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ORIGINAL PAPER

Lipid peroxidation, chloroplastic pigments and antioxidant strategies in *Carapa guianensis* (Aubl.) subjected to water-deficit and short-term rewetting

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Abstract The effects of drought on membrane lipids and leaf pigments and the ability of andiroba (*Carapa guianensis* Aubl.) plants to attenuate oxidative damage through antioxidant enzymes or adjusting carotenoids and glycinebetaine (GB) were examined. Assessments were performed when pre-dawn leaf water potential (Ψ_{pd}) of water-stressed plants reached −1.35 and −3.21 MPa (15 and 27 days after withholding irrigation) and 12 h after resuming watering (short-term rewetting, day 28). Oxidative damages to lipids were evident on day 15, in which drought caused an increase of 47% in malondialdehyde (MDA) content. On day 27, MDA content did not differ between treatments. The activity of superoxide dismutase remained unchanged over experimental period, while significant increases in the ascorbate peroxidase (APX, 110%) and catalase (CAT, 50%) activities were observed only on day 27. GB content was 62% (day 15) and 112% (day 27) higher in water-stressed plants than in control. Regardless of Ψ_{pd}, both chlorophyll (Chl) *a*, Chl *b* and total carotenoids remained unchanged between well-watered and water-stressed plants, indicating that drought did not result in degradation of leaflet pigments. On day 28, Ψ_{pd} of water-stressed plants increased near to control plants and both activities of APX and CAT did not differ between treatments. Altogether, adjustments in APX and CAT activity and in the GB content were efficient strategies to prevent expressive oxidative damages in water-stressed andiroba plants.

Keywords Antioxidant enzymes · Carotenoids · Cell damage · Drought stress · Glycinebetaine · Oxidative stress

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Introduction

Under moderate drought the decreases in net photosynthesis are commonly associated to stomatal constraints on CO_2 diffusion into leaves, reducing the active state of rubisco and favoring photorespiration in C_3 plants (Lawlor 1995). Nevertheless, prolonged drought affects negatively net photosynthesis by decreasing or inhibiting the activity of enzymes related to CO_2 fixation and this may precede inactivation of light capture and energy transfer between photosystems (Lawlor 1995). At least in parts, the imbalance between the photochemical and biochemical pathways of net photosynthesis lead to over-reduction of the photosynthetic electron chain, favoring generation of reactive oxygen species (ROS) such as superoxide radicals (O_2^-), hydrogen peroxide (H_2O_2), singlet oxygen ($^1O_2$), triplet chlorophyll, etc., (Asada 1999; Mittler 2002; Jaleel et al. 2009). These ROS are reactive to DNA, RNA, proteins and lipid cell membranes (Mittler 2002; Jaleel et al. 2009); and if plants fail to detoxify ROS, oxidative damage is shown in the whole plant as chlorotic and necrotic

lesions on damaged leaves (Karpinski et al. 1999). In woody species, lipid peroxidation, estimated as equivalents of malondialdehyde (MDA), has been reported in *Myracrodruon urundeuva* (Anacardiaceae) seedlings under drought conditions, and such damages were quickly attenuated at 6 and 54 h after resumption of irrigation (Queiroz et al. 2002). In *Coffea canephora*, the decrease in pre-dawn leaf water potential (Ψ_{pd}) from −0.20 to −3.00 MPa increased MDA production by 126% in the drought-tolerant clone (clone 120) against 330% in the drought-sensitive genotype (clone 109A), and electrolyte leakage indicated more pronounced membrane injury in clone 109A (Lima et al. 2002).

As a protective strategy to prevent oxidative damage, plants are endowed with a complex enzymatic system able to cope with ROS (Smirnoff 1995; Noctor and Foyer 1998; Asada 1999). It includes superoxide dismutase (SOD; EC 1.15.1.1) which catalyzes the reaction from superoxide radical (specially derived from Mehler's Reaction) to H_2O_2; catalase (CAT; EC 1.11.1.6), that produces H_2O and O_2 from H_2O_2; and enzymes from ascorbate–glutathione cycle, e.g. ascorbate peroxidase (APX; EC 1.11.1.11), which detoxify the H_2O_2 produced by SOD (Asada 1999; Mittler 2002; Jaleel et al. 2009). Cell protection may also be achieved by means of dissipating free excessive energy through lipid-soluble, membrane-associated antioxidants, such as tocopherol and carotenoids (Asada 1999; Mittler 2002; Jaleel et al. 2009). Recently, Raza et al. (2007) registered enhanced activities of SOD, CAT and peroxidase in response to application of exogenous glycinebetaine (GB), indicating that GB modulates antioxidant enzyme activities in wheat cultivars differing in salt tolerance. Moreover, Raza et al. (2007) inferred that GB might exert protective effects on cell membranes and, if so, minor lipid peroxidation would be expected. Thereby, coordinated activation of both enzymatic and non-enzymatic pathways of detoxifying ROS is of crucial importance to enable plants to tolerate or postpone drought efficiently.

Andiroba (*Carapa guianensis* Aubl.; Meliaceae) is an evergreen tropical tree species widely distributed over the Amazon Rain Forest that produces an excellent oil used to manufacture medicines, cosmetics, repellents and biofuels (Neves et al. 2004). This species remains productive at least for 40 years and for this reason it has been planted in agroforestry systems to recover degraded lands. However, much of the degraded lands in the Amazon are prone to suffer a prolonged dry season, in which the average monthly rainfall does not exceed 100 mm. Thus, limited soil water availability poses a problem for seedling survival and growth, mainly during the first years of cultivation in which the shallow root system does not attenuate drought effects by increasing water uptake satisfactorily. Considering that net photosynthesis in andiroba is significantly decreased under more negative leaf water potentials (Costa and Marenco 2007; Gonçalves et al. 2009) and only slight changes in the electron transfer reactions are observed (Gonçalves et al. 2009), thus the occurrence of oxidative damage in drought-stressed plants of andiroba is expected to some extent. Therefore, in this research we compared well-watered and water-stressed plants of andiroba to evaluate the magnitude of oxidative damage to membrane lipids (lipid peroxidation) and leaf content of chlorophyll (*a* and *b*). The ability of plants to cope with ROS through antioxidant enzymes (SOD, APX and CAT) and adjustments in the concentration of leaf carotenoids and GB were also examined. Finally, plant recovery was evaluated after stress cease, assessing Ψ_{pd} and biochemical analysis 12 h after irrigation was resumed (short-term rewetting).

Materials and methods

Plant material, growth conditions and sampling procedures

Andiroba (*Carapa guianensis* Aubl.) seeds were collected at the campus of "Universidade Federal Rural da Amazônia", Belém, PA, North Brazil (01°28′03″, 48°29′18″W) from 12 adult trees of around 15-years-old. Uniform seeds were immersed in distilled water at 25°C for 24 h and planted in polyethylene bags (15 × 27 cm, diameter × height) for seedling establishment. Five months later, uniform seedlings were selected according to their uniformity in relation to stem height and number of leaves and leaflets for experimental setup. The selected seedlings were transferred (one seedling per pot) to 20-L polyethylene pots filled with 16 kg of yellow loam latosol previously dried at room temperature and sifted to remove undesired elements. Acidity of substrate was adjusted to a pH of around 6.0 by adding 5-g dolomite calcareous per pot, and macronutrients (nitrogen, N; phosphate, P; and potassium, K) were supplied by adding 30-g NPK (10:10:10, w/w/w) per pot. Throughout the experiment, the plants were grown under greenhouse conditions, with an average of diurnal photosynthetic photon flux (PPF) of 490 μmol m^{-2} s^{-1}, and averages of diurnal relative air humidity (RH) and air temperature (T_{ar}) of 80% and 28°C, respectively. PPF was measured with a quantum sensor attached to a steady-state porometer (Li-1600; LiCor Bioscience, Lincoln, USA), and RH and T_{ar} were registered with a thermohygrometer (m5203, Incoterm Ind., Porto Alegre, Brazil) placed inside the greenhouse. Irrigation was performed daily to maintain soil near field capacity by replacing evapotranspired water, estimated by weighing each pot just prior to watering.

Weeds were manually controlled weekly. When 9-months old, plants were divided into two groups (treatments). In the first group, the plants were continuously watered as previous described (control plants) and in the second, irrigation was completely withheld and water-deficit developed naturally with progressive exhaustion of soil water (water-stressed plants). The effects of water-deficit on lipid peroxidation, leaf pigments and antioxidant enzymes were assessed 15 and 27 days after withhold irrigation (representing two water-deficit conditions) and 12 h after rewetting (short-term rewetting; day 28). For Ψ_{pd} evaluations, one leaflet of the third leaf-pair from the apices was selected from six different replicates per water regime treatments. For biochemical analysis, six leaflet discs (0.8 cm^2 each) per plant were collected from healthy, mature leaflets from a single leaf at the second or third pair from the apices, and immediately stored at −20°C until assays. Biochemical analyses were performed at most 2 weeks later. For the electrolyte leakage, eight leaflet discs (each 0.8 cm^2) per plant were collected and immediately assayed. Except for Ψ_{pd}, determined from 0430 to 0530 h, samples were collected from 1100 to 1300 h. After sampling on day 27, all plants were watered at 1700 h and Ψ_{pd}, electrolyte leakage and sampling for biochemical analysis were assessed on next morning to examine plant recovery during short-term rewetting.

Leaf water potential

Ψ_{pd} was measured using a Scholander-type pressure chamber (m670, Pms Instrument Co., Albany, USA) as described by Pinheiro et al. (2008).

Lipid peroxidation and electrolyte leakage

Lipid peroxidation was estimated as described in Cakmak and Horst (1991), with some modifications. Leaflet samples were ground in 3 mL 0.1% (w/v) trichloracetic acid (TCA), at 4°C, and the slurry was centrifuged at 15,000×*g* for 15 min. An aliquot of 0.5 mL from the supernatant was collected and added to 1.5 mL of 0.5% 2-thiobarbituric acid (TBA; prepared in 20% TCA). After shaking, the samples were incubated at 90°C for 20 min. The colorimetric reaction was stopped in an ice bath and samples were centrifuged at 13,000×*g* for 8 min at 25°C. The absorbance of supernatant was measured at 532 nm and corrected for non-specific turbidity by subtracting the absorbance at 600 nm. Lipid peroxidation was estimated as the content of total TBA reactive substances and expressed as equivalents of MDA, calculated from their extinction coefficient (155 mM^{-1} cm^{-1}). Electrolyte leakage was performed as described in Lima et al. (2002).

Chloroplastic pigments

Chloroplastic pigments were extracted by grinding frozen leaflet samples in 5 mL 80% (v/v) acetone plus 0.01 g $CaCO_3$ and the resultant slurry was centrifuged at 2,000×*g* for 10 min, at 4°C. The supernatant was collected and extraction procedures were repeated twice using the same volume of acetone. All supernatants were combined and resultant volume was adjusted to 25 mL using 80% (v/v) acetone. After homogenization, the absorbance of the extracts was measured at 470, 646.8, and 663.2 nm and concentrations of leaf pigments (chlorophyll *a*, Chl *a*; chlorophyll *b*, Chl *b*, and carotenoids) and Chl *a*/carotenoids ratio were estimated according to Lichthenthaler (1987). Results were expressed in g pigment kg^{-1} dry matter (DM).

Enzymatic assays

Frozen leaflet samples were ground using an ice-cold mortar and pestle and 3 mL of extraction buffer containing 100 mM K-phosphate buffer (pH 7.8), 0.1 mM EDTA, 14 mM 2-mercaptoethanol and 0.1% (v/v) Triton X-100 for SOD (EC 1.15.1.1); or 50 mM K-phosphate buffer (pH 7.0), 2 mM EDTA, 20 mM ascorbate and 0.1% (v/v) Triton X-100 for CAT (EC 1.11.1.6) and APX (EC 1.11.1.11). The resulting slurry was centrifuged at 15,000×*g* for 15 min at 4°C and the supernatant was used for total protein (Bradford 1976) and enzymatic assays. Total SOD activity was evaluated in the reaction medium containing 50 mM K-phosphate buffer (pH 7.8), 0.1 μM EDTA, 13 mM methionine, 75 μM nitrobluetetrazolium (NBT), 2 μM riboflavin and 10 μL enzyme extract. The activity of SOD was determined according to the ability of the enzyme to inhibit photochemical reduction of NBT on blue formazan followed by monitoring the absorbance of the reaction mixture at 560 nm (Giannopolitis and Ries 1977). Total CAT activity was performed following the rate of consumption of H_2O_2 at 240 nm (Havir and McHale 1987) in a reaction medium containing 50 mM K-phosphate buffer (pH 7.0), 12.5 mM H_2O_2 and 20 μL enzyme extract. Total APX activity was estimated by monitoring the decline in absorbance at 290 nm (Nakano and Asada 1981). Each 3 mL reaction medium contained 50 mM K-phosphate buffer (pH 7.0), 0.1 mM H_2O_2, 0.5 mM ascorbate and 50 μL enzyme extract. Interferences were corrected by running the assays using denatured enzyme extract, and results were expressed in unit of enzyme mg^{-1} protein as follows: 1 unit SOD is the amount of enzyme to cause 50% inhibition on NBT photoreduction; and 1 unit CAT (or APX) is the amount of enzyme required to decompose 1 μmol H_2O_2 (or ascorbate) min^{-1}.

Glycinebetaine

GB was determined according to Grieve and Grattan (1983), modified as following. Leaflet dried samples were ground to a fine powder and homogenized in 2 mL distilled water for 4 h, at 25°C, under continuous agitation. After centrifuging at 3,500 × *g* for 10 min, at 25°C, an aliquot of 250 μL from the supernatant was mixed with an equal volume of 2 N H_2SO_4 and incubated in an ice bath for 1 h. Then, 200 μL potassium iodide were added and, after vigorous shaking, the samples were incubated overnight (16 h) at 0°C. After centrifuging at 3,500 × *g* (15 min at 0°C), the supernatant was discarded and the pellet was washed twice in 2 mL 1 N H_2SO_4 at 8°C. The samples were centrifuged at 3,500 × *g*, for 5 min at 0°C, and the supernatant (H_2SO_4 phase) was discarded. The pellet was solved in 3 mL 1,2-dichloroethane (at 0°C) and the absorbance of the resultant extracts was measured at 365 nm. GB content was determined through standard curve using GB (SIGMA) as standard and results were expressed in μg GB g^{-1} DM.

Statistics

The plants were placed in a randomized complete design with two treatments (control and water-stressed plants) evaluated at three different times (Days after treatment differentiation: days 15, 27 and 28). A single plant per pot was considered an experimental replicate and six replicates per treatment were assayed. The effect of water-deficit on plants was studied into each experimental day. For this, data from each variable were subjected to analysis of variance and mean differences between control and water-stressed plants were tested for significance by the Student's *t* test ($P < 0.05$). A mean of six replicates ± standard deviation (SD) for each variable was used for plotting.

Results

Leaf water potential, electrolyte leakage and MDA

After 15 days of withholding irrigation, Ψ_{pd} decreased from −0.19 MPa in the control to −1.35 MPa in the water-stressed plants; and on day 27 Ψ_{pd} it decreased from −0.30 MPa (control) to −3.21 MPa (water-stressed) (Fig. 1a). When irrigation of water-stressed plants was resumed, Ψ_{pd} increased sharply from −3.21 MPa (Day 27) to −0.59 MPa (Day 28) (Fig. 1a). Averages of Ψ_{pd} on days 15 and 27 evidenced that water-stressed plants experienced two different water-deficit conditions and the increase on Ψ_{pd} of water-stressed plants next to control indicated an excellent ability of the plants to recover their turgor.

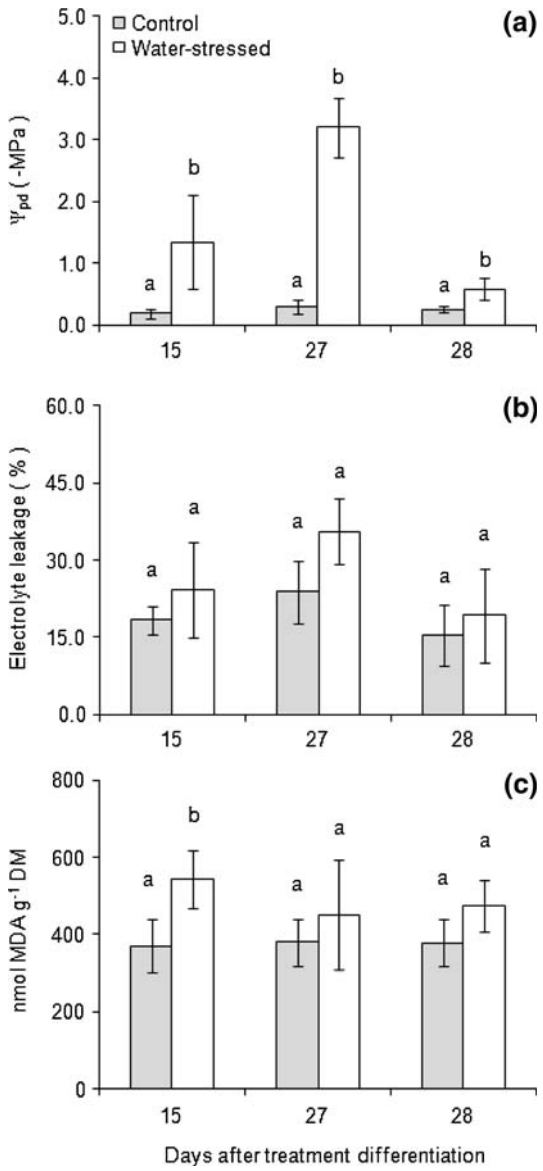

Fig. 1 Pre-dawn leaf water potential (Ψ_{pd}), electrolyte leakage and malondialdehyde (MDA) content in *C. guianensis* plants subjected to water-deficit (days 15 and 27) and short-term rewetting (day 28). Different *small letters* denote statistical significance between mean of well-watered and water-stressed plants as compared into the same experimental day (Student's *t* test, $P < 0.05$). Data are the mean of six replicates ± standard deviation

The electrolyte leakage did not differ between treatments regardless of the experimental period (Fig. 1b), while the effects of water-deficit on MDA content were evident only on day 15, being 47% higher in water-stressed plants than in the control (Fig. 1c).

Chloroplastic pigments

The contents of Chl *a*, Chl *b* and total carotenoids did not differ between treatments regardless of the experimental

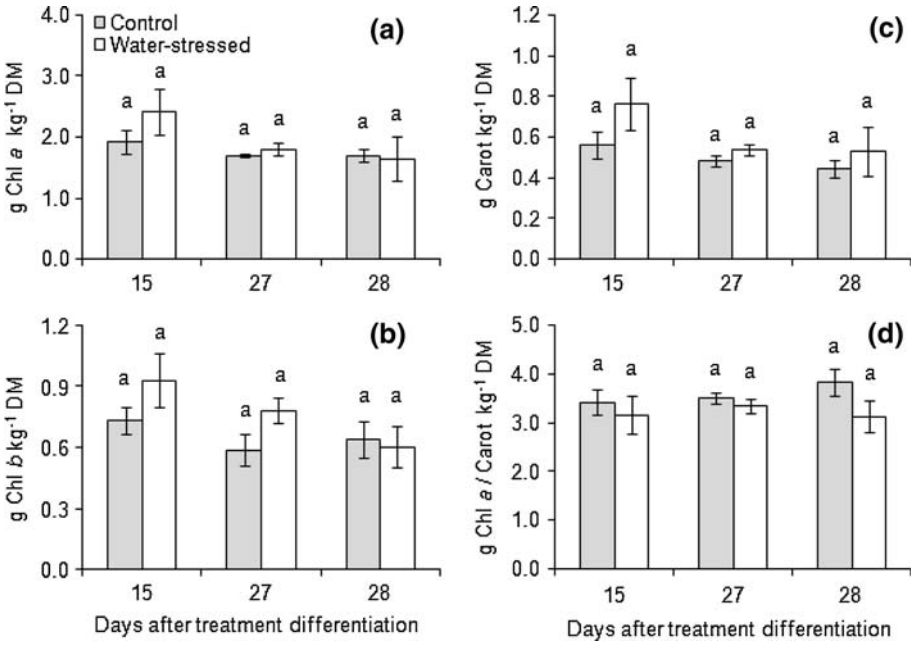

Fig. 2 Concentration of leaf chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), total carotenoids, and Chl *a*/carotenoids ratio in *C. guianensis* plants subjected to water-deficit (days 15 and 27) and short-term rewetting (day 28). Statistics as in Fig. 1

period (Fig. 2a, b, c) and as a consequence, Chl *a*/Carot ratio remained unchanged between well-watered and water-stressed plants (Fig. 2d). These results indicate that the water-deficit conditions experienced by water-stressed plants did not promote degradation of chloroplastic pigments, explaining the absence of chlorotic and necrotic lesions on the leaflets of those plants.

Enzyme activities and glycinebetaine

The activities of SOD, APX and CAT did not differ between well-watered and water-stressed plants on day 15 (Fig. 3). On day 27, SOD activity of water-stressed plants remained unchanged in relation to control plants (Fig. 3a); however, water-deficit caused an increase of about 111% in the APX activity (Fig. 3b) and 50% increase in the CAT activity (Fig. 3c). During short-term rewetting, the activities of SOD, APX and CAT did not differ between treatments (Fig. 3). Water-deficit resulted on 62% (day 15) and 112% (day 27) increases in GB and after resuming irrigation, the concentration of GB was 22% higher in the water-stressed plants than in the control (Fig. 4).

Discussion

Oxidative damages in water-stressed plants of *Myracrodruon urundeuva* (Queiroz et al. 2002), *Coffea canephora* (Lima et al. 2002; Pinheiro et al. 2004), *Momordica charantia* (Agarwal and Shaneen 2007) and *Picea asperata* (Duan et al. 2007) are generally associated to increased MDA content and if plants fail to remove excess of ROS, oxidative damages could be also manifested as chlorotic and necrotic lesions due to chlorophyll degradation, as previously reported in *Arabidopsis thaliana* (Karpinski et al. 1999), *Melissa officinalis* (Munné-Bosch and Alegre 1999) and *Rosmarinus officinalis* (Munné-Bosch and Alegre 2000). In the present study, the occurrence of oxidative stress was evaluated in terms of MDA content and electrolyte leakage as well as assessing possible variations in the leaf pigments. Although MDA assay presents some methodological limitations (Halliwell et al. 1992; Halliwell and Whiteman 2004), this is the most widely used assay to characterize oxidative damage in plants (Shulaev and Oliver 2006) because the aldehydic secondary products of lipid peroxidation are generally accepted markers of oxidative stress (Del Rio et al. 2005). Therefore, the MDA content indicated that young plants of andiroba suffered oxidative damage to lipids regardless of the water regime and experimental day of evaluation, and this was confirmed by electrolyte leakage assay.

In the well-watered plants of andiroba, the production of ROS at low levels (or steady-state level) is a byproduct from metabolic reactions involving electron transport, such as photochemical reactions of net photosynthesis, photorespiration and mitochondrial respiration (Polle 2001). Nevertheless, more significant damages could be mitigated by the constitutive activities of antioxidant enzymes (such as SOD, CAT and APX) and non-enzymatic antioxidants molecules (Polle 2001). This explains the residual MDA content and the constitutive activity of SOD, CAT and APX in the well-watered plants of andiroba, as previously observed in well-watered plants of *Coffea canephora* (Lima et al. 2002; Pinheiro et al. 2004) and in Kentucky

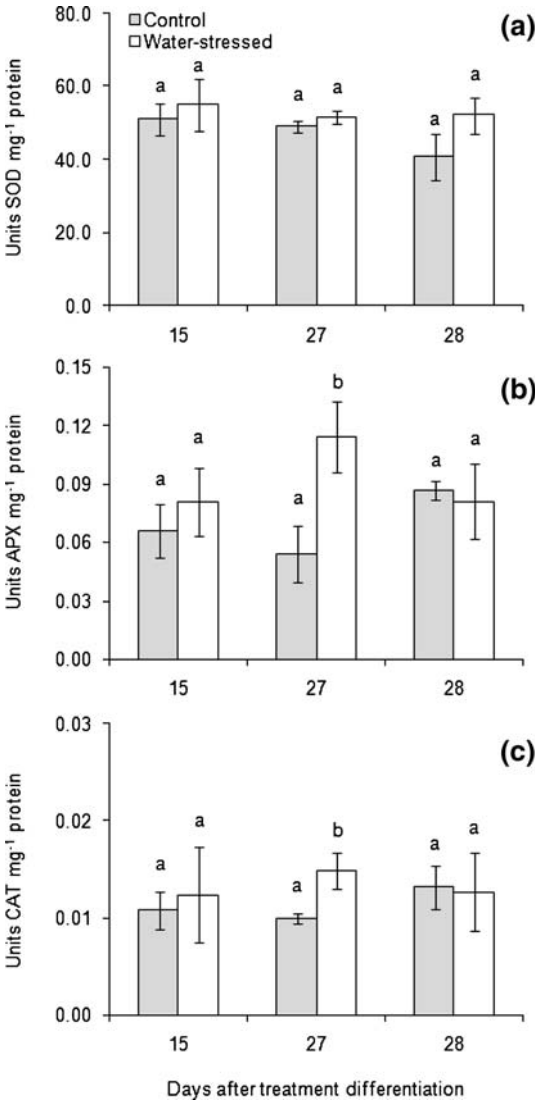

Fig. 3 Activities of superoxide dismutase (SOD), ascorbate peroxidase (APX), and catalase (CAT) in *C. guianensis* plants subjected to water-deficit (days 15 and 27) and short-term rewetting (day 28). Statistics as in Fig. 1

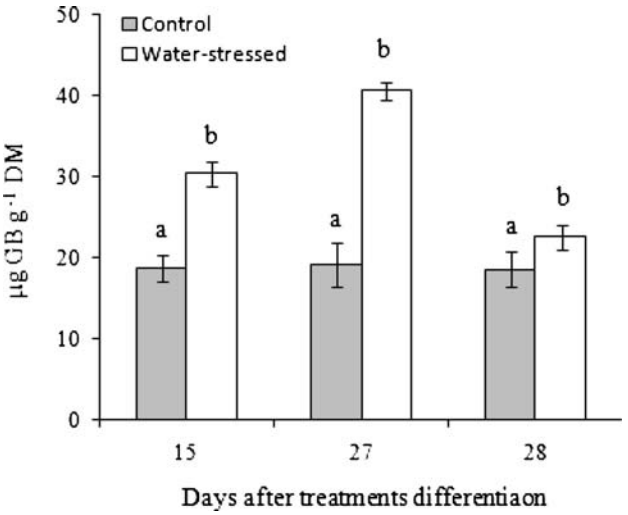

Fig. 4 Glycinebetaine content in *C. guianensis* plants subjected to water-deficit (days 15 and 27) and short-term rewetting (day 28). Statistics as in Fig. 1

bluegrass, in which constitutive activity of SOD, CAT and APX was correlated to constitutive gene expression (Bian and Jiang 2009).

In water-stressed plants of andiroba, Gonçalves et al. (2009) have observed that net photosynthesis was substantially suppressed (80% lower in relation to well-watered plants) 21 days after withholding irrigation (when leaf water potential measured at 0900 h reached −3.4 MPa), and this was accompanied by only few changes in the chlorophyll *a* fluorescence parameters. Considering that the experimental conditions (plant age, climatic conditions and stress imposition) and the internal water-deficit experienced by the water-stressed plants in this study (day 27) were quite similar to that reported by Gonçalves and co-workers, thus the maintenance of electron flux through photosystems in parallel to decreases in net photosynthesis could be expected to some extent and this could lead to over production of ROS (Lawlor 1995; Asada 1999). Despite we did not measure changes in chlorophyll *a* fluorescence, the unchanged averages of chloroplastic pigments (in special chlorophyll *a* and carotenoids) between well-watered and water-stressed plants regardless of Ψ_{pd} were indicative that water-deficit did not cause photo-oxidative damages to photosystems, granting the light capture for photochemical reactions (Lawlor 1995; Asada 1999). This explains, at least in part, the increased lipid peroxidation in water-stressed plants on day 15 (see MDA content, Fig. 1c), which was coincident to unchanged activity (in comparison to control plants) of antioxidant enzymes activity (SOD, CAT and APX). On the other hand, more expressive damages to lipids were attenuated on day 27 and this was due to the maintenance of SOD activity and to the increased activity of CAT and APX under drought conditions. Similar trend was previously reported in water-stressed *Coffea canephora* clone 120 (tolerant to drought), which decreased leaf MDA contents and electrolyte leakage more efficiently than in drought-sensitive clone 109A in response to the higher activity of SOD, CAT and APX (Lima et al. 2002). In water-stressed Kentucky bluegrass, the MDA content was efficiently controlled through the maintenance of SOD and CAT activities as well as by increased activities of APX, monodehydroascorbate reductase, and dehydroascorbate reductase (Bian and Jiang 2009).

Our results indicated a partial co-operation between antioxidant enzymes, since SOD activity in water-stressed plants remained constant in parallel to increased APX and

CAT activities on day 27. Thereby, we can infer that the oxidative damages were adequately attenuated under more negative Ψ_{pd}. The unchanged SOD activity in parallel to increased activities of APX and CAT (day 27) is quite acceptable because superoxide anions could also be mitigated through non-enzymatic pathways. For this reason, different responses (increases and decreases) in SOD activity under drought conditions have been reported, and this depends on plant species and stress severity (Dhindsa and Matowe 1981; Del Longo et al. 1993; Moran et al. 1994; van Rensburg and Krüger 1994; Schwanz et al. 1996; Sgherri et al. 2000; Martinez et al. 2001; Lima et al. 2002; Pinheiro et al. 2004; Bian and Jiang 2009). Thus, detoxifying of O_2^- in water-stressed andiroba plants could result in part from SOD activity in the chloroplasts (Corpas et al. 2001; Mittler 2002) as well as from its direct reaction with ascorbate and reduced glutathione (Smirnoff 1995; Mittler 2002; Jaleel et al. 2009) or GB (Smirnoff and Cumbes 1989; Shen et al. 1997).

Increases in the activity of antioxidant enzymes under stressful conditions could be attributed either to an increase in gene expression or simply to an increase in the enzyme activity in response to enzymatic modulators, with no significant effects in the gene expression. A relationship between antioxidant enzymes and expression of the correspondent genes was reported in Kentucky bluegrass (Bian and Jiang 2009) and by using transgenic plants (Allen et al. 1997). On the other hand, the application of exogenous GB enhanced endogenous GB in wheat cultivars differing in salt tolerance, modulating positively the activities of antioxidant enzymes in salt-tolerant genotypes (Raza et al. 2007). GB is a quaternary compound abundant in the chloroplast and commonly synthesized from serine via ethanolamine (Rhodes and Hanson 1993) in response to dehydration (Mohanty et al. 2002; Yang et al. 2003). Our data showed increased GB content under drought conditions, indicating that GB possibly co-operated with SOD in detoxifying O_2^- in the chloroplasts. Moreover, possible GB-enzyme modulation in water-stressed plants of andiroba was evident for APX and CAT, since higher (days 15 and 27) enzyme activities were coincident to higher (days 15 and 27) concentrations of GB.

The magnitude of damage during stress development is responsive to both stress period and intensity and this may determine plant ability to recover turgor and overall physiological processes after stress cessation (Sgherri et al. 2000). Here, we examined the recovery of water-stressed plants 12 h after resuming irrigation because previous results indicated that water-stressed plants of Brazilian mahogany (*Swietenia macrophylla*, another Meliaceae from the Amazon region) recovered its turgor during short-term rewetting (Cordeiro et al. 2009). In agreement, water-stressed plants of *Myracrodruon urundeuva* (Anacardiaceae), a typical species found in semiarid lands in Brazil, recovered turgor and decreased lipid peroxidation efficiently 6 h after resuming irrigation (Queiroz et al. 2002). By comparison, we can infer from our results that andiroba plants exhibited an efficient recovery in plant turgor during short-term rewetting. Although the mechanisms contributing to this have not been evaluated, the increased GB content in water-stressed plants during stress development and short-term rewetting strongly evidenced that GB may have improved water uptake from drying soil through osmotic adjustment (Subbarao et al. 2001; Munns 2002; Ashraf and Harris 2004). After stress cease, the activities of APX and CAT did not differ between treatments, and the decreases in MDA content in water-stressed plants indicated that production of H_2O_2 was attenuated during plant recovery. Altogether, we can conclude that both increases in the APX and CAT activity and in the GB content are efficient strategies to prevent expressive oxidative damages in water-stressed plants of andiroba.

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