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Variations in desiccation tolerance in seeds of *Eugenia pyriformis*: dispersal at different stages of maturation[1]

Variações da tolerância à dessecação em sementes de *Eugenia pyriformis*: dispersão em diferentes estádios de maturação

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ABSTRACT - *Eugenia pyriformis* Cambess., known locally as *uvaieira*, a species of fruit-bearing tree with both pharmacological and gastronomic potential, has seeds which are sensitive to desiccation. The aim of this study was to analyse whether the degree of tolerance to desiccation of uvaieira seeds depends on the stage of maturation of the seeds at shedding. This, in turn, depends on the environmental conditions in which the seeds develop, including the accumulation of degree-days and rainfall in the period. Seeds were collected from the ripe fruit of parent plants located in the states of São Paulo and Minas Gerais, Brazil, submitted to drying and analysed for water content and germination. A completely randomised design was used in a 20 x 3 factorial scheme (source of material x level of drying). The degree of desiccation tolerance differs between region and period of collection, even for the same parent plant when the seeds are collected in different years. The water and thermal conditions of the environment during seed development modify the maturation cycle, the physiological quality and the acquisition of desiccation tolerance. In *uvaieira* seeds, desiccation tolerance depends on the physiological maturity of the seeds at the time of dispersal, which is associated with the environmental conditions.

Key words: Myrtaceae. Uvaieira. Degree days. Physiological quality. Drying.

RESUMO - A uvaieira (*Eugenia pyriformis* Cambess.), espécie arbórea e frutífera, com potencial farmacológico e gastronômico, apresenta sementes sensíveis à dessecação. O objetivo deste trabalho foi analisar se o grau de tolerância à dessecação de sementes de uvaieira depende do grau de maturidade das sementes no momento de sua dispersão. Este, por sua vez, depende das condições ambientais nas quais as sementes se desenvolvem, incluindo-se o acúmulo de graus-dia e a chuva acumulada no período. As sementes foram coletadas de frutos maduros de matrizes localizadas em São Paulo e Minas Gerais, submetidas à secagem e analisadas quanto ao teor de água e germinação. Utilizou-se o delineamento inteiramente casualizado, em esquema fatorial 20 x 3 (origem do material x níveis de secagem). O grau de tolerância à dessecação difere entre as regiões e épocas de coleta, inclusive dentro da mesma matriz, quando as sementes são coletadas em anos distintos. As condições hídricas e térmicas do ambiente, durante o desenvolvimento das sementes, condicionam o ciclo de maturação, a qualidade fisiológica e a aquisição da tolerância à dessecação. A tolerância à dessecação de sementes de uvaieira depende da maturidade fisiológica das sementes no momento de sua dispersão, a qual está associada às condições ambientais.

Palavras-chave: Myrtaceae. Uvaieira. Graus-dia. Qualidade fisiológica. Secagem.

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INTRODUCTION

Known locally as *uvaieira*, *Eugenia pyriformis* Cambess. is a species of fruit-bearing tree with great gastronomic, industrial and medicinal potential; besides being appreciated for its fresh fruit, it is also widely used in agroforestry systems (LAMARCA *et al*., 2013b). It belongs to the family Myrtaceae, and occurs in tropical or subtropical regions of Argentina, Paraguay and Brazil. The seeds are intolerant to desiccation and short-term storage (DELGADO; BARBEDO, 2012; SCALON *et al*., 2012), with extensive germination plasticity (AMADOR; BARBEDO, 2011).

Seeds are crucial to most processes of crop production, both for their use directly in the field and in the production of seedlings. The vast majority have an exceptional capacity for storage, maintaining germination potential for several years and allowing their use at completely different times and places from those where they were produced. However, there is a group of seeds that, being sensitive to desiccation, can only be stored for extremely short periods, often preventing their use in production systems (ARAÚJO *et al.*, 2008; HAY; PROBERT, 2013).

Sensitivity to desiccation varies between species, ranging from the more sensitive to the more tolerant (PEREZ; HILL; WALTERS, 2012), with variations occurring within a single species, and depending on the environmental conditions in which the seeds are formed (DAWS *et al.*, 2006; DUSSERT *et al*., 2000; JOËT; OURCIVAL; DUSSERT, 2013; LAMARCA *et al*., 2013a.). This led to the assumption that changes in the desiccation tolerance of seeds may be due to variations in their degree of physiological maturity when dispersed (BARBEDO; CENTENO; FIGUEIREDO-RIBEIRO, 2013).

Development of the seed, which takes place from fertilisation of the ovule to maturity, is divided into three stages, stage I being marked by cell division and expansion, phase II by the accumulation of reserves and a progressive increase in dry matter, and phase III by drying at maturation, or desiccation. The transition from the second to the third stage roughly coincides with the development of desiccation tolerance (ANGELOVICI *et al*., 2010).

Physiological evidence suggests that recalcitrant seeds do not complete the second phase; with fruit abscission occurring before development is complete (DAWS *et al*., 2004; DELGADO; BARBEDO, 2012). However, studies with desiccation-intolerant seeds (*Aesculus hippocastanum* and *Acer pseudoplatanus*), collected at different locations in Europe, have shown that variations in air temperature, represented by the concept of degree-days, influence the physiological maturity of seeds, affecting acquisition of desiccation tolerance (DAWS *et al*., 2004, 2006). In seeds of *Euterpe edulis* and *Tapirira obtuse*, for example, variations have been seen in desiccation tolerance and storage, depending on the environmental conditions in which the seeds were formed (MARTINS *et al.*, 2009; PEREIRA *et al*., 2012).

As it has seeds that are desiccation-intolerant and of short-term storage, and as productive individuals are found over a wide range of latitudes and altitudes, the uvaieira is an interesting model for the physiological study of seeds. Analysis of the germination behaviour of seeds from different regions can provide important information about the degree of environmental interference on the characteristics of formed seeds. In this study, the hypothesis was considered and tested, that the level of desiccation tolerance in seeds of the uvaieira depends on the degree of maturity reached by the seeds at the time of dispersal. This in turn depends on the environmental conditions in which the seeds develop, including the accumulation of degree-days, and accumulated rainfall for the period.

MATERIAL AND METHODS

Seeds of the uvaieira were obtained from mature, recently dispersed fruits, based on information on maturation and dispersal from Lamarca *et al*. (2013a) and Teixeira and Barbedo (2012). The fruits came from 11 different regions, as described in Table 1. Codes were allocated for region, and period or altitude, as follows: Lavras (LAV), São Bento do Sapucaí (SBS), Campinas (CAM) São Paulo (SPA), Ibiúna (IBI), São Bernardo do Campo (SBC), Ribeirão Preto (RIB), Jumirim (JUM), Santo André (SAA), Itaberá (ITA) and Pariquera-Açu (PAR). In five of these regions (LAV, CAM, SPA, IBI, and SBC), seeds were obtained in different years from the same parent plants, identified by number (1, 2 and 3), and in SBS from parent plants at three different altitudes, also identified by number. Each collection, considering region and period, or region and altitude, was regarded as a different source of seed, also referred to as source of material.

During the period of maximum flowering for the species, the inflorescences of those trees with most flowers at anthesis were marked at each source. At the end of the period of fruit development and ripening, the mature, recently dispersed fruits were collected (up to 24 hours after dispersal), from which the seeds were manually extracted (TEIXEIRA; BARBEDO, 2012) and stored in a cold room at 7 °C until the start of the experiments

Table 1 - Source of uvaieira seeds (*Eugenia pyriformis* Cambess.), maturation cycle (time between flowering and dispersal), meteorological data of the collection sites during the cycle of seed formation, and physical characteristics of the collected material

Source of seed	Maturation cycle (total of cycle)	Min- Max (°C)	DD (°C day)	Rainfall (mm)	WC (g g^{-1})	DM (g $seed^{-1}$)
LAV1 - Lavras, MG (21°13' S, 44°58' W, 949 m; Cwa)	09/08/09 - 23/09/09 (45 days)	15 – 27	495	175.4	1.53 ± 0.10	0.59 ± 0.03
LAV2 - Lavras, MG (21°13' S, 44°58' W, 949 m; Cwa)	15/08/10 - 25/09/10 (41 days)	12 – 28	417	24.2	1.12 ± 0.06	0.80 ± 0.08
SBS1 - São Bento do Sapucaí, SP (22°41' S, 45°43' W, 884 m; Cfb)	24/08/10 - 07/10/10 (44 days)	12 – 27	426	177.1	1.87 ± 0.24	0.37 ± 0.06
SBS2 - São Bento do Sapucaí, SP (22°41' S, 45°45' W, 1022 m; Cfb)	26/08/10 - 15/10/10 (50 days)	11 – 26	448	177.1	1.34 ± 0.11	0.97 ± 0.07
SBS3 - São Bento do Sapucaí, SP (22°41' S, 45°46' W, 1121 m; Cfb)	26/08/10 - 21/10/10 (56 days)	11 – 26	472	252.4	1.12 ± 0.04	1.27 ± 0.04
CAM1 - Campinas, SP (22°52' S, 47°04' W, 645 m; Cwa)	01/08/09 - 18/09/09 (48 days)	14 – 26	479	162.7	1.58 ± 0.08	0.31 ± 0.03
CAM2 - Campinas, SP (22°52' S, 47°04' W, 645 m; Cwa)	10/08/10 - 19/09/10 (40 days)	14 – 28	451	6.3	1.19 ± 0.11	0.48 ± 0.05
CAM3 - Campinas, SP (22°52' S, 47°04' W, 645 m; Cwa)	06/08/11 - 14/09/11 (39 days)	14 – 28	442	36.7	1.44 ± 0.08	0.52 ± 0.04
SPA1 - São Paulo, SP (23°38' S, 46°37' W, 785 m; Cwb)	25/08/09 - 12/10/09 (48 days)	15 – 24	458	232.1	2.16 ± 0.44	0.19 ± 0.04
SPA2 - São Paulo, SP (23°38'S, 46°37'W, 785 m; Cwb)	26/08/10 - 09/10/10 (44 days)	14 – 25	428	128.8	1.82 ± 0.15	0.23 ± 0.03
SPA3 - São Paulo, SP (23°38' S, 46°37' W, 785 m; Cwb)	31/08/11 - 10/10/11 (40 days)	13 – 25	374	99.1	1.90 ± 0.14	0.24 ± 0.02
IBI1 - Ibiúna, SP (23°39' S, 47°09' W, 917 m; Cfb)	12/09/10 - 23/10/10 (41 days)	12 – 27	413	123.6	1.53 ± 0.11	0.38 ± 0.05
IBI2 - Ibiúna, SP (23°39' S, 47°09' W, 917 m; Cfb)	04/09/11 - 12/10/11 (38 days)	10 – 29	380	103.2	1.71 ± 0.18	0.19 ± 0.03
SBC1 - São Bernardo do Campo, SP (23°42' S, 46°33' W, 786 m; Cwb)	16/08/10 - 03/10/10 (48 days)	13 – 25	458	104.3	1.27 ± 0.07	0.55 ± 0.03
SBC2 - São Bernardo do Campo, SP (23°42' S, 46°33' W, 786 m; Cwb)	16/08/11 - 01/10/11 (46 days)	13 – 25	406	68.5	1.38 ± 0.10	0.39 ± 0.02
SAA - Santo André, SP (23°40' S, 46°32' W, 791 m; Cwb)	14/08/07 - 27/09/07 (44 days)	13 – 26	431	3.2	1.56 ± 0.07	0.48 ± 0.05
JUM - Jumirim, SP (22°05' S, 47°47' W, 540 m; Cwa)	05/08/10 - 19/09/10 (45 days)	12 – 29	481	12.6	1.47 ± 0.09	0.43 ± 0.06
RIB - Ribeirão Preto, SP (21°10' S, 47°52' W, 593 m; Cwa)	14/08/10 - 17/09/10 (34 days)	14 – 31	440	6.9	1.70 ± 0.08	0.48 ± 0.04
ITA - Itaberá, SP (23°52' S, 49°06' W, 683 m; Cfa)	17/08/10 - 23/09/10 (37 days)	11 – 26	341	1.8	1.93 ± 0.22	0.42 ± 0.02
PAR - Pariquera-Açú, SP (24°37' S, 47°53' W, 28 m; Af)	23/08/10 - 11/10/10 (49 days)	15 – 25	501	87.4	1.49 ± 0.13	0.67 ± 0.02

Min: minimum temperature; Max: maximum temperature; DD: Degree-days; Rainfall: accumulated rainfall for the period. Water content (WC) and dry matter (DM): mean values ± standard deviation. Köppen climate classification: Cwa - temperate humid climate with dry winters and hot summers; Cwb - temperate humid climate with dry winters and temperate summers; Cfa - subtropical climate; Cfb - maritime climate; Af - equatorial climate or tropical humid

(DELGADO; BARBEDO, 2007), but not for more than seven days after collection.

From weather stations located close to the collection areas, data were obtained of the daily rainfall (mm) and the maximum and minimum air temperature (°C). The accumulated rainfall (mm) and degree-days (°C day) were calculated for the period between flowering and seed dispersal, as per equations proposed by Villa Nova *et al*. (1972), considering a basal temperature of 10 °C (PEDRO JUNIOR *et al*., 1977).

After collection, the seeds were characterised for water content, dry matter content and germination. The water content and dry matter content were determined gravimetrically by oven method at 103 °C for 17 hours (BRASIL, 2009), the results being shown as g of water per g of dry matter (g g^{-1}) for water content, and g $seed^{-1}$ for dry matter content.

Germination tests were carried out in germination chambers at 25 °C under constant light and 100% relative humidity, using roll paper as substrate (filter paper), with two sheets for the base and one as cover (BRASIL, 2009). Germination was evaluated every 3 days for 70 days (DELGADO; BARBEDO, 2007; LAMARCA; SILVA; BARBEDO, 2011), recording those seeds with a primary root, to calculate germinated seeds, and those that had produced normal seedlings, to calculate germination; both results were given as a percentage. The germination speed index (GSI) was also calculated, using the formula proposed by Maguire (1962).

After characterisation, the seeds underwent controlled drying in a forced air circulation oven; for this, they were placed on shelves lined with a single layer of polyethylene screen, with no overlaps. Drying was carried out intermittently, with 10 hours at 40 °C followed by 14 hours at 20-25 °C (DELGADO; BARBEDO, 2007). Periodically, based on the value for seed dry matter, samples were taken and evaluated for water content, dry matter content and germination, as described above. This procedure was repeated until the seeds reached two pre-established levels, 1.00 g g^{-1} and 0.67 g g^{-1}, i.e. when 50% of the vigour and germination are lost respectively (DELGADO; BARBEDO, 2007). Levels of drying were thus created: non-dried seeds (D_0), seeds dried to the first level (D_I) and seeds dried to the second level (D_{II}).

The experimental design was completely randomised, in a 20 x 3 factorial scheme (source of material x level of drying), with three replications. The resulting data were submitted to variance analysis (F-test) at a significance level of 5%. There was no need for data transformation, and mean values were compared by Tukey’s test at the 5% significance level (SANTANA; RANAL, 2004). Simple correlation coefficients were then calculated for all combinations of the meteorological data with the physical and physiological data of the seeds, and the significance determined by t-test at 5% probability.

RESULTS AND DISCUSSION

Analysis of variance (Table 2) showed a significant interaction between the factors source of material and level of seed drying, for the data on germinated seeds, germination and GSI, with a difference in the desiccation tolerance of the seeds for source therefore becoming evident.

The increase in drying decreased the values for germinated seeds (Table 3), germination (Table 4) and SGI (Table 5). It was also found that, depending on the source of the material, this decrease occurred at the first or second level of drying (in some cases, at both), showing that there were differences in the desiccation tolerance of the seeds. Thus seeds coming from LAV1, SBS1, CAM1, CAM3, SPA1, SPA3, IBI1, SAA and PAR showed a reduction for all physiological variables shortly after the first level of drying, unlike the seeds

Table 2 - Summary of analysis of variance for the variables germinated seeds (GS), germination (G) and germination speed index (GSI) in the uvaieira (*Eugenia pyriformis* Cambess.) from different sources and at three levels of drying

Cause of variation	DF	------------GS--------------		--------------G---------------		------------GSI-------------	
		MS	F	MS	F	MS	F
Source of material (A)	19	938.905	12.3*	1845.046	28.5*	0.416	91.5*
Level of drying (B)	2	34661.239	452.8*	42953.867	663.6*	6.392	1406.6*
A x B	38	573.578	7.5*	818.884	12.7*	0.127	27.9*
Residual error	120	76.544		64.733		0.004	
CV (%)		12.10		14.35		12.06	

*indicates significant at 5% by F-test. DF = degrees of freedom and MS = mean square from RIB, LAV2, SBS2, SBS3, CAM2, JUM, SPA2, IBI2, SBC1, SBC2 and ITA, which showed a reduction after the second level (Tables 3, 4 and 5).

When each variable is considered individually, it is found that the differences in desiccation tolerance occurred even when comparing seeds from the same region but from different altitudes or periods, for example germinated seeds from SBS, LAV, CAM SPA, IBI and SBC (Table 3).

These results support the idea that desiccation tolerance is not established absolutely, but rather in a continuous process, and may vary not only inter- but also intra-species (WALTERS, 2000; DAWS *et al.*, 2004; DELGADO; BARBEDO, 2012; PEREZ; HILL, WALTERS, 2012). These differences had already been seen in seeds of various species of *Eugenia*, among which *E. pyriformis* is among the most sensitive to desiccation (DELGADO; BARBEDO, 2007). However, there were still no studies into the species, where production years and places of origin were varied.

As mentioned above, the desiccation tolerance of the seeds varied with both region and year of production, showing the influence of environmental conditions on this characteristic. Data of the maturation cycle (which varied from 34 to 56 days), accumulated degree-days (341 to 501 degree-days), maximum air temperature (24 to 31 °C) and minimum air temperature (10 to 15 °C), accumulated rainfall in the period (1.8 to 252.4 mm), water content (1.12 to 2.16 g g^{-1}) and seed dry matter content (1.27 to 0.19 g $seed^{-1}$), for the period of development/maturation (Table 1), showed wide variation for the different regions and years of production. It was found that years/regions with greater amounts of accumulated rainfall or a greater accumulation of degree-days resulted in the longest maturation cycles (Table 1), moreover with a positive correlation (Table 6), suggesting that those variables

Table 3 - Germinated seeds of the uvaieira (*Eugenia pyriformis* Cambess.) from different sources and at three levels of drying. D_0 - non-dried seeds; D_I - 1st level of drying; D_{II} - 2nd level of drying

Source of material (Water content for level of drying, g g^{-1})	Level of drying*		
	D_0	D_I	D_{II}
LAV1 (D_0 = 1.53; D_I = 1.00; D_{II} = 0.70)	100 aA	77 abcdeB	33 defC
LAV2 (D_0 = 1.12; D_I = 1.00; D_{II} = 0.67)	100 aA	100 aA	62 abcB
SBS1 (D_0 = 1.87; D_I = 1.17; D_{II} = 0.67)	98 abA	69 bcdeB	44 bcdeC
SBS2 (D_0 = 1.34; D_I = 1.04; D_{II} = 0.64)	97 abA	100 aA	62 abcB
SBS3 (D_0 = 1.12; D_I = 0.96; D_{II} = 0.64)	92 abA	88 abcA	52 abcdB
CAM1 (D_0 = 1.58; D_I = 0.96; D_{II} = 0.79)	93 abA	75 abcdeB	15 fC
CAM2 (D_0 =1.19; D_I = 0.96; D_{II} = 0.64)	98 abA	93 abA	50 bcdeB
CAM3 (D_0 = 1.44; D_I = 0.96; D_{II} = 0.70)	93 abA	53 efB	25 efC
SPA1 (D_0 = 2.16; D_I = 1.00; D_{II} = 0.75)	85 abcA	52 efB	38 defB
SPA2 (D_0 = 1.82; D_I = 1.17; D_{II} = 0.67)	63 cB	83 abcdA	52 abcdB
SPA3 (D_0 = 1.90; D_I = 1.08; D_{II} = 0.70)	92 abA	60 defB	38 cdefC
IBI1 (D_0 = 1.53; D_I = 0.96; D_{II} = 0.64)	93 abA	76 abcdeB	36 defC
IBI2 (D_0 = 1.71; D_I = 1.22; D_{II} = 0.85)	88 abcA	90 abcA	62 abcB
SBC1 (D_0 = 1.27; D_I = 1.04; D_{II} = 0.75)	73 bcA	88 abcA	77 aA
SBC2 (D_0 = 1.38; D_I = 1.08; D_{II} = 0.75)	90 abA	90 abcA	68 abB
SAA (D_0 = 1.56; D_I = 0.96; D_{II} = 0.67)	100 aA	37 fB	33 defB
JUM (D_0 = 1.47; D_I = 1.00; D_{II} = 0.69)	98 abA	98 aA	25 efC
RIB (D_0 = 1.70; D_I = 0.96; D_{II} = 0.72)	98 abA	100 aA	55 abcdB
ITA (D_0 = 1.93; D_I = 1.13; D_{II} = 0.70)	100 aA	100 aA	42 cdeB
PAR (D_0 = 1.49; D_I = 1.00; D_{II} = 0.85)	82 abcA	65 cdeB	40 cdefC
CV (%)	12.10		

*Mean values followed by the same letter (lowercase compares source of material and uppercase compares levels of drying) do not differ by Tukey's test at 5%

Table 4 - Germination in seeds of the uvaieira (*Eugenia pyriformis* Cambess.) from different sources and at three levels of drying. D_0 - non-dried seeds; D_I - 1st level of drying; S_{II} - 2nd level of drying

Source of material (Water content for level of drying, g g^{-1})	Level of drying*		
	D_0	D_I	D_{II}
LAV1 (D_0 = 1.53; D_I = 1.00; D_{II} = 0.70)	98 aA	47 deB	10 deC
LAV2 (D_0 = 1.12; D_I = 1.00; D_{II} = 0.67)	100 aA	100 aA	47 abB
SBS1 (D_0 = 1.87; D_I = 1.17; D_{II} = 0.67)	87 abcdA	38 defB	18 deC
SBS2 (D_0 = 1.34; D_I = 1.04; D_{II} = 0.64)	85 abcdA	90 abA	42 abcB
SBS3 (D_0 = 1.12; D_I = 0.96; D_{II} = 0.64)	77 abcdeA	77 abA	32 abcB
CAM1 (D_0 = 1.58; D_I = 0.96; D_{II} = 0.79)	73 bcdeA	52 cdB	2 eC
CAM2 (D_0 =1.19; D_I = 0.96; D_{II} = 0.64)	90 abcA	77 abA	30 bcdB
CAM3 (D_0 = 1.44; D_I = 0.96; D_{II} = 0.70)	87 abcdA	38 defB	15 deC
SPA1 (D_0 = 2.16; D_I = 1.00; D_{II} = 0.75)	60 efA	25 efB	18 cdeB
SPA2 (D_0 = 1.82; D_I = 1.17; D_{II} = 0.67)	58 efB	57 bcA	42 abcC
SPA3 (D_0 = 1.90; D_I = 1.08; D_{II} = 0.70)	82 abcdeA	40 defB	25 bcdeB
IBI1 (D_0 = 1.53; D_I = 0.96; D_{II} = 0.64)	72 cdeA	33 defB	18 deB
IBI2 (D_0 = 1.71; D_I = 1.22; D_{II} = 0.85)	47 fA	37 defAB	23 bcdeB
SBC1 (D_0 = 1.27; D_I = 1.04; D_{II} = 0.75)	65 defA	78 abA	63 aA
SBC2 (D_0 = 1.38; D_I = 1.08; D_{II} = 0.75)	88 abcdeA	40 defB	25 bcdeB
SAA (D_0 = 1.56; D_I = 0.96; D_{II} = 0.67)	97 abA	17 fB	23 bcdeB
JUM (D_0 = 1.47; D_I = 1.00; D_{II} = 0.69)	92 abcA	93 abA	15 deB
RIB (D_0 = 1.70; D_I = 0.96; D_{II} = 0.72)	88 abcdA	90 abA	42 abcB
ITA (D_0 = 1.93; D_I = 1.13; D_{II} = 0.70)	87 abcdA	88 abA	23 bcdeB
PAR (D_0 = 1.49; D_I = 1.00; D_{II} = 0.85)	74 bcdeA	31 defB	18 deB
CV (%)		14.35	

*Mean values followed by the same letter (lowercase compares source of material and uppercase compares levels of drying) do not differ by Tukey's test at 5%

Table 5 - Germination speed index in seeds of the uvaieira (*Eugenia pyriformis* Cambess.) from different sources and at three levels of drying. D_0 - non-dried seeds; D_I - 1st level of drying; D_{II} - 2nd level of drying

Source of material (Water content for level of drying, g g^{-1})	Level of drying		
	D_0	D_I	D_{II}
LAV1 (D_0 = 1.53; D_I = 1.00; D_{II} = 0.70)	0.93 cdA	0.35 fgB	0.14 cdefC
LAV2 (D_0 = 1.12; D_I = 1.00; D_{II} = 0.67)	1.09 bcA	1.21 bA	0.31 bcB
SBS1 (D_0 = 1.87; D_I = 1.17; D_{II} = 0.67)	0.70 efgA	0.26 ghB	0.12 cdefC
SBS2 (D_0 = 1.34; D_I = 1.04; D_{II} = 0.64)	0.86 deA	0.68 deB	0.30 bcdC
SBS3 (D_0 = 1.12; D_I = 0.96; D_{II} = 0.64)	0.82 deA	0.96 bcA	0.26 bcdeC
CAM1 (D_0 = 1.58; D_I = 0.96; D_{II} = 0.79)	0.81 defA	0.38 fgB	0.06 fC
CAM2 (D_0 = 1.19; D_I = 0.96; D_{II} = 0.64)	1.22 bA	0.62 deB	0.21bcdefC
CAM3 (D_0 = 1.44; D_I = 0.96; D_{II} = 0.70)	0.72 efgA	0.25 ghB	0.31 cdefB
SPA1 (D_0 = 2.16; D_I = 1.00; D_{II} = 0.75)	0.59 ghiA	0.23 ghB	0.20 bcdefB
SPA2 (D_0 = 1.82; D_I = 1.17; D_{II} = 0.67)	0.63 fghA	0.65 deA	0.37 abB
SPA3 (D_0 = 1.90; D_I = 1.08; D_{II} = 0.70)	0.70 efgA	0.31 fgB	0.17 cdefB

Table 5 Continued

IBI1 (D_0 = 1.53; D_I = 0.96; D_{II} = 0.64)	0.89 deA	0.33 fgB	0.14 cdefC
IBI2 (D_0 = 1.71; D_I = 1.22; D_{II} = 0.85)	0.73 efgA	0.51 efB	0.40 abC
SBC1 (D_0 = 1.27; D_I = 1.04; D_{II} = 0.75)	0.87 deA	0.97 bcA	0.51 aB
SBC2 (D_0 = 1.38; D_I = 1.08; D_{II} = 0.75)	0.88 deA	0.77 cdA	0.31 bcB
SAA (D_0 = 1.56; D_I = 0.96; D_{II} = 0.67)	0.42 iA	0.09 hB	0.08 efB
JUM (D_0 = 1.47; D_I = 1.00; D_{II} = 0.69)	1.42 aA	0.69 deB	0.10 defC
RIB (D_0 = 1.70; D_I = 0.96; D_{II} = 0.72)	1.20 bA	1.40 aB	0.28 bcdC
ITA (D_0 = 1.93; D_I = 1.13; D_{II} = 0.70)	1.43 aA	1.02 bB	0.18 bcdefC
PAR (D_0 = 1.49; D_I = 1.00; D_{II} = 0.85)	0.44 hiA	0.23 ghB	0.11 cdefB
CV (%)		12.06	

*Mean values followed by the same letter (lowercase compares source of material and uppercase compares levels of drying) do not differ by Tukey's test at 5%

Table 6 - Simple correlation coefficients (r) between meteorological data and physical and physiological data in seeds of the uvaieira (*Eugenia pyriformis* Cambess.) from different sources

	DD	Rain	DM	GSD_I	GSD_{II}	GD_0	GD_I	GD_{II}	$GSID_0$	$GSID_I$	$GSID_{II}$
Cycle	0.60*	0.61*	0.53*	-0.03	-0.02	-0.13	-0.09	0.07	-0.39	0.21	-0.03
Min	0.54*	-0.07	-0.26	-0.43	-0.49*	0.13	-0.26	-0.33	-0.26	-0.38	-0.39
Max	-0.02	-0.40	0.03	0.46*	0.06	0.28	0.30	-0.11	0.56*	0.15	0.03
DD		0.23	0.37	0.02	-0.34	0.12	0.09	-0.29	-0.16	0.03	-0.32
Rain			0.16	-0.05	-0.03	-0.30	-0.13	-0.11	-0.13	0.03	0.06
WC			-0.71*	-0.51*	-0.37	-0.27	-0.59*	0.43	-0.01	-0.66*	0.29
DM				0.36	0.34	0.28	0.46*	0.36	0.01	0.51*	0.17
GSD_0				0.10	-0.24	0.65*	0.07	-0.32	0.46*	-0.14	-0.46*
GSD_I					0.53*	0.80*	0.56*	0.65*	0.88*	0.05	0.65*
GSD_{II}						-0.06	0.51*	0.87*	0.05	0.65*	0.88*
GD_0							0.35	0.09	0.45*	0.09	-0.29
GD_I								0.61*	0.47*	0.88*	0.52*
GD_{II}									-0.02	0.71*	0.82*
$GSID_0$										0.33	-0.01
$GSID_I$											0.71*

Cycle = maturation cycle; Min = mimimum temperature; Max = maximum temperature; DD = degree-days; Rain = accumulated rainfall; WC = water content; DM = dry matter; GSD_0 = non-dried germinated seeds; GSD_I = germinated seeds at the 1st level of drying; GSD_{II} = germinated seeds at the 2nd level of drying; GD_0 = non-dried germination; GD_I = germination at the 1st level of drying; GD_{II} = germination at the 2nd level of drying; $GSID_0$ = non-dried germination speed index; $GSID_I$ = germination speed index at the 1st level of drying; $GSID_{II}$ = germination speed index at the 2st level of drying. (*) = r significant at 5% probability. Data not shown, or with no asterisk, correspond to non-significant correlations

also influence the cycle of seed formation. This result is similar to those obtained by Lamarca *et al*. (2013a) for the same species. Considering that accumulated degree-days showed a wide variation, and therefore in this case did not define the time of fruit and seed dispersal, it can be assumed that the amount of rainfall has a significant influence on the maturation cycle of the seeds in the uvaieira. Having a positive correlation, the greater the rainfall, the longer the development cycle of the uvaieira seeds. However, this influence does not translate into extending the maturation process, since there was no correlation between accumulated rainfall and water content or dry matter content of the dispersed seeds (Table 6). On the other hand, the maximum and minimum temperatures alone were not correlated with the cycle, and therefore have little influence on it (Table 6). Although the maturation cycles of seeds are programmed genetically, comparing collections made in any one region (from the same parent plants in CAM, SPA, LAV, IBI and SBC), but at different periods, it is found that in years of high rainfall, the cycles were longer and, consequently, there was a greater accumulation of degree-days.

A general analysis of the results showed that the water and thermal conditions of the environment indeed have a great influence on the maturation of uvaieira seeds, both for the cycle and the final quality of the produced seeds, especially the level of desiccation tolerance. For Daws *et al.* (2004, 2006), Dussert *et al.* (2000) and Joët, Ourcival and Dussert (2013), variations in desiccation tolerance within populations of the same species are a result of environmental conditions, which may lead to early seed dispersal, that is before they complete maturation. This probably happened with the uvaieira seeds from the different sources, creating differences in the progress of the development and maturation process. Thus, desiccation tolerance in this case could progress further, for more favourable water and thermal conditions of the environment, resulting in a longer period of maturation. It is interesting to note that all the seeds that showed less than 50% germination (except for CAM3) or a GSI less than or equal to 0.20 after the second level of drying, were dispersed with a water content greater or equal to 1.50 g g^{-1} (60% wet basis).

It is a fact that variations in the level of desiccation tolerance among the sources were enough to identify the influence of the environment on desiccation tolerance. Analysing the seeds from different altitudes at SBS for example, it can be seen that at higher altitudes, with lower air temperatures (maximum and minimum), the period of maturation was longer, increasing the total of degree-days. On average, for each 100-meter increase in altitude, the air temperature decreases by 0.6 °C (PEREIRA; ANGELOCCI; SENTELHAS, 2002). This increase apparently affects the maturation cycle and the accumulation of degree-days. Seeds formed at these higher altitudes (SBS2 and SBS3) for example, were dispersed with a lower water content and greater quantity of dry matter, resulting in less sensitivity to desiccation. This suggests that the seeds with a higher water content at the time of dispersal were more sensitive to desiccation due to their lesser maturity, as suggested by Barbedo, Centeno and Figueiredo-Ribeiro (2013), and also verified during the maturation of desiccation-tolerant seeds (LEDUC *et al.*, 2012; SCHWALLIER; BHOOPALAN; BLACKMAN, 2011.). When analysing the results for seeds from the same parent plants but in different years, this effect from maturity becomes clearer. The seeds from LAV, CAM and SPA for example, became more sensitive to desiccation the higher their water content at the time of dispersal, as seen from the values after the first and/or second level of drying.

The air temperature, represented by the concept of degree-days, shows a strong relationship to seed development and maturation, as well as the acquisition of desiccation tolerance. Daws *et al*. (2004, 2006) for example, found that regions that favoured the greatest accumulation of degree-days during formation saw the dispersal of seeds that were more vigorous and more tolerant to desiccation; such was not observed in this study. In this work, the lower the minimum temperature, or higher the maximum temperature, the more tolerant to desiccation the seeds became. In other words, the sum of degree-days seems to influence desiccation tolerance, but must be associated with a minimum in temperature range.

Finally, variations in the degree of desiccation tolerance between the regions and collection times of the uvaieira seeds are dependent on the source of the material. It should also be noted that the water and thermal conditions of the environment might influence the maturation cycle, as well as the physiological quality and acquisition of desiccation tolerance of the seeds. Desiccation tolerance in seeds of the uvaieira depends therefore on their degree of maturation at the time of dispersal, confirming the assertion of Barbedo, Centeno and Figueiredo-Ribeiro (2013) that the level of recalcitrance in the seeds depends on the point of physiological maturity at the time they detach from the mother plant.

CONCLUSION

Desiccation tolerance in seeds of the uvaieira depends on the stage of physiological maturity at the time of dispersal, which in turn depends on the water and thermal conditions of the environment during formation.

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