DOI: 10.5433/1679-0359.2016v37n4p1733

Quantification of storage proteins during seed imbibition of native species from the brazilian Caatinga vegetation

Quantificação de proteínas de reserva durante a embebição de sementes de espécies nativas da Caatinga

Fabrício Francisco Santos da Silva[1]; Bárbara França Dantas[2*]

Abstract

Poincianella pyramidalis (Fabaceae), *Schinopsis brasiliensis* (Anacardiaceae) and *Sideroxylon obtusifolium* (Sapotaceae) are native species of the Caatinga vegetation from northeastern Brazil and have both biological importance and potential economic uses. Little is known about the water uptake and degradation of storage proteins during seed germination of these species. The aim of this study was to evaluate the imbibition and quantify the amount of storage proteins during seed germination of *P. pyramidalis*, *S. brasiliensis* and *S. obtusifolium*. Two lots of *S. obtusifolium* seeds with different vigour were used. Four replicates of 20 seeds of *P. pyramidalis, S. brasiliensis* and *S. obtusifolium*, were sown onto gerboxes with blotting paper soaked in distilled water and incubated during 72, 200 and 624 hours. Before and after imbibition seeds were weighed and frozen at until the sequential extraction and analysis of the seed storage proteins. Based on our results, we conclude that seed germination of *P. pyramidalis*, *S. brasiliensis* and *S. obtusifolium* has a well-defined triphasic imbibition. All storage proteins content of *P. pyramidalis* and *S. brasiliensis* seeds degraded along with the seed imbibition. Likewise, the content of albumins, globulins and glutelins decreased as *S. obtusifolium* seeds absorbed water.

Key words: Germination. *Poincianella pyramidalis*. Reserve mobilisation. *Schinopsis brasiliensis*. *Sideroxylon obtusifolium*. Tropical dry forest.

Resumo

Poincianella pyramidalis (Fabaceae), *Schinopsis brasiliensis* (Anacardiaceae) e *Sideroxylon obtusifolium* (Sapotaceae) são espécies nativas da Caatinga e que apresentam grande importância biológica e potencial econômico. Pouco se sabe sobre a absorção de água e degradação de proteínas de reserva durante a germinação dessas espécies. O objetivo deste trabalho foi avaliar a embebição e quantificação de proteínas de reserva durante o processo germinativo de sementes de *P. pyramidalis*, *S. brasiliensis* and *S. obtusifolium*. Dois lotes de sementes de *S. obtusifolium* de vigor diferente foram utilizados. Quatro repetições de 20 sementes de *P. pyramidalis, S. brasiliensis* e *S. obtusifolium*, foram colocados em gerbox com papel germitest umedecido com água destilada e incubados durante 72, 200 e 624 horas. Antes e após a embebição as sementes foram pesadas até a extração sequencial e quantificação de proteínas de reserva. A germinação das sementes de *P. pyramidalis*, *S. brasiliensis* e *S. obtusifolium* tem um padrão de embebição trifásico bem definido. Assim, podemos concluir que a germinação das sementes de *P. pyramidalis*, *S. brasiliensis* e *S. obtusifolium* apresenta modelo trifásico na embebição bem definido. O conteúdo de proteínas de reserva de *P. pyramidalis* e *S. brasiliensis* degrada na medida em que suas sementes embebem. Os teores de albuminas, globulinas e glutelinas reduzem na medida em que as sementes de *S. obtusifolium* embebem.

Palavras-chave: Floresta tropical seca. Germinação. *Poincianella pyramidalis*. Mobilização de reservas. *Schinopsis brasiliensis*. *Sideroxylon obtusifolium*.

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[1] Discente de Doutorado, Universidade Estadual de Feira de Santana, UEFS, Feira de Santana, BA, Brasil. E-mail: fabriciofrancisco2006@gmail.com

[2] Pesquisadora, Embrapa Semiárido, Petrolina, PE, Brasil. E-mail: barbara.dantas@embrapa.br

[*] Author for correspondence

Recebido para publicação 08/07/14 Aprovado em 04/05/16

Introduction

Caatinga, the most important ecosystem in semi-arid, northeastern Brazil, was reduced by less than 50% of its original area during the last 100 years. For several decades, it has been undergoing a strong anthropic pressure, mainly due to extractive activities. Its vegetation is a mosaic of different successional stages. This tropical dry forest can be considered a relic vegetation that presents floristic, physiognomic and ecological peculiarities (MENDES, 1997). With a desert physiognomy, the Caatinga has a low rainfall of approximately 250 to 800 mm annually. The temperature ranges between 24 and 26 °C and varies little throughout the year (MAIA, 2004).

Seeds of only 25% of the Caatinga species have been studied (MEIADO et al., 2012). Therefore, more basic seed biology studies are necessary for prioritising the conservation actions for this ecosystem. The basis for success in the propagation of forest species is the use of viable and vigorous seeds. Thus, studies on seed metabolic processes are of vital importance to understand germination (MATA-ATAÍDE et al., 2014).

Certain native species to the Caatinga, such as *Poincianella pyramidalis* (Tul.) L.P. Queiroz (Fabaceae), *Schinopsis brasiliensis* Engl. (Anacardiaceae) and *Sideroxylon obtusifolium* (Roem. & Schult.) T.D. Penn (Sapotaceae), have a significant biological importance and economic potential. *P. pyramidalis* is an autochoric, deciduous, pioneer and endemic species from the Caatinga that occurs in both degraded and well preserved environments. It adapts to different soils but especially to rocky soils. The flowering occurs between October and February, and the fructification occurs from December to June (MACIEL et al., 2012). Their trunks are often used as beehives. *P. pyramidalis* has forage, wood and medicinal potentials, and it can also be used for reforestation (CARVALHO, 2014).

S. obtusifolium is a semideciduous, native tree species to the Caatinga, and it is on the list of threatened species due to the lack of information about its biology according to the Brazilian Institute of Environment and Renewable Natural Resources (BRASIL, 2008). Its smooth ovoid fleshy drupes are dispersed by birds (SIQUEIRA FILHO et al., 2013). This species can be used for various purposes such as urban landscaping (DANTAS; SOUZA, 2004), recovery of riparian vegetation (FERRAZ et al., 2006; RIBEIRO-FILHO et al., 2009) and for medicinal uses (AGRA et al., 2007).

S. brasiliensis is, according to IBAMA, an endangered species from the Caatinga vegetation (BRASIL, 2008). The wood of this species is especially used for interior works, carpentry, milling, struts, pylons, poles, beams and structural railway sleepers (MAIA, 2004). It’s an anemochoric, deciduous, heliophytic and climax species that grows in calcareous soils or rocky outcrops, whose flowering occurrs between June and July and fructification between August and December (MACIEL et al., 2012). *S. brasiliensis* presents forage, wood and medicinal potential (CARVALHO, 2008).

The process of water imbibition by seeds follows a triphasic pattern. The reactivation of metabolism known as Phase I (PI) is characterised by a rapid water uptake that occurs as a result of the matric potential of various seed tissues; therefore, this phase does not depend on the seed to be alive or not. At this time, there is also a rapid increase in the respiration of seeds. Subsequently, when there is a reduction in the imbibition rate and respiratory intensity, Phase II (PII) initiates. In this phase, metabolic processes essential for the embryonic growth begin, and the enhanced germination is completed with the root protrusion. Then, Phase III (PIII) follows. Phase III presents an active absorption of water; the embryo has already started its growth, and thus, the formation and growth of new cells require water. PII and PIII are achieved only by living and non-dormant seeds. When germination begins, there is an activation of the protein synthesis and the formation of hydrolytic enzymes that promote the mobilisation of reserves, among which are the storage proteins. These proteins, in turn, form the basis of agriculture because of the variety of essential functions that they perform as food (CARVALHO; NAKAGAWA, 2012; BEWLEY et al., 2013).

For seedling recruitment, the mobilisation of storage proteins is crucial during imbibition and seed germination (TAN-WILSON, WILSON, 2012). Osborne (1924) classified the seed storage proteins based on their solubility in different solvents. Albumins are water-soluble proteins, globulins are soluble in saline solutions, prolamins are soluble in hydroalcoholic solutions, and glutelins are soluble in diluted acidic or basic solutions. Most studies related to seed storage proteins involve crops such as legumes, cucurbits, brassicas, among others (BEWLEY et al., 2013). According to Mata-Ataíde et al. (2014), information on the metabolic processes (physiological and biochemical) involved in germination are incipient for most native species, especially during water uptake by seeds. This study aimed at comparing the imbibition curves during the germination of *P. pyramidalis*, *S. brasiliensis* and *S. obtusifolium* as well as the quantification of their storage proteins during seed germination and water uptake by seeds.

Materials and Methods

We used seeds from three native species from the Caatinga, *Poincianella pyramidalis*, *Schinopsis brasiliensis* and *Sideroxylon obtusifolium*. The fruits of these three species were harvested from 10 parental plants in Juazeiro, Bahia State, Brazil (9° 33' 22" S, 40° 40' 0" W), in 2009. In the same year, fruits of *S. obtusifolium* were also harvested from 10 parental plants in Boa Vista, Paraíba State, Brazil (7° 15' 35" S, 36° 14' 26 ″ W). For this species, two lots were formed: lot A (harvested at Juazeiro-BA) and lot B (harvested at Boa Vista-PB). All the seeds were collected from adult plants in well preserved populations of the Caatinga area.

The seed water content was determined at 105 ± 3 °C for 24 h (BRASIL, 2009) using two samples of 25 seeds for each species. The results were expressed as the mean percentage of each sample.

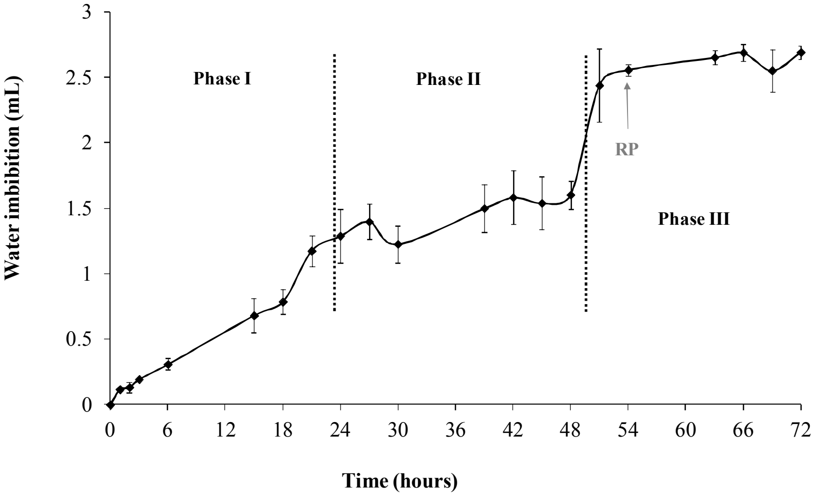
Seeds of *S. brasiliensis* and *S. obtusifolium* presented seed coat dormancy. To overcome this physiological barrier, it was necessary to perform a cut on the opposite side of the hilum before placing the seeds for soaking. To obtain an imbibition curve, the seeds were placed in a gerbox on two layers of Germitest paper, soaked with 15 mL of distilled water and left at 30 ºC with a photoperiod of 12 h. Each lot was divided into four replicates of 20 seeds and soaked for 72, 200 and 624 h for *P. pyramidalis*, *S. brasiliensis* and *S. obtusifolium*, respectively. The germination was evaluated at different time intervals for each species. The intervals for *P. pyramidalis* were one, two and three hours and, thereafter, every three hours for 72 hours. The intervals for *S. brasiliensis* were one, two, and four hours, every 4 h until a period of 96 h and every 8 h until a total of 200 h. The intervals for *S. obtusifolium* were eight, 18, 24 hours and, thereafter, every 24 h until 624 h. After the incubation intervals, the seedlings were frozen at –20 °C until the sequential extraction and analysis of the seed storage proteins, which occurred a few days later.

For the sequential extraction of storage proteins, seeds were homogenized in 10 mL of distilled water. After incubation at 30 °C for 30 minutes, samples were centrifuged at 3000*x*g for 20 minutes. The supernatant was recovered and the pellet resuspended with 5 mL distilled water. This procedure was repeated twice, i.e., incubation, centrifugation and supernatant recovery. Afterwards, we obtained the albumin fraction. The residue obtained after the extraction of the albumin fraction similarly underwent the extraction of the globulin fraction using NaCl (1%) as solvent. Likewise, for the extraction of prolamins and glutelins, we used ethanol (70%) and NaOH (0.1 mol L^{-1}), respectively (ARAGÃO et al., 2003). The proteins were quantified according to Bradford (1976) using bovine serum albumin (BSA) as a reference curve.

Results and Discussion

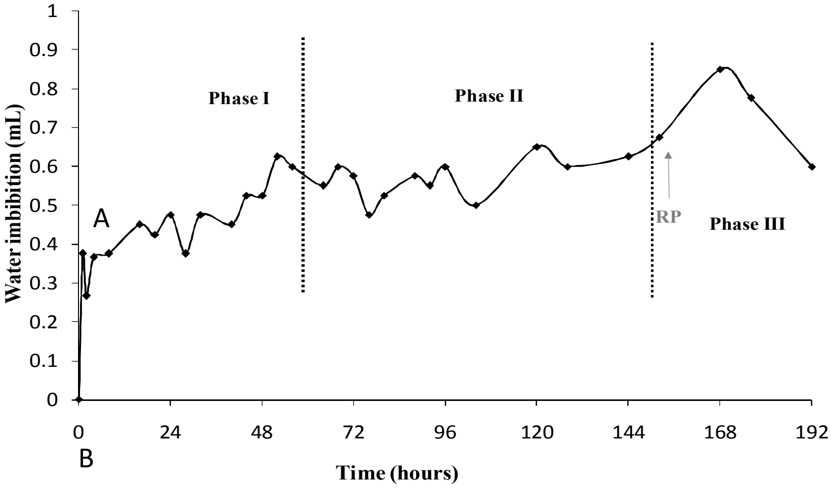
Seeds of *Poincianella pyramidalis* had an average of 9.46% moisture content before they were subjected to water imbibition. Its germination was adjusted to a triphasic model, in which phase I (PI) was completed after 24 h of imbibition, and phase III (PIII) began after 51 h imbibition. At 54 h of soaking, the root protrusion of 10% of seedlings was recorded. Seeds of *P. pyramidalis* showed a rapid absorption of water after 48 h of soaking and reached an increase of approximately 76% of the initial weight at root protrusion (Figure 1).

Figure 1. Water imbibition during the germination of *Poincianella pyramidalis* seeds (Tul.) L.P. Queiroz (Fabaceae) *RP= root protrusion.



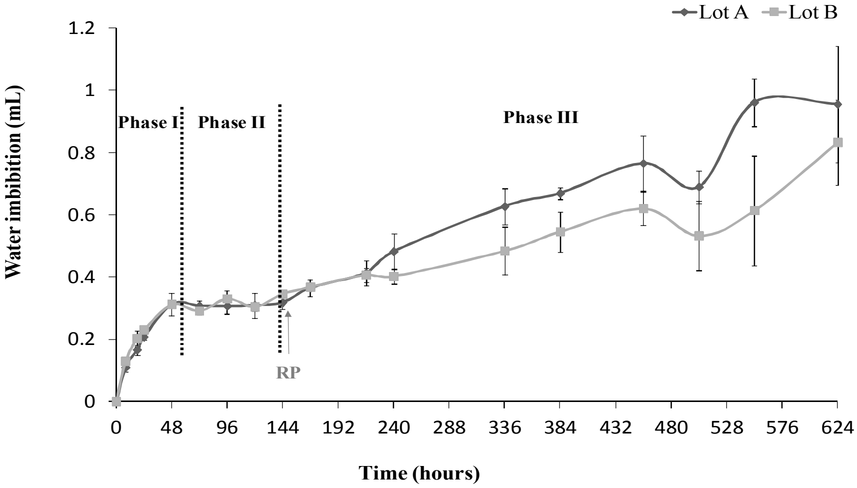
Seeds of *Schinopsis brasiliensis* had an average of 9% moisture content before imbibition. PI was characterised by a rapid water absorption until 48 h. PII or lag phase, a slower phase than the previous one, was initiated within 56 h of soaking and continued until 144 h. PIII began at 152 h when 12.5% of the seeds showed root protrusion and visible growth of the embryonic axis (Figure 2).

Figure 2. Water imbibition during the germination of *Schinopsis brasiliensis* seeds Engl. (Anacardiaceae). *RP= root protrusion.



Seeds of *Sideroxylon obtusifolium* from lots A and B had an average water content of 8.07% and 6.14, respectively, before the imbibition. Both lots had a triphasic pattern of imbibition during germination. PI was characterised by a rapid absorption of water that was completed in 48 h. PII was approximately three times slower than the previous phase. PIII started after 144h, when 25% and 40% of the seeds from lots A and B, respectively, showed visible growth of the embryo axis (Figure 3).

Figure 3. Water imbibition during the germination of *Sideroxylon obtusifolium* seeds (Roem. & Schult.) T.D.Penn. (Sapotaceae). *RP= root protrusion.



The duration of each imbibition phase depends on certain seed properties, among which we highlight the amount of hydratable compounds and the coat permeability to water and oxygen. Likewise, the environmental conditions where seeds are found are also important, such as the relative humidity, temperature, composition and characteristics of the substrate (GARCÍA-AGUSTÍN; PRIMO-MILLO, 1996). Water uptake, when dry quiescent or dormant seeds resume growth of embryonic axis, is a vital process for germination. This depends on three factors: permeability and seed coating, availability of water and chemical composition of seeds (COPELAND; MCDONALD, 2001a).In the current study, we observed that the three Caatinga tree species showed different imbibition patterns. Seeds of *P. pyramidalis*, whose germination occurred in less than three days, showed a fast weight gain in the first 24 h of water uptake. These findings corroborate those from other studies in which *Simarouba amara* Aubl. (Simaroubaceae), *Protium widgrenii* Engl. (Burseraceae), and *Mimosa verrucosa* Benth. (Fabaceae), which are fast germinating Cerrado and Caatinga species, respectively, showed a fast weight gain in PI (GOLDMAN et al., 1987; SEIFFERT, 2003; SILVA, 2011).

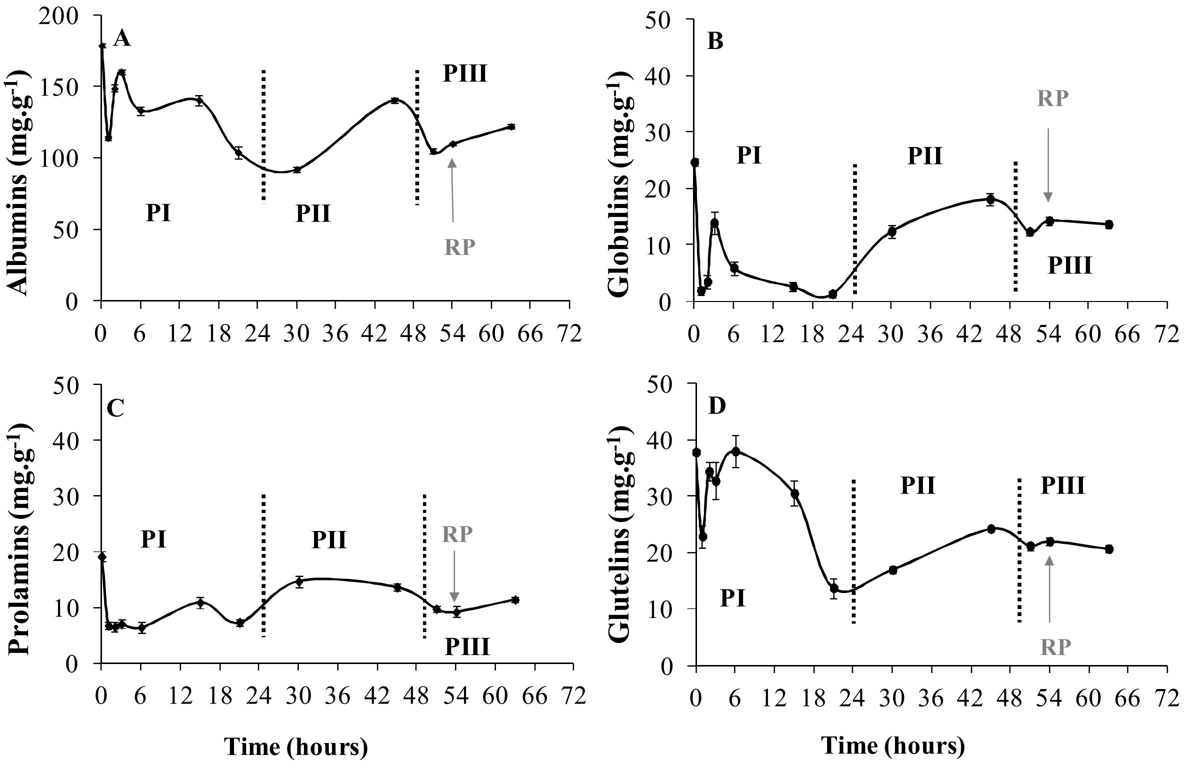
Seeds of *S. obtusifolium* and *S. brasiliensis* had a slower water uptake and a slower germination. Although seeds from both species took approximately 6 days to initiate the radicle protrusion, their imbibition patterns were completely different. *S. brasiliensis* seeds had a smooth imbibition curve, in which the first two imbibition phases were hardly distinguishable. In contrast, *S. obtusifolium* seeds showed well characterised imbibition phases during water uptake (Figures 2 and 3).

Seeds of *P. pyramidalis* and *S. obtusifolium* presented a fast water uptake in PI followed by a phase II, where water absorption by seeds is stabilized, reaching a plateau, which can be observed in. Seeds of *S. brasiliensis* seemed to uptake water in an ascending trend and with little, if any, change in the water uptake in PII. In addition, PIII was characterised by the radicle protrusion and the resumption of the water uptake. However, unlike PI, this phase showed an active water absorption (BEWLEY et al., 2013). *P. pyramidalis* seeds presented a sharp increase in the water uptake, while *S. obtusifolium* seeds showed a smoother increase. For *S. brasiliensis* seeds, PIII was distinguishable only by the onset of the radicle protrusion.

Knowledge of the chemical composition of seeds allows the identification of possible sources of raw materials for industrial purposes, basic sources of food and the identification of substances that influence the seed germination and seedling vigour. Most of the current information on the chemical composition of seeds is related to cultivated species. However, seeds of wild plants have received increasing attention because of the search for new sources of food and raw materials (COPELAND; MCDONALD, 2001b).

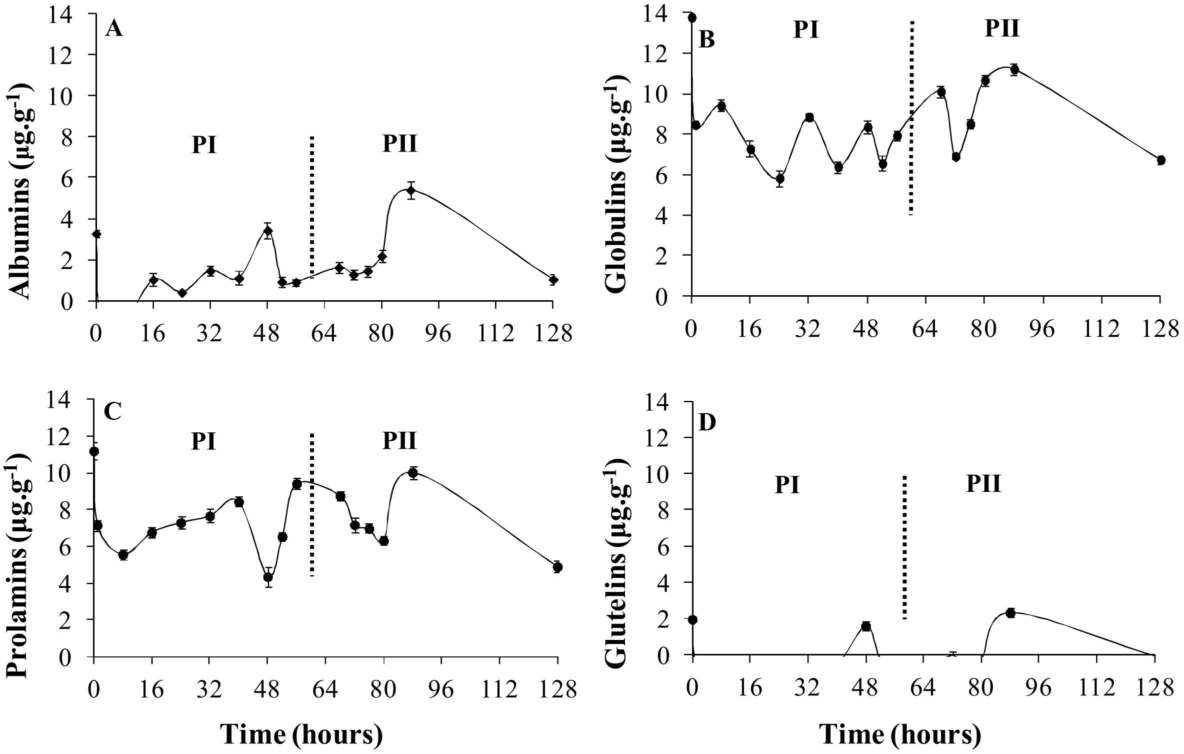
The content of albumin, globulin and glutelin varied during the first hours of imbibition in seeds of *P. pyramidalis* (Figures 4A, B and D). According to Bewley et al. (2013), in the first hours of imbibition, a large amount of exudates (sugars, ions, amino acids and proteins) are leached into the surrounding medium. The content of albumins, enzymes, in general, and other water-soluble proteins decreased during PI, and these substances were produced again during PII (Figures 4A). The same result was observed for the globulin content (Figures 4B). Moreover, the contents of prolamins and glutelins decreased after the onset of the water uptake and remained at approximately half of the initial value until the completion of germination (Figures 4C and D).

Figure 4. Content of storage proteins: albumins (**A**), globulins (**B**), prolamins (**C**) and glutelins (**D**); (mg of casein.g^{-1} fresh matter) in seeds of *Poincianella pyramidalis* (Tul.) L.P. Queiroz (Fabaceae). *RP= root protrusion; PI= Phase I, PII= Phase II, PIII= Phase III.



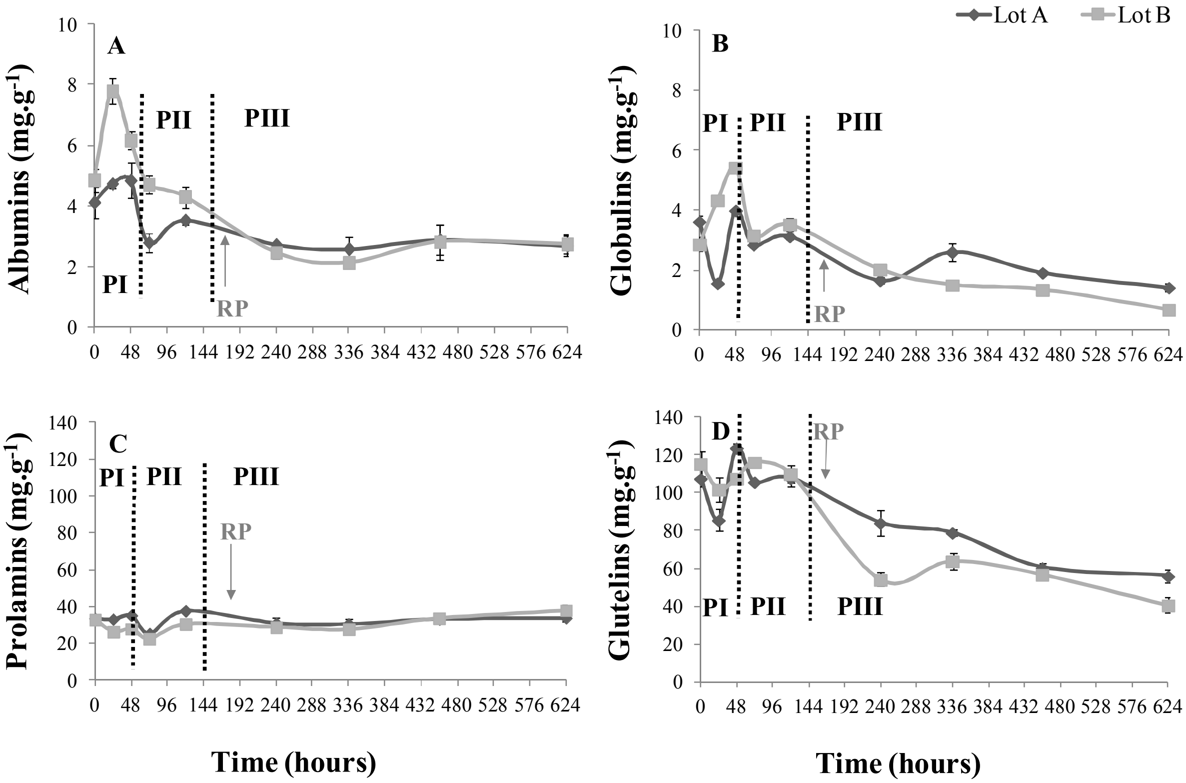
The content of seed storage proteins in *S. brasiliensis* showed a large variation during the first hours of imbibition (Figure 5). The initial levels of albumin, globulins and prolamins in the seeds showed a decrease at the beginning of the water uptake. These levels remained oscillating in the same proportion until the end of PII, i.e., 128h (Figures 5A, B, C). The seeds of *S. brasiliensis* showed low levels of glutelins (2 µg g^{-1}; Figure 5D). Among the seed storage proteins, globulins showed the highest concentrations in seeds, which ranged from 13.8 to 6.7 µg g^{-1} at the beginning and at the end of the germination process, respectively (Figure 5B).

Figure 5. Content of storage proteins: albumins (**A**), globulins (**B**), prolamins (**C**) and glutelins (**D**); (µg of casein.g^{-1} fresh matter) in seeds of *Schinopsis brasiliensis* Engl. (Anacardiaceae). *RP= root protrusion; PI= Phase I, PII= Phase II.



At the end of PI, the seeds of *S. obtusifolium* showed an increase in water-soluble proteins (e.g., the albumin fraction), which probably initiated the degradation of proteins. After 48 h of imbibition during PII, a decrease in the water uptake (Figure 3) was followed by a decrease in the levels of proteins, with the exception of prolamins (Figure 6 C). In PIII, the resumption of the water uptake was followed by a sharp drop in the levels of albumins, globulins and glutelins, which reflect a mobilisation of these proteins from the cotyledons to the embryonic axis (Figures 6 A, B and D).

Figure 6. Content of storage proteins: albumins (A), globulins (B), prolamins (C) and glutelins (D); (mg of casein.g^{-1} fresh matter) in seeds of *Sideroxylon obtusifolium* (Roem. & Schult.) T.D.Penn. (Sapotaceae). *RP= root protrusion; PI= Phase I, PII= Phase II, PIII= Phase III.



One of the characteristics of seed proteins is that while some of them are metabolically active, such as enzymes, most of them are metabolically inactive. The latter ones are called storage proteins and account for approximately 80% of all the proteins located in protein bodies within seeds (MAYER; POLJAKOFF-MAYBER, 1963). Proteins in seeds have the major function of nitrogen supply to the embryo and seedling in its early stage of development. The synthesis of these proteins is regulated during seed development and is tissue-specific, i.e., they are only synthesised in seed tissues and are not found in any other tissues except for lecithin (globulin), which can be found at the tips of growing roots (TAN-WILSON; WILSON, 2012). The synthesis of protein is extremely important during germination. Its onset after imbibition is independent of the RNA synthesis, while the DNA synthesis occurs only after the beginning of the embryonic axis growth (MUNTZ et al., 2001).

The seed total protein content gradually decreased over the imbibition period (MATA-ATAÍDE et al., 2013). Suda and Giorgini (2000) found that the albumin content of *Euphorbia heterophylla* L. (Euphorbiaceae) seeds remained constant until 72 h after the beginning of imbibition, and afterwards, it decreased; the glutelin content decreased after 48 h, and the globulin content steadily declined during imbibition. In the present study with seeds of *P. pyramidalis, S. obtusifolium* and *S. brasiliensis*, the increase in the initial albumin levels can be explained by the rehydration and biosynthesis of functional proteins (enzymes); however, unlike the seeds of *A. leiocarpa*, *P. widgrenii* and *E. heterophylla*, the albumins were metabolised during the germination process (PONTES et al., 2002; SEIFFERT, 2003; SUDA; GIORGINI 2000).

Albumins, globulins and glutelins have similar and specific metabolisation patterns during the *P. pyramidalis* and *S. obtusifolium* germination process. In *P. pyramidalis* seeds, the high protein level at the onset of imbibition declined until the beginning of PII, when it increased until the radicle protrusion; at this point, we observed a slight decrease. In *S. obtusifolium* seeds, we observed a constant decrease in the albumin, globulin and glutelin levels throughout germination. For these two species, the prolamin levels showed little, if any, variation during germination. Contrasting to *P. pyramidalis; S. obtusifolium* and *S. brasiliensis* seeds had a low protein content, which slightly increased until the end of PII, and then, it decreased again (Figures 4, 5 and 6).

The relative proportions of these storage protein fractions varied from one species to another and even between varieties of same species; however, this variation was independent from the environmental variation (MASOUMI et al., 2012). Hence, it can be concluded that the concentration of different storage proteins varies with species.

The cotyledons are important sources of nutrition for the embryo axis from the onset of germination until the seedlings become autotrophic. According to Kim et al. (2011), the temporal profiles of the protein expression in cotyledons dramatically changed during seed germination and seedling growth. Likewise, the mobilisation of storage protein subunits was differentially regulated during seed germination and seedling growth. The ability of cotyledons to support the seedling growth by transforming the seed storage reserves into soluble components used in the development of new tissues of the embryonic axis appears to be related to the seed vigour. More vigorous seeds have more accumulated reserves and are more efficient in their mobilisation. In a previous study, more vigorous seeds of *Avena strigosa* Schreb. (Poaceae) had higher initial levels of soluble proteins and showed a higher protein degradation during germination (SCHUCH et al., 1999). Similar results were found in the present study with seeds of *S. obtusifolium* in which the seeds from lot B were more vigorous than seeds from lot A (SILVA; DANTAS, 2013) and showed a higher degradation of proteins during germination.

Conclusions

Thus, we can conclude that the seed germination of *P. pyramidalis*, *S. brasiliensis* and *S. obtusifolium* has a well-defined triphasic imbibition. The storage proteins of *P. pyramidalis* and *S. brasiliensis* seeds were degraded along with the water uptake. Albumins, globulins and glutelins decrease as *S. obtusifolium* seeds absorbed water.

Acknowledgements

This study was financially supported by the National Counsel of Technological and Scientific Development (CNPq), Brazil.

The authors would like to thank Dr. Marcos Vinicius Meiado for his significant contribution to the paper.

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