



Is the loss of desiccation tolerance in orthodox seeds affected by provenance?



W.V.S. Pereira^{a,*}, J.M.R. Faria^a, A.C. José^a, O.A.O. Tonetti^a, W. Ligterink^b, H.W.M. Hilhorst^b

^a Departamento de Ciências Florestais, Universidade Federal de Lavras, Campus Universitário, 37200-000 Lavras, Brazil

^b Laboratory of Plant Physiology, Wageningen University and Research, Droevendaalsesteeg 1, 6708 PB, Wageningen, The Netherlands

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ABSTRACT

There is little information about the influence of the environment on seed morphological and physiological characteristics, especially on desiccation tolerance. Therefore, the objective of this study was to investigate the loss of desiccation tolerance in germinating orthodox seeds of the tree species *Copaifera langsdorffii* from different provenances. Seeds were harvested from the Cerrado *stricto sensu* in Montes Claros and Lavras, and the riparian forest in Lavras. These cities are located, respectively, in the north and south of the State of Minas Gerais, Brazil. The climate in the north of the State shows higher temperatures and lower precipitation than the south. For each provenance, a seed imbibition curve was constructed by measuring the increase in seed water content with incubation time. Seeds were then imbibed for different periods of time, dried and subsequently rehydrated in order to assess survival (desiccation tolerance). Additionally, the effect of pre-imbibition over water and scarification on desiccation tolerance was assessed for seeds from Montes Claros. It was observed that seeds from the Cerrado of Montes Claros are more desiccation-tolerant than those from Lavras, highlighting that the maternal environment influences desiccation tolerance. Pre-imbibition and scarification did not influence desiccation tolerance.

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1. Introduction

The most common definition of desiccation tolerance is the ability to survive almost complete water loss and subsequent recovery of normal metabolism after rehydration (Oliver et al., 2000; Hoekstra et al., 2001). Alpert (2000) defined desiccation tolerance as the ability to equilibrate the internal water content with moderately dry air and restore normal metabolism after rehydration. This ability is found in all groups of organisms, from microorganisms to a few species of animals (Alpert, 2000). In plants this ability is mostly observed in seeds, pollen and spores (Hoekstra, 2005), which can be dispersed from the parent plant when in a dry state. Seeds may be divided into three broad groups based on their desiccation tolerance: those that are tolerant to drying, cold temperatures and storage for long periods ('orthodox'), those which do not survive drying, cold temperatures and storage ('recalcitrant') (Roberts, 1973), and those that survive moderate drying and cooling and can be stored for periods longer than those belonging to

the recalcitrant group, but shorter than the orthodox (intermediate) (Ellis et al., 1990).

During their life cycle, orthodox seeds alternate between phases of tolerance and sensitivity to desiccation. At the initial stages of embryo development and growth (seed formation), when metabolic activity and water content are high, seeds are sensitive to desiccation (Parcy et al., 1994). At the maturation phase, orthodox seeds are induced to become tolerant to desiccation and may survive drying either before or after dispersion, until the commencement of germination. When seeds are imbibed and the germination process begins, desiccation tolerance is progressively lost (Nedeva and Nikolova, 1997). Thus, at both formation and germination, orthodox seeds display recalcitrant behaviour. Considering these factors and the difficulties in studying desiccation sensitivity in recalcitrant seeds, Sun et al. (1999) proposed the use of germinating orthodox seeds as a model system to understand desiccation sensitivity.

During the germination of orthodox seeds, reserve mobilization begins, general metabolism is reactivated and desiccation tolerance mechanisms are deactivated (Kermode and Finch-Savage, 2002). Based on the three phases of water uptake by a mature, dry seed (Bewley et al., 2013), most orthodox seeds retain desiccation tolerance during phase one and start to lose it by the end of phase two. Among the orthodox seeds that have been reported in the literature, desiccation tolerance is lost around the time of radicle protrusion, and this behaviour is

* Corresponding author at: Laboratório de Sementes Florestais/Departamento de Ciências Florestais, Universidade Federal de Lavras, P.O. Box 3037, Campus Universitário, Lavras, MG, Brazil.

E-mail addresses: wvcentesp@gmail.com (W.V.S. Pereira), jmfaria@dcf.ufla.br (J.M.R. Faria), acjose@dcf.ufla.br (A.C. José), oaotonetti@gmail.com (O.A.O. Tonetti), wilco.ligterink@wur.nl (W. Ligterink), henk.hilhorst@wur.nl (H.W.M. Hilhorst).

associated with intense metabolism in phase two (Faria et al., 2005; Masetto et al., 2008; Guimarães et al., 2011). A different response to desiccation at early germination has been reported for orthodox seeds from neotropical species (Daws et al., 2007), for the Brazilian species *Senna multijuga* (Rodrigues-Junior et al., 2014) and for *Copaifera langsdorffii* (Pereira et al., 2014). These seeds became completely desiccation sensitive prior to radicle protrusion and this may have started even as early as phase 1, as in for *C. langsdorffii*.

Many studies have reported on the desiccation tolerance and sensitivity of seeds, either related to the acquisition of desiccation tolerance during development (Ooms et al., 1993; Vertucci and Farrant, 1995; Cordova-Tellez and Burris, 2002; Sreedhar et al., 2002; Aberlenc-Bertossi et al., 2003; Ali et al., 2007) or its loss during germination (Lin et al., 1998; Reisdorph and Koster, 1999; Koster et al., 2003; Faria et al., 2005; Guimarães et al., 2011; Pereira et al., 2014; Rodrigues-Junior et al., 2014). Some studies on desiccation sensitivity in intermediate and recalcitrant seeds have also been carried out (Berjak, 1993; Wesley-Smith et al., 2001; Faria et al., 2004), as well as on the classification of seeds regarding desiccation tolerance and storage behaviour (Davide et al., 2003; Carvalho et al., 2006; José et al., 2007).

For both desiccation sensitive and -tolerant seeds, studies have been undertaken to understand the mechanisms of desiccation tolerance and the responses of seeds to drying (Leprince, 1993; Finch-Savage et al., 1996; Hoekstra et al., 2001; Vicré et al., 2004; Berjak, 2006). Also, studies have been performed on the reestablishment of desiccation tolerance in germinating orthodox seeds (Buitink et al., 2003; Faria et al., 2005; Maia et al., 2011). A few studies have related desiccation sensitivity to the maternal environment (Daws et al., 2004; Daws et al., 2006; Pereira et al., 2012), but there are no studies on possible effects of the maternal environment on the loss of desiccation tolerance during germination of orthodox seeds.

It has been reported that the maternal environment exerts a considerable influence on performance of the mature seed (Guterman, 2000; Donohue, 2005; Jurado and Flores, 2005; Bognounou et al., 2010; Jacobs and Lesmeister, 2012). The phenotypic and physiological properties of seeds are influenced by maternal environmental conditions, such as day length, temperature, water availability, soil characteristics and even the action of herbivores (Wulff, 1986; Fenner, 1991; Delph et al., 1997). These characteristics influence seed vigour and germination, as well as seedling establishment and growth (Stearns, 1960; Daws et al., 2006). Some authors have reported an effect of maternal environmental temperatures on seed dormancy (Fenner, 1991; Pritchard et al., 1999). Desiccation sensitivity is also influenced by climatic factors, as observed for recalcitrant seeds of *Aesculus hippocastanum* and *Acer pseudoplatanus*; therefore, it is important to consider the environmental influence on the response to desiccation in seeds (Daws et al., 2004; Daws et al., 2006).

C. langsdorffii (copaiba; Fabaceae) is a species within the *Copaifera* genus (Veiga Junior and Pinto, 2002; Guerra et al., 2006). It is an important tree species in Brazil because of its medicinal properties and wood (Jeller and Perez, 1997; Lorenzi, 2002; Veiga Junior and Pinto, 2002; Freire et al., 2006). Copaiba seeds are reported to have occasional dormancy by a combination of germination inhibitors and physical dormancy caused by tegument impermeability, resulting in non-uniform imbibition and germination (Fowler and Bianchetti, 2000). Mechanical scarification or immersion in water at room temperature for 96 h are recommended for dormancy release (Fowler and Bianchetti, 2000; Lima et al., 2008; Pereira et al., 2014). As this species is reported to grow in different environments (Queiroz et al., 2014), studying the possible effects of the environment on the loss of desiccation tolerance in germinating *C. langsdorffii* seeds can be useful to explain the uncommon behaviour regarding the loss of desiccation tolerance observed for this species (Pereira et al., 2014). Furthermore, such studies can contribute to the understanding of the effects of the environment on seed characteristics. Therefore, the objective of this study was to characterize the loss of desiccation tolerance during early germination of orthodox seeds of *C. langsdorffii* from different provenances.

2. Materials and methods

2.1. Seed material and storage conditions

Copaifera langsdorffii (Desfontaines) seeds were collected after dispersal (seeds on the ground after natural opening of the fruits) from the Cerrado *stricto sensu* at Montes Claros and Lavras, state of Minas Gerais (MG), Brazil. Seeds were also collected from the riparian forests near Lavras. Seeds were collected in July 2011 and only one seed collection was carried out for each provenance. After collection, the initial seed water content (fresh basis) was assessed gravimetrically in four replicates of 10 seeds by drying at 103 ± 2 °C for 17 h (ISTA, 2004). Meteorological data of the collection year (January 2011 to January 2012), were obtained from the meteorological station of the State University of Montes Claros (Unimontes) and from the Federal University of Lavras (UFLA). These data are presented in Fig. 1.

Seeds with a water content higher than $10 \pm 2\%$ were dried in a plastic box of 0.134 m^3 , containing an internal fan and desiccant material (silica gel), creating an atmosphere of $13 \pm 2\%$ relative humidity. Seeds were placed in a monolayer over a net suspended at 1/3 of the box height. Seeds were dried until they reached $10 \pm 2\%$ water content, based on Eq. (1) which calculates a target weight (Hong and Ellis, 1996). When the target weight was reached, the water content was confirmed as before (ISTA, 2004), dry seeds were then stored in semipermeable plastic bags in a dry, cold chamber (40% relative humidity and 5 °C) until the experiments were performed, seven months after collection. At the beginning of the experiments, water content was assessed again following the method described above (ISTA, 2004).

$$\text{Target Weight} = \frac{(100 - iWC)}{(100 - tWC)} \times iW \quad (1)$$

Formula used for calculation of the target seed weight (g) during drying. iWC = Initial Water Content (%); tWC = Target Water Content (%); iW = Initial Weight (g).

2.2. Loss of desiccation tolerance during germination

An imbibition curve was first constructed to determine the sampling points for the desiccation tolerance experiments. For all tests, seeds were mechanically scarified, using sandpaper, at the lateral area at a point which did not result in damage to the axis. Thirty seeds from each provenance were imbibed in a paper roll (Germilab Paper from JProLab®, 28×38 cm, 65 g/m^2 , neutral pH, white colour), moistened with 3 times its weight of tap water and incubated at 25 °C in constant light). Regularly, seeds were removed from the paper roll and individually weighed. Seed water content after storage was measured as before, regarding these values as the “target water content” for the desiccation tolerance experiments.

Using the imbibition curve as guidance, seeds were sampled every 24 h during imbibition to establish the timing of the loss of desiccation tolerance. At each sampling interval, four replicates of 25 seeds were collected, weighed (“initial weight”) and the water content measured as before, regarding this value as the “initial water content” (Eq. (1)). Seeds were then placed in a single layer at 1/3 height of a 363 cm^3 plastic box (“gerbox”) filled with 100 mL of blue silica gel and dried until they reached the water content observed before the beginning of the imbibition (target water content). Seeds were weighed at regular intervals until the target weight was reached (Eq. (1); (Hong and Ellis, 1996). After reaching the initial water content, the seeds were maintained in this state for 72 h. For this, seeds were kept in the same gerbox but with 1/3 of the volume of silica gel used for drying, which did not allow drying or increase of moisture content. Seeds were then submitted to pre-humidification, by placing them in a single layer over a net at 1/2 height of a sealed gerbox filled with 50 mL of water (without direct contact between water and seeds) and kept at 25 °C under constant

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