosynthetic apparatus. This result was an attenuation of the emitted fluorescence and advanced (except for O) transient occurrence, probably the consequence of the lower Chl a concentration and limitations concerning the flow of electrons through PSII (Strasser et al., 1995). Strauss et al. (2006) also reported the maintenance of all transients O-J-I-P during chilling conditions, suggesting that the O-J-I-P transients can be useful in ranking chilling tolerance in soybean genotypes. Soybean chilling (6 °C), however, resulted in a greater increase in the transient J than that of the control (20 °C) with low variations in the I and none in O and the P. In contrast, in the current investigation, decreases were observed in all transients in the chilling treatments, including

4. Discussion

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in the J transient. This transient is usually interpreted as evidence of accumulation of the fraction of the reduced QA pool (Strasser et al., 1995), possibly due to decreased electron transport beyond QA−. These findings suggest that PsII electron transport beyond QA− was not inhibited in chilling coffee seedlings.

The dv/dt0 (Table 2) is a measurement of the fraction of QA in the reduced state (QA−) at a determined time, in relation to the initial state (in F0 all QA is oxidized) (Force et al., 2003). In this study, the dv/dt0 and the PsII quantum yield obtained consolidate the evidence that photosynthetic activity saturation in coffee seedlings occurred long before the saturation in the accumulation of chloroplast pigments. The PsII quantum yield or the relative rate of photochemistry refers only to a fraction of the total concentration of the pigments. Others inactive PsII exist that can resume photochemical activity (Cogdell, 2006) and do not contribute to the fluorescence variables analyzed, but which add to the total concentration of the pigments (Bowyer and Leegood, 1997). Therefore, these plants did not carry out “luxury acquisition” by accumulating the double of the concentration of the pigments necessary to achieve the saturation of the photosynthetic activity; rather they made an investment that allows them to survive under the varying conditions of their habitat.

Liperoxidative activities, expressed as MDA concentrations, were increased in the control and chilling temperature (Fig. 4). However, during chilling the increase was much lower than that of the control plants. Lipid peroxidation triggers the action of free radicals (Olson, 1995; Qiu and Liang, 1995) and the carotenoids are physiologically important in protecting these (Schindler and Lichtenthaler, 1994). However, in this study, at 25 °C, the increase in lipid peroxidation occurred together with increased carotenoids (Fig. 1C). This finding suggests a partial inability of these pigments to inhibit the peroxidation action of free radicals. During the chilling treatment, the level of chloroplast membrane degradation was initially stable. During this stage, it is probable that no free radicals were produced due to the inhibition of the electron flux by low temperature. There was, however, an increase in lipid peroxidation in control plants (25 °C) and a tendency towards increased peroxidation in chilled plants (10 °C) (Fig. 4). According to Mano et al. (1997), when electron transfer through PsII is inhibited or inactivated by light stress, the formation of MDA is stimulated. At low temperature, the entire metabolism was affected, including that of free radicals production, resulting in a lower peroxidation activity in chloroplast membranes.

In conclusion, these results indicate that saturation of the photosynthetic activity of coffee seedlings takes place before the saturation of the accumulation of chloroplast pigments. Data show that the accumulation of pigments, particularly PsII, during the green process is before the seedling’s metabolic needs for the maintenance of photosynthetic activity. The chilling temperature inhibited the accumulation of chloroplast pigments and, in turn, altered the capacity of the photosynthetic tissue of etiolated coffee seedlings for the capture and transfer of photon energy into the PsII RC. Finally, the O-J-I-P transient was more effective than Fv/Fm and Fv'/Fm' for discriminating small differences in the assembly of PsII in cotyledon leaves exposed to low temperature.

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The authors dedicate this work to Prof. Dr Antônio C. N. Magalhães (in memoriam) for his exemplary supervision of Oliveira and Alves.

References


