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Seed reserve composition and mobilization during germination and early seedling establishment of *Cereus jamacaru* D.C. ssp. *jamacaru* (Cactaceae)

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ABSTRACT

Cereus jamacaru, a Cactaceae found throughout northeast Brazil, is widely used as cattle food and as an ornamental and medicinal plant. However, there has been little information about the physiological and biochemical aspects involved in its germination. The aim of this study was to investigate its reserve mobilization during germination and early seedling growth. For this, *C. jamacaru* seeds were germinated in a growth chamber and collected at 0, 2, 4, 5, 6, 8 and 12 days after imbibition for morphological and biochemical analyses. Dry seeds had wrinkled seed coats and large, curved embryos. Lipids were the most abundant reserve, comprising approximately 55% and 65% of the dry mass for cotyledons and the hypocotyl-radicle axis, respectively. Soluble sugars and starch were the minor reserves, corresponding to approximately 2.2% of the cotyledons' dry mass, although their levels showed significant changes during germination. Soluble proteins corresponded to 40% of the cotyledons' dry mass, which was reduced by 81% at the final period of germination compared to dry seeds. *C. jamacaru* seed can be classified as an oil seed due to its high lipid content. Moreover, lipids were the main reserve mobilized during germination because their levels were strongly reduced after seed germination, while proteins were the second most utilized reserve in this process.

Key words: Cactaceae, carbohydrates, cytochemistry, lipids, morphology, proteins.

INTRODUCTION

Seed germination is composed of two distinct metabolic processes: reserve mobilization by hydrolytic enzymes and the use of the hydrolysis products for the formation of new cell structures (Fu et al. 2005, Soltani et al. 2006). The mobilization of food reserves also provides energy to fuel growth until the seedling becomes photoautotrophic (Pritchard et al. 2002). Carbohydrates, lipids and proteins, which are stored during the later stages of seed formation, are considered the major reserves in most seeds (Bewley 1997, Suda and Giorgini 2000, Lima et al. 2008).

Cactaceae are widely distributed in the American continent and consist of approximately 1500 to 2000 species (Rojas-Aréchiga and Vásquez-Yanes 2000). Cactus seeds present considerable

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variations in form, size, structure, embryo characteristics, color of the testa and number among species and sometimes within the same species (Rojas-Aréchiga and Vásquez-Yanes 2000). These authors also reported features of cactus seed germination such as predation, dissemination, dormancy, soil seed bank, longevity, propagation and conservation (Rojas-Aréchiga and Vásquez-Yanes 2000). However, there is no current information about seed reserve mobilization within the Cactaceae family. In addition, although the third highest level of species diversity in the Cactaceae family is found in Brazil (Taylor and Zappi 2004), few studies have been conducted with cacti inhabiting the Caatinga vegetation, a semiarid ecosystem that characterizes northeastern Brazil (Meiado et al. 2008).

Cereus jamacaru D.C. ssp. *jamacaru* is a columnar cactus popularly known as 'mandacaru' that is widely distributed in the semi-arid tropic of Brazil, being used as an ornamental plant and as cattle feed (Taylor and Zappi 2004). Farmers also use their fruit as food, and infusions of their stems and roots are professed to be efficient for treating respiratory diseases (Mors et al. 2000, Lorenzi and Matos 2002). Recently, Meiado et al. (2010) classified *C. jamacaru* as a positive photoblastic species and showed that saline and water stresses negatively affected its germination. They also reported that the high seed germination capacity of *C. jamacaru* while under the influence of different environmental factors was associated with high fruit production per individual and the high seed production per fruit. In addition, it could compensate for the low level of recruitment and should favor the occurrence and the wide distribution of the species in the Caatinga vegetation.

As *C. jamacaru* is well adapted to Brazil's semi-arid region, knowledge about the reserve of these seeds is important for understanding how the reserves can provide enough energy for seed germination. Moreover, information regarding the way in which an embryo mobilizes seed reserves during the early stage of germination and seedling development can provide insights into the metabolic processes of germination and the relative nutritional importance of different reserve compounds, which can be considered crucial for successful seedling development. Therefore, the aim of this study was to evaluate the reserve mobilization process during the seed germination and early seedling growth of this species and to contribute with more information about the related biochemical and physiological aspects of this process.

MATERIALS AND METHODS

Plant Material and Germination

Mature fruits with *C. jamacaru* seeds were collected in Crateús, Ceará, Brazil. The seeds were harvested and stored at 4°C in glass pots until use. Seeds were treated with 5% sodium hypochlorite for 5 min and washed with distilled water prior to germination on two paper sheets moistened with distilled water (4.5 mL) in plastic boxes (14 x 14 x 3.5 cm), which were placed in a germination chamber at 25°C under continuous white light from 0.012 W m^{-2} nm^{-1} lamps for a 12 h photoperiod. The seeds that were used had a medium mass of 3 mg per unit. Seed germination was defined as a radicle protrusion out of the seed coat that was 1 mm in length. The seeds were harvested at 0 (dry seed), 2 (imbibed seed), 4 (beginning of seed coat ruptured), 5 (radicle after protrusion) and 6 days after imbibition (DAI) (epicotyl elongation), and seedlings were harvested at 8 and 12 DAI. The radicle protrusion occurred between 4 and 5 DAI. Four replicates of 100 seeds were used for each evaluation period.

Morphological and Cytochemical Analyses

Seeds at 0 and 5 DAI, with and without a seed coat, were evaluated morphologically according to Beltrati (1995) using a stereoscopic microscope. For cytochemical analyses, seeds with a seed coat at 0 and 6 DAI were fixed with a solution of 40 g L^{-1} paraformaldehyde in 0.1 mol L^{-1} phosphate

buffer (pH 7.2) and 10 g L^{-1} glutaraldehyde for 24 h at ambient temperature (Karnovsky 1965). The material was then dehydrated in a graded ethanol series and embedded with a Historesin Embedding Kit (Jung Heidelberg, Germany). The tissue blocks were sectioned at 5 μm on a Leica RM 2065 microtome (Heidelberg, Germany). Thereafter, the seed cross sections were subjected to the following cytochemical stains: xylidine Ponceau (XP) for proteins (Vidal 1970), periodic acid/Schiff (PAS) for polysaccharides (Maia 1979), Lugol's reagent for starch (Berlyn and Miksche 1976) and Sudan IV for lipid bodies (Gerlach 1984). The cross sections were analyzed by light microscopy.

Biochemical Analyses

Seeds without a seed coat at 0, 2, 4, 5 and 6 DAI and seedlings at 8 and 12 DAI were separated into cotyledons and the hypocotyl-radicle axis. These structures were then freeze-dried, and the tissue dry mass was obtained. The materials were stored at 4°C until use.

For total lipid determination, the following procedure was performed at room temperature. Initially, 15 mg of dry mass (cotyledon or hypocotyl-radicle axis) was ground and homogenized in 1.5 mL of a chloroform/methanol mixture (2:1 v/v) according to Bligh and Dyer (1959). After the separation step, the lipid phase was collected and dried. Soon after, the lipid content was determined by gravimetry.

For soluble sugar and free amino acid determinations, 15 mg of cotyledon or hypocotyl-radicle axis dry mass was ground and homogenized in 1.5 mL of 80% ethanol (v/v), and then the mixture was warmed at 75°C for 1 h. After centrifugation at 12,000 x g for 10 min, the supernatant was collected, and the pellet was re-extracted twice for 30 min each. Supernatants from both extractions were then combined. The amount of total soluble sugars was then determined according to Dubois et al. (1956) using glucose as a standard. Free amino acids (FAA) were determined using the Yemm and Cocking (1955) method with glycine as a standard. Reducing sugars were estimated according to the Miller (1959) method, whereas non-reducing sugars were estimated by the difference between the total soluble and reducing sugars. Starch was determined according to McCready et al. (1950) using glucose as a standard.

Proteins were extracted according to their solubility (Osborne 1924). The material was subjected to consecutive extractions with distilled water (albumins), 5% (w/v) sodium chloride (globulins), 60% (v/v) ethanol (prolamins) and 0.4% (w/v) sodium hydroxide. The alkali-soluble protein is referred to in the present study as salt insoluble protein (SIP). Extracts were centrifuged at 12,000 x g at 4°C for 10 min. An aliquot of each extract was taken for the quantification of proteins by the Bradford (1976) method using bovine serum albumin (BSA) as a standard. Total soluble protein (TSP) was calculated as the sum of all protein fractions.

Experiments for the biochemical analyses were set up in a completely randomized design, and each treatment had four replicates of 100 seeds each. Differences in biochemical parameters among treatments were tested for statistical significance using a one-way ANOVA followed by a Tukey's honestly significant difference test. Data are expressed as a mean of four independent values ± the standard error (SE). All statistical analyses were carried out using the program ASSISTAT 7.0 ($P < 0.05$).

RESULTS

Morphological and Cytochemical Analyses

Seeds were oblong-oval in shape, with wrinkled testae and a black seed coat (Fig. 1A). The bulk of the seed at 5 DAI was a large curved embryo, which was peripheral, cylindrical, perispermous and campylotropous, with two convex-plane cotyledons observed after the radicle protrusion (Fig. 1B).

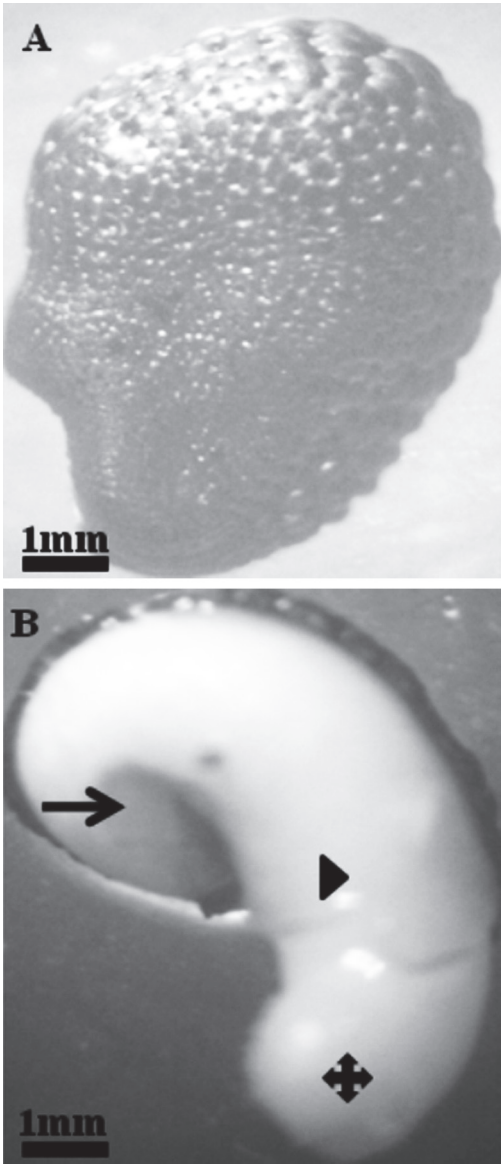

Fig. 1 - Dry seed (A), seed at 5 DAI (B) partially without seed coat showing cotyledons (→), hypocotyl- radicle axis (▶) and radicle after protusion (✥).

The seeds were evaluated by cytochemical analyses during germination (Fig. 2). A large number of lipid bodies were detected in dry seeds (Fig. 2A); however, after germination at 6 DAI, these structures were reduced (Fig. 2B). A considerable number of protein bodies present in dry seeds (Fig. 2C) were reduced or fused after the radicle had protruded at 6 DAI (Fig. 2D). Cell walls were thin both in dry seeds (Fig. 2E) and at 6 DAI (Fig. 2F); moreover, starch grains were evident in the last period (6 DAI) (Fig. 2F), which was confirmed by the positive reaction with Lugol's reagent (Fig. 2H).

Seed Reserve Mobilization

Lipids were the most abundant reserve compounds in dry seeds, accounting for 55% and 65% of the cotyledon and the hypocotyl-radicle axis dry mass, respectively (Table I). Proteins were the second most represented compound, comprising 40% of the cotyledons and 30% of the hypocotyl-radicle axis. Other compounds were not as abundant, with 1.9%, 0.5% and 0.3% of the cotyledon dry mass composed of soluble sugars, free amino acids and starch, respectively, with similar percentages observed in the hypocotyl-radicle axis (Table I).

The lipid content was slightly changed in cotyledons until 6 DAI, except by a significant increase at 5DAI; however, a strong reduction was observed at 8 and 12 DAI, corresponding to 37% and 66%, respectively, compared to dry seeds (Table IIA). On the other hand, the lipid content of the hypocotyl-radicle axis remained practically unchanged until 6 DAI; thereafter significant increase occurred from 8 DAI ($F_{(6,21)}$= 24.13, $P < 0.001$, Table IIB).

The soluble sugar content also showed significant differences ($P < 0.01$), with the highest values at 8 DAI, showing an increase of 262% in the cotyledons and ($F_{(6,21)}$= 42.96, $P < 0.01$, Table IIA) 255% in the hypocotyl-radicle axis ($F_{(6,21)}$= 42.96, $P < 0.001$, Table IIB), compared to dry seeds. Reduced sugars were unchanged in the cotyledons (Table IIA), whereas in the hypocotyl-radicle axis there were significant changes, with the highest values at 8 and 12 DAI ($F_{(6,21)}$= 17.30, $P < 0.001$, Table IIB). The non-reducing sugars were highest at 8 and 12 DAI in cotyledons and at 6 and 8 DAI in the hypocotyl-radicle axis.

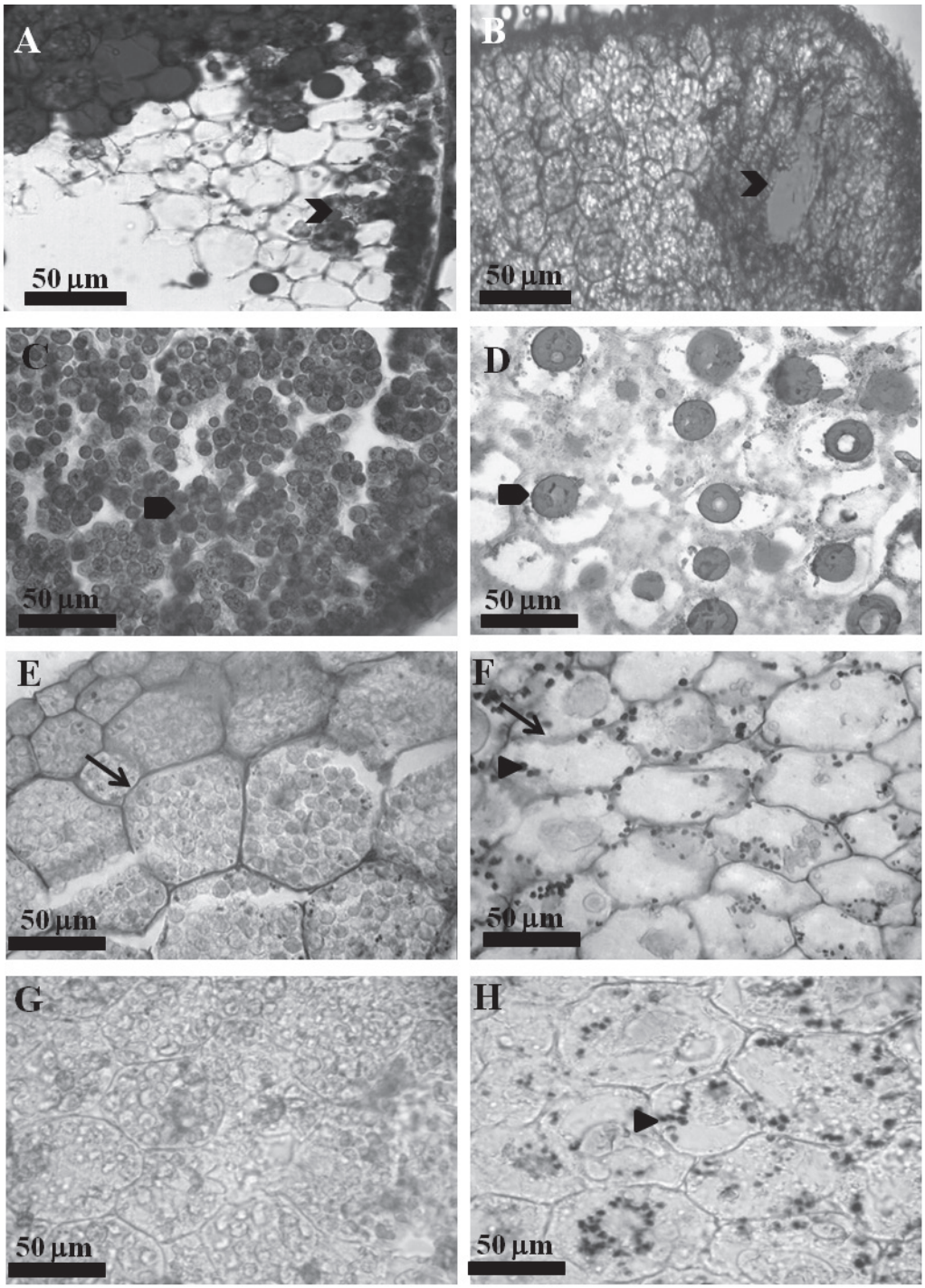

Fig. 2 - Cotyledon cross sections at 0 (A) and 6 days after imbibition (DAI) (B), showing lipid bodies (➧) stained by Sudan IV, protein bodies (➡) at 0 (C) and 6 DAI (D) stained by xylidine Ponceau. Sections at 0 (E) and 6 DAI (F) showing cell-wall (→) and PAS-positive reactions indicating starch grains (▶, F). Sections at 0 (G) and 6 DAI (H) stained by lugol, confirming starch grains (▶, H).

TABLE I
Percentage composition (%) of cotyledons and hypocotyl-radicle axis in *Cereus jamacaru* dry seeds. Mean values (n=4).

Seed dry compounds	Cotyledons	Hipocotyl-radicle axis
Lipids	55.0	65.0
Soluble sugars	1.9	1.9
Starch	0.3	0.4
Soluble Proteins	40.0	30.0
Free amino acids	0.5	0.4
Other compounds	2.3	2.3

TABLE II
Changes in lipid, sugars (soluble, reducing and non-reducing) and starch contents in *Cereus jamacaru* seed cotyledons (A) and hypocotyl-radicle axis (B).

Cotyledon compounds (mg g^{-1} cotyledon dry mass) (A)					
DAI	Lipids	Soluble sugars	Reducing sugars	Non-reducing sugars	Starch
0	377.3 ± 11.6 bc	13.0 ± 1.7 d	10.8 ± 1.2 ab	2.2 ± 0.9 d	1.9 ± 0.2 c
2	355.0 ± 10.4 c	35.4 ± 1.9 b	10.3 ± 0.4 ab	25.1 ± 1.9 b	2.4 ± 0.2 c
4	500.0 ± 32.4 a	21.8 ± 0.1 cd	10.4 ± 1.0 ab	11.4 ± 1.1 c	4.0 ± 0.1 c
5	447.5 ± 18.0 ab	14.3 ± 0.7 d	10.1 ± 0.3 ab	4.2 ± 0.8 cd	11.7 ± 0.5 ab
6	355.0 ± 30.5 c	24.8 ± 2.0 c	12.5 ± 0.6 a	12.3 ± 1.4 c	11.7 ± 0.4 ab
8	238.7 ± 15.9 d	47.0 ± 3.1 a	7.3 ± 0.4 b	39.7 ± 3.4 a	13.9 ± 0.8 a
12	130.0 ± 5.8 e	44.1 ± 3.2 ab	10.2 ± 1.2 ab	33.9 ± 2.1 a	10.1 ± 0.7 b
Hypocotyl-radicle compounds (mg g^{-1} hypocotyl-radicle axis dry mass) (B)					
DAI	Lipids	Soluble sugars	Reducing sugars	Non-reducing sugars	Starch
0	454.0 ± 17.7 b	13.0 ± 0.7 d	5.6 ± 0.7 c	7.4 ± 0.2 c	2.7 ± 0.1 e
2	464.3 ± 7.9 b	31.7 ± 1.3 bc	4.8 ± 0.6 c	26.9 ± 1.0 b	3.8 ± 0.3 de
4	461.0 ± 16.1 b	26.1 ± 2.2 c	4.8 ± 0.1 c	21.3 ± 2.2 b	7.8 ± 0.6 cd
5	445.0 ± 9.6 b	29.5 ± 1.4 bc	7.1 ± 0.5 bc	22.4 ± 1.0 b	13.9 ± 0.9 a
6	362.0 ± 18.1 b	34.2 ± 0.7 bc	7.0 ± 0.7 bc	27.2 ± 1.2 ab	12.8 ± 0.5 ab
8	1025.0 ± 25.0 a	46.1 ± 2.3 a	11.4 ± 1.4 ab	34.7 ± 2.9 a	9.5 ± 1.7 bc
12	884.8 ± 41.8 a	36.8 ± 3.4 b	15.3 ± 1.7 a	21.5 ± 2.9 b	7.3 ± 1.2 cd

Values are means ± standard error ($n=4$). Different letters indicate significant difference at $P \leq 0.05$ according to Tukey Test. DAI=Days after imbibition.

The major reserve proteins in dry seeds were albumins and SIP, which accounted for 31% and 53% of the TSP in the cotyledon dry mass, respectively (Table IIIA). The albumin, globulin and SIP contents in the cotyledons and the hypocotyl-radicle axis were significantly reduced (between 77% to 94%) at 12 DAI compared to dry seeds ($P < 0.001$, Table III). The prolamins did not change significantly during the imbibition in the cotyledons ($F_{(6,21)}= 1.57$, $P > 0.05$, Table IIIA), whereas the total protein content was significantly reduced in both the cotyledons ($F_{(6,21)}= 99.86$, $P < 0.001$, Table IIIA) and the hypocotyl-radicle axis ($F_{(6,21)}= 42.35$, $P < 0.001$, Table IIIB), and was accompanied by an increase in free amino acid levels, which were highest at 8 and 12 DAI.

TABLE III

Changes in albumin, globulin, prolamin, salt insoluble protein (SIP), free amino acids (FAA) and total protein (TP) contents in *Cereus jamacaru* seed cotyledons (A) and hypocotyl-radicle axis (B). The total protein (TP) corresponds to the sum of albumins, globulins, prolamins and glutelins.

Cotyledon proteins (mg g^{-1} cotyledon dry mass) (A)						
DAI	Albumins	Globulins	Prolamins	SIP	TP	Free amino acids
0	84.0 ± 2.0 b	41.5 ± 2.9 ab	3.8 ± 0.9ns	145.1 ± 11.0 a	274.4 ± 11.7 ab	3.7 ± 0.2 d
2	124.5 ± 8.4 a	44.1 ± 3.4 ab	4.9 ± 0.4ns	124.5 ± 3.8 ab	298.0 ± 6.8 a	4.3 ± 0.6 d
4	120.1 ± 9.6 a	46.0 ± 1.7 a	4.7 ± 0.7ns	111.0 ± 8.1 ab	281.8 ± 9.2 ab	4.2 ± 0.3 d
5	107.6 ± 8.2 ab	41.8 ± 7.2 ab	6.2 ± 1.1ns	115.2 ± 11.4 ab	270.8 ± 11.5 ab	9.4 ± 0.8 c
6	114.4 ± 7.2 a	28.8 ± 3.0 b	4.5 ± 0.5ns	100.2 ± 11.4 bc	247.9 ± 15.6 b	13.8 ± 0.7 b
8	4.5 ± 0.6 c	6.9 ± 0.5 c	5.6 ± 0.6ns	67.6 ± 9.8 cd	84.6 ± 9.8 c	18.5 ± 1.1 a
12	5.3 ± 0.4 c	6.3 ± 0.5 c	5.9 ± 0.5ns	33.9 ± 3.5 d	51.4 ± 3.9 c	20.7 ± 1.0 a
Hypocotyl-radicle proteins (mg g^{-1} hypocotyl-radicle dry mass) (B)						
DAI	Albumins	Globulins	Prolamins	SIP	TP	Free amino acids
0	26.7 ± 1.9 b	24.5 ± 3.8 c	5.4 ± 0.2 ab	159.8 ± 10.9 a	216.4 ± 15.0 a	2.7 ± 0.2 c
2	27.4 ± 0.8 b	34.1 ± 2.1 abc	6.1 ± 0.4 ab	161.5 ± 17.6 a	229.1 ± 18.6 a	4.7 ± 0.1 c
4	30.9 ± 1.5 ab	40.5 ± 1.5 a	5.5 ± 0.5 ab	112.1 ± 6.7 bc	189.0 ± 7.3 a	6.3 ± 0.5 c
5	32.5 ± 1.0 a	36.1 ± 1.8 ab	6.1 ± 0.1 ab	118.9 ± 10.7 ab	193.6 ± 11.8 a	13.6 ± 0.7 b
6	29.6 ± 0.8 ab	28.5 ± 3.4 bc	6.5 ± 0.1 a	67.2 ± 7.9 cd	131.8 ± 9.5 b	20.4 ± 0.5 a
8	6.7 ± 0.5 c	7.1 ± 0.1 d	5.3 ± 0.1 ab	53.8 ± 6.8 d	72.9 ± 7.2 c	18.6 ± 0.6 a
12	2.8 ± 0.4 c	6.0 ± 0.5 d	5.0 ± 0.3 b	24.2 ± 1.4 d	38.0 ± 1.2 c	17.0 ± 1.6 ab

Values are means ± standard error ($n=4$). Different letters indicate significant difference at $P \leq 0.05$ according to Tukey Test. DAI=Days after imbibition.

DISCUSSION

Similar to *C. jamacaru*, seeds of *Opuntia tomentosa* (Orozco-Segovia et al. 2007) and *Pilosocereus pachycladus* (Abud et al. 2010) are also campylotropous and perispermous. Additionally, Abud et al. (2010) observed seeds with a wrinkled, black seed coat and an embryo consisting of a well-developed hypocotyl-radicle axis and reduced plane-convex cotyledons for *P. pachycladus*.

In the present study, lipid reserves were laid down in oil bodies, and these structures were abundant in the cotyledons. Moreover, the high lipid content (55% in the cotyledon of dry seeds) suggests that this species is an oil seed, which is supported by the presence of the high levels of these reserves until 6 DAI and their strong reduction at 8 DAI. In addition, although the lipid had increased at 4 DAI compared to dry seed, it is important to highlight that this content remained the same at 5 DAI, which in turn did not differ significantly from that of quiescent seeds. In addition, the lipid content did not differ statistically at 2 and 6 DAI when compared to dry seed. Thus, it could be suggested that the lipid content was unchanged until 6 DAI. Surprisingly, the lipid content increased in the hypoctyl-radicle axis at 8 and 12 DAI. We speculate that this increase could be related to the fact that, during this period, this structure became green (data not shown), which may have occurred due to an increase in chloroplasts, which are organelles that are rich in membrane lipids. Similarly, the lipids in *Euphorbia heterophylla* were the most abundant reserve, comprising 60% of the content in dry seed, and this content was reduced by 70% during seed germination (Suda and Giorgini 2000).

The lipid content was also high in the cactus species *Pachycereus pringlei*, *Pachycereus pecten-aboriginum*, *Carnegiea gigantea*, *Stenocereus thurberi* and *Stenocereus gummosus*, which ranged from 28 to 31% among these species (Ortega-Nieblas et al. 2001). In addition, Lim et al. (2010) also observed that the pitaya (*Hylocereus* cacti) seeds contained a high amount of oil, 18% (*Hylocereus polyrhizus*) and 28% (*Hylocereus undatus*). It was also verified that a higher content of lipids (27%) was found in *Opuntia ficus indica* seeds (Kossori et al. 1998). It is important to note that seed reserves during germination and the mobilization process in Cactaceae species have not been previously reported in the literature.

As for the other reserves, the soluble sugars and starch were the less abundant reserve compounds in this study, indicating that they are not strongly involved in the seed reserve mobilization of *Cereus jamacaru*. In seeds of *Euphorbia heterophylla*, soluble sugars comprised approximately 4% of the seed dry mass, and starch was not detected in the endosperm of *E. heterophylla*, which supports the results of this study in which starch was barely detected. In seeds of *Myracrodruon urundeuva*, an arborescent species of the Anacardiaceae family, soluble sugars represented only 3.5% and starch represented 0.1% of dry seeds (Abdala et al. 2002). In addition, soluble sugar and starch contents showed low levels in French beans (Cortelazzo et al. 2005) and *Dalbergia miscolobium* (Silva et al. 1998). Notably, in the Kossori et al. (1998) study on the composition of the cactaceae seeds of *Opuntia ficus indica*, the levels of starch and soluble carbohydrates corresponded to 21 and 6%, respectively.

Proteins corresponded to the second most abundant seed reserve used in the heterotrophic development of this species. These reserves corresponded to 31% of the total reserves; consequently, a large number of protein bodies were observed in the cotyledons, and a strong protein mobilization was observed after the radicle protrusion. Protein depletion was accompanied by an increase in the free amino acid content, suggesting that, during seed mobilization, they are transferred to the growing embryo. Although protein mobilization has not been studied in cactus seeds, studies involving the composition of *Opuntia* seeds showed that proteins represent a large amount of the reserves, which corresponded to 46% of the total dry mass of the seeds (Kossori et al. 1998). In seeds of the columnar cactus from the Sonoran Desert (*Stenocereus thurberi*, *Carnegiea gigantea*, *Stenocereus gummosus* and *Pachycereus pringlei*), the protein content varied between 20-22% among species (Ortega-Nieblas et al. 2001). In addition, Costa et al. (2001) isolated and characterized a reserve protein from the seeds of *C. jamacaru* that showed a similar amino acid composition to the 2S albumin storage protein family. The authors named the protein cactin and discussed its potential use as a molecular marker in the Cactaceae family (Costa et al. 2001).

The total amount of seed reserves available for a developing seedling and the duration of a strict dependency of the seed for a given resource may vary among species in relation to three characteristics: seed size (total seed mass); seed quality (concentration of the focal resource); and the major function of the cotyledons (whether the cotyledons serve as a photosynthetic or storage organ of seed reserves after germination). Light-demanding species tend to have small seeds and photosynthetic cotyledons (Kitajima 2002), which correspond to characteristics also observed for the seeds discussed in this study.

The high lipid content in *C. jamacaru* seeds can be considered an adaptive trait of this species that enables the development of seedlings in adverse environmental conditions due to the high-energy content of this reserve. Moreover, Kitajima (1996) reported that the high lipid content in some species should indicate a compensatory selection (more energy/volume) in small seeds, which also contributes to the stronger selection of these seeds for dispersal. In addition, in oil seeds, lipids are preferably stored in the form of triacylglycerols, which are non-polar

and can be stored in a nearly anhydrous form. Their complete oxidation yields more than twice as much energy as protein or carbohydrate hydrolysis on a per unit volume basis (Murphy 2001, Quettier and Eastmond 2009). In plants, the main site of TAG storage is in the embryo and/or endosperm tissues of the seeds, depending on the species (Graham 2008). When the seeds germinate, the TAGs are degraded to produce a carbon source that will fuel the embryo's postgerminative growth and allow it to become a photosynthetically active seedling with a root system and leaves (Graham 2008).

In conclusion, our results suggest that the period of the most intense mobilization of seed reserves that were stored in cotyledons occurred at germination, and that the reserves were strongly reduced at the seedling growth stage. Moreover, these seeds can be classified as oil seeds due to the high lipid content observed in dry and germinating seeds. The lipids, as the main reserve mobilized, perform an important role as a fuel source for germination and early seedling development, and could be crucial for seed germination and successful seedling establishment under adverse conditions. Finally, as studies about the morphology and reserve mobilization of *C. jamacaru* seeds have not yet been reported in the literature, we can assume that our results provide insights into the physiological and biochemical mechanisms involved during the seed germination of this cactus.

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RESUMO

Cereus jamacaru, uma cactácea encontrada comumente no nordeste brasileiro, é amplamente usada como planta forrageira e como ornamental e medicinal. No entanto, existem poucas informações sobre os aspectos fisiológicos e bioquímicos relacionados à sua germinação. O objetivo desse estudo foi avaliar a mobilização de reservas durante a germinação e o crescimento inicial de plântulas de *C. jamacaru*. Para isso, as sementes foram germinadas em câmaras de germinação e coletadas aos 0, 2, 4, 5, 6, 8 e 12 dias após a germinação para as análises fisiológicas e bioquímicas. As sementes quiescentes apresentaram tegumento espesso e rugoso e embriões curvados. Os lipídios foram as reservas mais abundantes, correspondendo aproximadamente a 55% e 65% da massa seca dos cotilédones e eixo hipocótilo-radícula, respectivamente. Os açúcares solúveis e o amido foram as reservas menos abundantes, correspondendo aproximadamente a 2,2% da massa seca dos cotilédones, embora suas reservas tenham apresentado mudanças significativas durante a germinação. As proteínas solúveis corresponderam a 40% da massa seca dos cotilédones, que foi reduzida a 81% no período final de germinação comparado a sementes quiescentes. As sementes de *C. jamacaru* podem ser consideradas oleaginosas devido ao seu alto conteúdo de lipídios. Além disso, os lipídios foram as principais reservas mobilizadas durante a germinação porque seus níveis foram fortemente reduzidos durante esse período, enquanto que as proteínas foram a segunda reserva mais utilizada nesse processo.

Palavras-chaves: Cactaceae, carboidratos, citoquímica, lipídios, morfologia, proteínas.

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