

Tolerance to Desiccation of *Diospyros inconstans* Jacq. (Ebenaceae) Seeds at Different Maturity Stages

Edvânia da Silva Carvalho¹ 

Manuela Oliveira de Souza¹ 

Josival Santos Souza¹ 

Darlene Pereira da Silva¹ 

Jiovana Pereira Amorim Santos¹ 

Andrea Vita Reis Mendonça¹ 

¹Universidade Federal do Recôncavo da Bahia (UFBA), Cruz das Almas, BA, Brasil

Abstract

Classifying seeds in terms of desiccation tolerance is the first step in determining the potential and most appropriate conditions for storage. This study aimed to characterize the tolerance to desiccation of *Diospyros inconstans* seeds from fruits at different maturity stages. Germination tests were performed in a 3 x 6 factorial scheme, with seeds from fruits at three maturity stages (unripe, intermediate and ripe) and six moisture contents (initial, 20%, 15%, 10%, 5% and 2.5%). Accumulated germination was analyzed by the nonlinear models Gompertz and Logistic. The percentages of normal seedlings and unviable seeds were subjected to analyses of variance and regression. *Diospyros inconstans* seeds are tolerant to desiccation. The tolerance is higher in seeds from fruit with intermediate maturation than unripe and ripe fruits.

Keywords: 'fruta de jacu', germination, moisture content.

1. INTRODUCTION

Tolerance to desiccation consists in the capacity of some organisms to survive under extreme reduction in their moisture content, without undergoing lethal damage (Leprince & Buitink, 2010). Changes in cell membrane structure, accumulation of non-reducing sugars such as sucrose and oligosaccharides, and LEA protein synthesis are some of the physiological and biochemical modifications that promote desiccation tolerance in seeds (Black & Pritchard, 2002; Finch-Savage, 2003; Marcos-Filho, 2015; Bewley & Nonogaki, 2017; Colville, 2017).

The degree of tolerance to desiccation and to storage at low temperatures is the basis for the classification of seeds into the orthodox (tolerant of desiccation and storage at negative temperatures), intermediate (partially desiccant tolerant and sensitive to storage at negative temperatures) and recalcitrant categories (intolerant to desiccation and storage at negative temperatures) (Roberts, 1973; Ellis et al., 1990) and determines the potential and most appropriate conditions for storage.

Such information is of great interest for the management of *ex situ* conservation of plant species (Hong & Ellis, 1996).

Desiccation-tolerant seeds do not exhibit these characteristics at all stages of development (Ellis & Hong, 1992). When collected unripe or after maturity, these seeds may be sensitive to damage caused by desiccation (Hong & Ellis, 1996; Berjak & Pammenter, 2008), so the most indicated time to collect these seeds is when physiological maturity and tolerance are reached together (Ellis et al., 1987).

There is little information in the literature on desiccation tolerance of seeds of forest species, such as *Diospyros inconstans*, popularly known in Portuguese as 'fruta de jacu' or 'marmelinho'. This native species of shrubby to arboreal habit has wide distribution in the Brazilian territory, being found in the plant formations of almost all biomes (Wallnofer, 2015; Flora do Brasil, 2020). It has ornamental potential for use in urban forestry and is recommended for the composition of heterogeneous reforestation, due to the attractiveness of its fruits to the fauna (Cipriani et al., 2017).

In view of the above, the present study was carried out to characterize the tolerance to desiccation of *D. inconstans* seeds at different maturity stages.

2. MATERIAL AND METHODS

The experiment was conducted at the Laboratory of Ecology and Forest Restoration, of the Forestry Engineering

sector, of the Federal University of Recôncavo da Bahia, on the campus of Cruz das Almas, Bahia, Brazil.

Diospyros inconstans fruits at different maturity stages (Figure 1) were collected from 17 mother plants, in a region of pasture of the Environmental Protection Area of the *Pedra do Cavalo* pond, in the district of Ipuacú, Feira de Santana, Bahia, Brazil (12°21'38.0"S and 39°02'26.0"W) in November 2018.

Fruits	Seeds	Fruit color	Fruit maturity
		GREEN	UNRIPE
		GREENISH-BROWN	INTERMEDIATE
		PURPLE	RIPE

Figure 1. Visual aspect of fruits and seeds of *Diospyros inconstans* Jacq. at different maturity stages

The climate of the region is Asa, megathermal with rainy season in winter and dry season in summer (Santos et al., 2018). Average annual rainfall and temperature are 720.7 mm and 25.2 °C, respectively (Santos et al., 2018).

After collection, the fruits were taken to the laboratory and visually separated based on epicarp color into three maturity stages (Figure 1). The seeds were manually extracted from the fruits, washed in running water and arranged on trays for superficial drying for three days at room temperature (average of 25 °C), before installing the experiment. The moisture content of the seeds freshly collected and after surface drying (initial moisture content the experiment) was determined by the oven method at 105 ± 2 °C for 24 hours (Brasil, 2009).

Tolerance to desiccation was evaluated according to the methodology proposed by Hong & Ellis (1996). From the moisture content (%) and initial mass (g) of the seeds, the final mass (g) corresponding to the moisture contents of 20%, 15%, 10%, 5% and 2.5% was estimated for each maturity condition by the formula: mass of seed (g) at DMC% = [(100 - initial MC%) x initial seed mass (g)]/

(100 - DMC%), which DMC% is desired moisture content. To obtain these moisture contents, the seeds were dried with blue silica gel (1-3 mm) in 700-cm³ polystyrene boxes sealed with PVC film, at 20 °C ± 2 °C (adapted from Hong & Ellis, 1996). In the first 24 hours of drying, the seeds were weighed every three hours and, after this period, every day, until they reached the target mass, and then subjected to the germination test.

In the germination tests, the seeds were arranged in germitest paper rolls, moistened with distilled water in the proportion of 2.5 times the weight (g) of the dry paper (Brasil, 2009). The rolls were placed in transparent plastic bags and put in a B.O.D. germination chamber with constant temperature of 25 °C and photoperiod of 12 hours of light (Cipriani et al., 2017). The evaluations were performed daily, with counting of germinated seeds (minimum radicle length of 2 mm), dead seeds, hard seeds, normal seedlings and abnormal seedlings (Brasil, 2009) for 90 days.

The experimental design was completely randomized, in a 3 x 6 factorial scheme, with three maturity stages

(unripe, intermediate and ripe) and six moisture contents (initial, 20%, 15%, 10%, 5% and 2.5%). Each treatment comprised four replicates of 25 seeds.

At the end of the experiment, the viability of hard seeds was confirmed by the 0.5% tetrazolium test, with seed exposure time of two hours, at a temperature of 30 °C (Silva et al., 2016).

Germination curves were analyzed by fitting the nonlinear models Gompertz: $Y = \Theta_a \cdot \exp[-\exp(\Theta_b \cdot (x - \Theta_c))]$ (Souza et al., 2014) and Logistic: $Y = \Theta_a / (1 + \exp(-(x - \Theta_i) / \Theta_s))$ (Zeviani et al., 2013), where Y = germination accumulated in time t; Θ_a = asymptotic value, representing the maximum percentage of accumulated germination; exp = base of the Napierian logarithm; x = value of the independent variable (time required for germination to occur), given in days; Θ_b = relative growth at the inflection point; Θ_c = time required for 37% of the seeds to germinate; Θ_i = time required for 50% of the seeds to germinate; Θ_s = parameter related to the function rate, without biological interpretation.

The parameters of the models were estimated by the method of least squares and Gauss Newton using the nls function in R software version 3.1.3 (R Development Core Team, 2019). The most adequate model to describe the germination curves was selected based on the Akaike information criterion (AIC) (Akaike, 1974) and Bayesian

information criterion (BIC) (Schwarz, 1978), and the best fit equations were those with the lowest values of these criteria (Emiliano et al., 2014).

Data relative to the percentage of normal seedlings and unviable seeds (dead seeds + abnormal seedlings) were subjected to analyses of variance and regression in R software version 3.1.3 (R Development Core Team, 2019).

3. RESULTS AND DISCUSSION

The moisture content of the freshly collected seeds was 45.2% in the seeds of unripe fruits, 46.3% in the seeds of intermediate fruits and 41% in the seeds of ripe fruits. This moisture content is similar to that obtained for the seeds of ripe fruits of the species *Diospyros brasiliensis* (43.3%) e *Diospyros hispida* (49.5%) in the study by Mayrink et al. (2016).

The drying time for *D. inconstans* seeds is shown in Table 1. Unripe seeds took the longest time to reach the moisture content of 2.5% (1,248 hours). Intermediate seeds were the slowest ones to reach moisture contents of 20% (63 hours), 15% (97 hours) and 10% (352 hours). The drying of ripe seeds was the fastest for all final moisture contents (Table 1).

Table 1. Drying time (hours) for seeds from unripe, intermediate and ripe fruits of *Diospyros inconstans* Jacq. to reach the target moisture contents.

Maturity	Initial moisture content (%)	Final moisture content (%)	Time (hours)
Unripe	25.8	20	23
		15	24
		10	262
		5	743
		2.5	1.248
Intermediate	32.8	20	63
		15	93
		10	35
		5	744
		2.5	784
Ripe	20.9	20	1
		15	18
		10	64
		5	262
		2.5	352

The estimated parameters and selection criteria of the Gompertz and Logistic models for the germination of *D. inconstans* seeds are presented in Table 2. In general, the Gompertz model resulted in better fits for all maturity stages tested.

The accumulated germination (Θ_a) was above 90% for the seeds at the three maturity stages evaluated, regardless of the moisture content, except for unripe seeds at 2.5%, for which the estimated accumulated germination was 85% (Table 2). Although *D. inconstans* seeds are dispersed with high moisture content, a common characteristic in recalcitrant species that do not tolerate desiccation, the maintenance of a high percentage of germination in seeds that had their moisture content reduced to 5% or less, demonstrates the capacity of tolerance to desiccation and indicates intermediate or orthodox behavior regarding storage (Hong & Ellis, 1996). Seeds of *Diospyros brasiliensis* and *Diospyros hispida*, dispersed with moisture content above 40%, showed 60% and 63% germination when desiccated to 5% moisture content and were classified as intermediate, after storage for three months at -18 °C (Mayrinck et al., 2016). Similar behavior was observed by Pritchard et al. (2004) and Daws et al. (2006) for several tropical forest species and led these authors to conclude that seed moisture content at shedding is not a good predictor of desiccation tolerance.

Seed desiccation tolerance is commonly found in pioneer species that grow in seasonal and/or arid environments, while sensitive to desiccation seeds are more common in non-pioneer species and humid environments and little seasonal (Twelddde, 2003). *Diospyros inconstans* is a demanding light climax species (Callegaro et al., 2014) with predominant occurrence in seasonally dry tropical forests (Wallnofer, 2015). Despite being a species classified as climax, in the region of Feira de Santana where the seeds of the present study were collected, this species occurs in clearings in pasture areas and behaves like a pioneer. In this region, precipitation is seasonal and the temperature varies throughout the year (Santos et al., 2018). From an ecological point of view, desiccation tolerance represents a defense strategy to delay germination until conditions are suitable for efficient seedling establishment (Colville, 2017). Thus, the presence of tolerance to desiccation in

seeds of this population may contribute to keeping the seeds viable in the soil bank during the dry season, until the arrival of the rainy season and milder temperatures.

Seeds subjected to artificial drying tolerate desiccation as long as they have already acquired this characteristic in the field (Ellis et al., 1987; Kerbauy, 2008). For many species, tolerance to desiccation is acquired in the middle of the maturation phase (Hong & Ellis, 1992; Buitink & Leprince, 2018). This condition prepares the seed to survive the rapid reduction of moisture content during drying. With the reduction in moisture content, the seed becomes quiescent and tolerant to various environmental stresses, including high temperature and low atmospheric vapor pressure (Buitink & Leprince, 2018). Thus, the tolerance to desiccation represents a survival strategy to delay germination until the conditions are adequate for the efficient establishment of seedlings (Barbedo & Marcos-Filho, 1998; Angelovicki, 2010).

Seed germination speed is one of the criteria associated with the vigor of seed lots (Krzyanoswski & Neto, 2001), lots that germinate faster are considered more vigorous. The parameter Θ_c of the Gompertz model is one of the tools that can be used to compare the physiological potential between seed lots (Souza et al., 2014). According to the model, lower values of this parameter indicate that the accumulated germination of 37% will be reached faster and, consequently, greater the vigor of the seed lot.

In unripe seeds, the time for germination to reach 37% ranged from 14.4 to 18.1 days among the different levels of drying, with the shortest time observed for seeds desiccated to 5% (Table 2). For seeds from intermediate fruits, the time to reach this same germination percentage was shorter and ranged from 13.1 to 15.9, with the shortest time reached at 2.5% moisture content (Table 2). For seeds from ripe fruits, the time varied from 14.5 and 16.9 days, and the shortest time was also observed at 2.5% (Table 2). These results suggest that seeds from intermediate fruit were more vigorous.

The percentage of normal seedlings was influenced by the desiccation in seeds from unripe fruits. At the highest moisture contents, the percentage of normal seedlings was higher (p-value = 0.022) and, consequently, the percentage of unviable seeds decreased (p-value = 0.013) (Figure 2).

Table 2. Estimates of the parameters of Gompertz model (Θ_a, Θ_b and Θ_c) and logistic model (Θ_a, Θ_i and Θ_j) and of the selection criteria (R^2 , AIC and BIC) fitted to the data of germination of *Diospyros inconstans* Jacq. seeds from unripe, intermediate and ripe fruits.

Unripe																		
Gompertz																		
%Moisture of seeds																		
Parameters	25.8% (Initial)			20.0%			15.0%			10.0%			5.0%			2.5%		
	Value	LL	UL	Value	LL	UL	Value	LL	UL	Value	LL	UL	Value	LL	UL	Value	LL	UL
Θ_a	97.0	96.3	97.5	97.0	96.6	97.4	91.3	90.3	92.4	96.5	95.7	97.2	97.2	96.6	97.8	84.9	84.1	85.6
Θ_b	-0.22	-0.24	-0.21	-0.28	-0.29	-0.27	-0.18	-0.19	-0.16	-0.26	-0.28	-0.24	-0.23	-0.24	-0.21	-0.27	-0.29	-0.24
Θ_c	16.0	15.6	16.0	15.1	15.0	15.2	18.1	17.7	18.5	15.1	14.9	15.4	14.4	14.1	14.7	17.4	17.2	17.7
S%	4.8	-	-	3.3	-	-	9.5	-	-	6.8	-	-	5.0	-	-	7.4	-	-
R^2	0.98	-	-	0.98	-	-	0.91	-	-	0.94	-	-	0.92	-	-	0.89	-	-
AIC	1916.6	-	-	1707.5	-	-	2256.9	-	-	2127.9	-	-	1892.9	-	-	2015.4	-	-
BIC	1931.8	-	-	1722.8	-	-	2272.1	-	-	2143.1	-	-	1907.9	-	-	2030.1	-	-
Logistic																		
%Moisture of seeds																		
Parameters	25.8% (Initial)			20.0%			15.0%			10.0%			5.0%			2.5%		
	Value	LL	UL	Value	LL	UL	Value	LL	UL	Value	LL	UL	Value	LL	UL	Value	LL	UL
Θ_a	96.6	96.1	97.1	96.7	96.4	97.1	90.8	89.8	91.8	96.0	95.3	96.8	96.8	96.2	97.4	84.6	83.9	85.3
Θ_i	18.1	17.9	18.3	16.8	16.6	16.9	20.6	20.1	21.0	16.8	16.5	17.1	16.4	16.1	16.6	19.1	18.8	19.4
Θ_j	3.1	2.9	3.2	2.5	2.4	2.6	4.0	3.6	4.4	2.6	2.4	2.9	3.1	2.8	3.3	2.6	2.3	2.9
S	4.2	-	-	3.1	-	-	7.7	-	-	6.3	-	-	5.2	-	-	5.8	-	-
S%	5.0	-	-	3.3	-	-	9.7	-	-	7.2	-	-	5.8	-	-	7.4	-	-
R^2	0.98	-	-	0.98	-	-	0.91	-	-	0.93	-	-	0.92	-	-	0.90	-	-
AIC	1949.5	-	-	1703.3	-	-	2275.8	-	-	2164.3	-	-	1993.8	-	-	2013.6	-	-
BIC	1964.8	-	-	1718.6	-	-	2290.9	-	-	2179.5	-	-	2009.0	-	-	2028.7	-	-
Intermediate																		
Gompertz																		
%Moisture of seeds																		
Parameters	32.8% (Initial)			20.0%			15.0%			10.0%			5.0%			2.5%		
	Value	LL	UL	Value	LL	UL	Value	LL	UL	Value	LL	UL	Value	LL	UL	Value	LL	UL
Θ_a	93.9	93.1	94.7	96.2	95.4	97.0	96.4	95.7	97.1	99.0	98.5	99.5	95.6	95.0	96.2	97.8	97.3	98.3
Θ_b	-0.21	-0.23	-0.19	-0.24	-0.26	-0.22	-0.26	-0.28	-0.24	-0.31	-0.33	-0.30	-0.29	-0.32	-0.27	-0.25	-0.26	-0.23
Θ_c	15.4	15.1	15.7	15.1	14.9	15.4	15.9	15.7	16.2	14.1	14.0	14.3	14.4	14.2	14.7	13.1	12.9	13.3
S%	7.6	-	-	7.3	-	-	6.7	-	-	4.5	-	-	5.4	-	-	4.4	-	-
R^2	0.9	-	-	0.9	-	-	0.9	-	-	1.0	-	-	0.9	-	-	0.9	-	-
AIC	2177.2	-	-	2177.7	-	-	2090.7	-	-	1868.9	-	-	1950.7	-	-	1855.7	-	-
BIC	2192.4	-	-	2192.3	-	-	2105.9	-	-	1884.1	-	-	1965.8	-	-	1870.9	-	-

Continue...

Table 2. Continued...

Logistic																		
%Moisture of seeds																		
Parameters	32.8% (Initial)			20.0%			15.0%			10.0%			5.0%			2.5%		
	Value	LL	UL	Value	LL	UL	Value	LL	UL	Value	LL	UL	Value	LL	UL	Value	LL	UL
Θ_a	93.5	92.7	94.4	95.9	95.1	96.7	96.1	95.5	96.8	98.8	98.3	99.3	95.4	94.8	96.0	97.5	97.0	98.0
Θ_b	17.5	17.1	17.8	17.0	16.7	17.3	17.7	17.5	18.0	15.5	15.4	15.7	15.9	15.7	16.1	14.7	14.5	14.9
Θ_c	3.4	3.1	3.7	2.9	2.7	3.2	2.7	2.4	2.9	2.3	2.1	2.5	2.6	2.4	2.8	3.1	2.9	3.3
S%	7.9	-	-	7.6	-	-	6.5	-	-	4.7	-	-	5.8	-	-	4.6	-	-
R ²	0.9	-	-	0.9	-	-	0.9	-	-	1.0	-	-	0.9	-	-	0.9	-	-
AIC	2203.7	-	-	2203.0	-	-	2078.0	-	-	1899.5	-	-	1994.0	-	-	1878.4	-	-
BIC	2219.0	-	-	2218.2	-	-	2093.2	-	-	1914.6	-	-	2009.1	-	-	1893.6	-	-
Ripe																		
Gompertz																		
%Moisture of seeds																		
Parameters	25.8% (Initial)			20.0%			15.0%			10.0%			5.0%			2.5%		
	Value	LL	UL	Value	LL	UL	Value	LL	UL	Value	LL	UL	Value	LL	UL	Value	LL	UL
Θ_a	93.5	92.9	94.2	94.9	94.1	95.6	97.8	97.3	98.2	99.1	98.7	99.6	91.4	90.9	91.8	96.7	96.2	97.2
Θ_b	-0.24	-0.25	-0.22	-0.17	-0.18	-0.16	-0.34	-0.36	-0.32	-0.29	-0.31	-0.28	-0.31	-0.32	-0.29	-0.25	-0.26	-0.23
Θ_c	15.4	15.2	15.6	16.9	16.6	17.2	14.7	14.6	14.9	15.0	14.8	15.1	15.0	14.9	15.2	14.5	14.4	14.7
S%	5.9	-	-	6.5	-	-	4.3	-	-	3.8	-	-	4.3	-	-	4.5	-	-
R ²	0.95	-	-	0.96	-	-	0.96	-	-	0.97	-	-	0.97	-	-	0.96	-	-
AIC	1988.5	-	-	2058.2	-	-	1829.6	-	-	1754.3	-	-	1787.6	-	-	1849.1	-	-
BIC	2003.7	-	-	2073.5	-	-	1844.8	-	-	1769.5	-	-	1802.8	-	-	1864.3	-	-
Logistic																		
%Moisture of seeds																		
Parameters	25.8% (Initial)			20.0%			15.0%			10.0%			5.0%			2.5%		
	Value	LL	UL	Value	LL	UL	Value	LL	UL	Value	LL	UL	Value	LL	UL	Value	LL	UL
Θ_a	93.2	92.6	93.9	94.4	3.6	95.1	97.5	97.0	98.0	98.9	98.5	99.4	91.1	90.6	91.5	96.4	95.9	97.0
Θ_b	17.3	17.0	17.5	19.4	19.1	19.7	16.0	15.9	16.2	16.5	16.4	16.7	16.5	16.3	16.6	16.3	16.1	16.5
Θ_c	3.0	2.8	3.3	4.1	3.8	4.4	2.0	1.9	2.2	2.5	2.3	2.6	2.2	2.1	2.4	3.0	2.8	3.2
S%	6.2	-	-	7.0	-	-	4.7	-	-	4.2	-	-	4.5	-	-	4.8	-	-
R ²	0.93	-	-	0.95	-	-	0.96	-	-	0.97	-	-	0.97	-	-	0.95	-	-
AIC	2022.5	-	-	2111.5	-	-	1881.9	-	-	1810.2	-	-	1828.7	-	-	1888.1	-	-
BIC	2037.7	-	-	2126.8	-	-	1897.1	-	-	1825.4	-	-	1843.7	-	-	1903.3	-	-

Where: Θ_a = maximum percentage of accumulated germination; Θ_b = relative growth at the inflection point; Θ_c = time required for 37% of the seeds to germinate; Θ = time required for 50% of the seeds to germinate; Θ = parameter related to the function rate, without biological interpretation; S% = standard deviation in percentage; R² = coefficient of determination; AIC= Akaike information criterion; BIC= Schwarz's Bayesian information criterion. LL = lower limit; UL = upper limit.

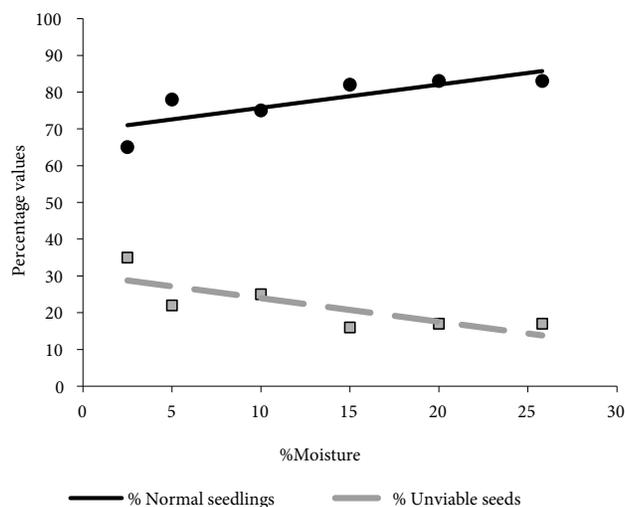


Figure 2. Percentage of normal seedlings (%NS = $0.6314x + 69.427$; $R^2 = 0.66$) and unviable seeds (%US = $-0.4688x + 27.028$; $R^2 = 0.63$) as a function the moisture content in seeds from unripe fruits of *Diospyros inconstans* Jacq. Where: R^2 = coefficient of determination.

For seeds from fruits at intermediate maturity stage, the percentage of normal seedlings (p-value = 0.11) and the percentage of unviable seeds (p-value = 0.10) were not influenced by desiccation. The average percentage of normal seedling was around 80% for all moisture contents tested.

For seeds from ripe fruits, the percentage of normal seedlings (p-value = 0.02) and the percentage of unviable seeds (p-value = 0.02) responded to the moisture content of the seeds, according to fourth-degree equations (Figure 3). The highest percentage of normal seedlings occurred at the moisture contents 11%. At moisture content of 5%, the lowest percentage of normal seedlings was obtained (72.6).

The ability to form normal seedlings is one of the indicators of seed physiological maturity (Ellis et al., 1987). Therefore, knowing that tolerance to desiccation is gradually acquired throughout development, the reduction in the ability of unripe seeds to form normal seedlings when desiccated to 10% indicates that at this stage, the seeds have not fully reached desiccation tolerance. Several studies report that seeds that are tolerant to desiccation, when collected early, are sensitive to this condition (Ellis et al., 1987; Ellis et al., 1991; Sun & Leopold, 1993; Teixeira et al., 2018).

In seeds from intermediate fruits, the maintenance of a high percentage of normal seedling formation up to the moisture level of 2.5% demonstrates that at this stage the seeds already have full tolerance to desiccation. Hong et al. (1991) observed tolerance to desiccation in seeds from *Coffea arabica* L. fruits at intermediate stage of maturity.

The higher sensitivity of ripe seeds to desiccation may have resulted from their longer time of exposure to the field conditions. According to Hong & Ellis (1996), seeds obtained in stressful environments, such as those with high temperatures, when collected after maturity, can also be sensitive to desiccation damage.

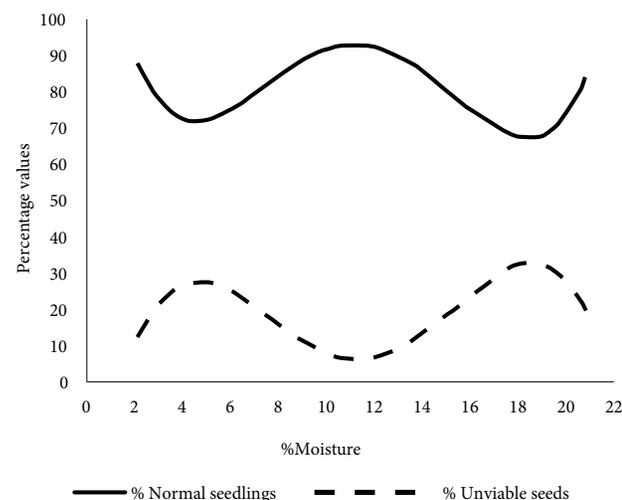


Figure 3. Percentage of normal seedlings (%NS = $0.0106x^4 - 0.4894x^3 + 7.5368x^2 - 43.537x + 156.37$; $R^2 = 0.88$) and % Unviable seeds (%US = $-0.0106x^4 + 0.4894x^3 - 7.5368x^2 + 43.537x - 56.372$; $R^2 = 0.89$) as a function of the moisture content in seeds from ripe fruits of *Diospyros inconstans* Jacq. Where: R^2 = coefficient of determination.

4. CONCLUSIONS

Diospyros inconstans seeds tolerate desiccation up to 2.5% moisture content. Tolerance is higher in fruit seeds with intermediate maturation than in green and ripe fruits.

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CORRESPONDENCE TO

Edvânia da Silva Carvalho

Universidade Federal do Recôncavo da Bahia, Rua Rui Barbosa, 710, 44380000 Cruz das Almas, BA, Brasil

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