Tropical Ecology **58**(2): 241–250, 2017 ISSN 0564-3295

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Non-deep physiological dormancy, desiccation and low-temperature sensitivity in seeds of *Garcinia gummi-gutta* (Clusiaceae): A tropical evergreen recalcitrant species

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Abstract: This study aimed to determine seed dormancy, desiccation, low-temperature sensitivity and storage behavior of seeds of *Garcinia gummi-gutta,* a medicinally important tropical evergreen tree. These seed characteristics serve as important ecological traits to regulate the regeneration strategy of plants by synchronizing seed germination timing with the wet season. De-coated fresh seeds imbibed water and had > 90% germination within four weeks, but seeds with an intact seed coat required about 24 weeks of warm temperature to attain 90% germination. Desiccation of intact seeds with silica gel at 15, 25 and 35 ºC revealed that the rate of desiccation varies with temperature. The critical moisture content (CMC), which is the moisture content below which there is a rapid fall in viability, for *G. gummi-gutta* seeds is ~34% and seeds completely lose viability at 24 and 17% moisture content (MC) at 25 and 35 ºC, respectively. Based on these results, fresh seeds with MC of 43% and reduced MC of 34% were stored at six temperatures ranging from –10 to 35 ºC for a period of 18 months. Rapid decline in germination was recorded at –10, 5 and 35 ºC. However, at 15 ºC, seeds with both 43% and 34% MC retained 90% viability for 18 months. The half viability period (P_{50}) indicated that an optimum condition for long-term seed storage is 15 ºC with 34% MC. We conclude that seeds of *G. gummi-gutta* have non-deep physiological dormancy (PD) and are sensitive to desiccation and low temperature. Inspite of their recalcitrant nature, the seeds of *G. gummi-gutta* have PD, thus the species is classified as a tropical dormant recalcitrant.

Key words: Critical moisture content, half viability period, physiological dormancy, seed storage.

Handling Editor: Christina Alba

Introduction

Tropical forests are one of the most important landscapes and are constantly threatened due to over exploitation by increased anthropogenic activities (Wright 2005) like habitat destruction uninhibited logging, land use changes, and increased demand for various forest produces (Chomitz 2007). One of the major consequences is reduced biodiversity, which has cascading effects in terms of lost ecological services and availability of forest products (Lamb *et al.* 2005). This necessitates the restoration of ecological balance and conservation of biodiversity. For *ex-situ* conservation and

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reintroduction of a species it is imperative to understand seed behavior. Seed storage behavior is dependent on seed sensitivity to desiccation. It has been estimated that nearly half of all tropical plant species produce seeds that are desiccation sensitive (Hill *et al.* 2012). These seeds are characterized by loss in viability with a decrease in moisture content below a critical level. Due to inherent high moisture content, recalcitrant seeds germinate rapidly and are considered non-dormant or viviparous (Tweddle *et al.* 2003). However, there have been reports of delayed germination in some recalcitrant species (Hong & Ellis 1990; Hong *et al.* 1998; Msanga 1998). Baskin & Baskin (2005) stressed that even with recalcitrant seeds, attention needs to be given to the time required for germination to occur. If fresh and untreated seeds require more than four weeks to germinate, the seeds are considered dormant (Baskin and Baskin 2005; Sautu *et al.* 2007). For example, this is the case with recalcitrant seeds of *Garcinia livingstonii* and *Ocotea usambarensis,* where germination continued for seven weeks, indicating that at least some seeds of these species have physiological dormancy (Msanga 1998; Baskin & Baskin 2005). Seeds with an impermeable seed coat have physical dormancy (PY), while those with fully developed embryos and a permeable seed coat, but with a physiological inhibition mechanism in the embryo that prevents radical emergence, have physiological dormancy (PD) (Baskin & Baskin 1998, 2004, 2014). Further, it is known that PD is prominent in tropical rainforest species, decreasing from evergreen to deciduous forests but increasing slightly in savanna and montane forests. In contrast, PY increases from evergreen to savanna forests but decreases in montane forests (Baskin & Baskin 2005). The pattern of PD being predominant in evergreen forests may be attributed to those species that have seeding time at the end of or beyond the rainy season; in these species, PD would facilitate overcoming the prevailing low moisture conditions. In tropical evergreen forests, seeds are exposed to high temperatures between the time of seed dispersal and germination, and the high temperatures facilitate a warm stratification and promote loss of seed dormancy in PD seeds (Baskin & Baskin 1998). According to Garwood (1983), physiological dormancy appears to be the dormancy class of the majority of dormant seeds dispersed in the late rainy season. However, evolutionary origins and biogeography of seed dormancy in tree species of rainforest ecosystems is not yet well understood.

In tropical evergreen forests, most species have recalcitrant seeds and the storage of these seeds is a challenge. At maturity these seeds have high moisture content and if the moisture content drops below a certain species-specific critical level then they lose viability (Baskin & Baskin 1998), as in the case of *Garcinia mangostana* (24%), *G. motleyana* (< 35%) (Normah *et al.* 1997), *Cryptocarya floribunda* (~31%) (Thapliyal *et al.* 2004), *Humboldtia laurifolia* (20%) (Jayasuriya *et al.* 2010), *Treculia africana* (≤ 24.1%) (Oboho & Ngalum 2014) and *Artocarpus heterophyllus* (~60%) (Adelina *et al.* 2014) and *Podocarpus nagi* (~16%) (Ming-Yue *et al.* 2015). Sensitivity of recalcitrant seeds to desiccation varies by species, with those that are sensitive having a short life span and those that are tolerant having a relatively long life span (Farrant *et al.* 1988). Among and within a species, recalcitrant seeds vary in water content at shedding, the extent of dehydration they tolerate, storage lifespan in the hydrated state, their response to low temperatures and drying rate (Berjak *et al.* 1993; Finch-Savage 1992; Pritchard 1991; Tompsett & Pritchard 1998). Rate of dehydration significantly affects the desiccation tolerance of recalcitrant seeds, with faster drying rates conferring greater tolerance to desiccation (Berjak & Pammenter 1997; Rosa *et al.* 2005). During drying, aqueous-based metabolism continues, but becomes unbalanced, resulting in failure of anti-oxidant systems and leading to generation of reactive oxygen species (ROS) (Finch-Savage *et al.* 1994; Varghese *et al.* 2011; Vertucci and Farrent 1995). This metabolism-linked damage (Walters *et al.* 2001) causes damage to cell membranes, proteins and DNA, leading to loss of viability (McDonald 1999). Under conditions of rapid drying, the time during which metabolism-linked damage occurs is curtailed, so viability is retained at lower moisture content (Berjak & Pammenter 2013). With slower drying, the seed tissues spend a longer time exposed to inter-mediate water contents that allow deleterious, aqueous-based processes to cause serious damage to membrane structure.

Garcinia gummi-gutta (L.) N. Robson (syn. *G. cambogia, Mangostana cambogia*; Family Clusiaceae or Guttiferae), commonly known as Gamboge or Brindal berry, is a medium-sized, dioecious tree endemic to rainforests of Western Ghats of India and Sri Lanka. It grows up to an altitude of 1800 m with mean annual temperature and mean annual rainfall of 15–30 °C and 1500-4000 mm, respectively. The fruits of *G. gummi-gutta* are used in treatment of rheumatism, bowel complaint and obesity (Orwa *et al.* 2009; USDA-ARS 2013). The extraction of Hydroxy Citric Acid from the fruit rind for its anti-obesity property has created a huge international market, and the uninhibited extraction of fruits will have ecological ramifications, not only in terms of availability of fruits for frugivores, but also on the regeneration and future survival of the species (Rai 2004). Additionally, ants devour seed kernels of *G. gummi-gutta*, which reduces the chances of seed survival with time (Rai 2003).

Fruits of *G. gummi-gutta* are fleshy and bear five to seven seeds. The fruiting season coincides with the southwest monsoon. Seeds with intact seed coats require 20 weeks for initiation of germination under controlled nursery conditions, whereas the de-coated seeds germinate in three weeks (Joshi *et al.* 2006). Earlier studies in *G. gummi-gutta* have suggested seed-coat-imposed dormancy due to impermeability of water (*i.e.*, PY; Chacko & Pillai 1997; Joshi *et al*. 2006; Mathew & George 1995), which is unexpected considering the phylogeny of seed dormancy patterns in Clusiaceae inferred by Baskin & Baskin (1998). Most genera in the Clusiaceae family grow in evergreen and semi-evergreen tropical forests and are known for producing either non-dormant or physiologically dormant seeds (Baskin & Baskin 1998). Since fresh mature seeds of *G. gummi-gutta* require more than four weeks to germinate and the majority of its congeners have PD seeds, this study was conducted to determine the nature of seed dormancy in *G. gummi-gutta*. The seeds of *G. gummi-gutta* have also been reported to be recalcitrant (Chacko & Pillai 1997) and have viability of maximum 60 days when stored at 15 °C (Malik *et al.* 2005). However, Rai (2003) has reported that in nature, the seeds germinate after eight months under natural conditions. Therefore, along with dormancy behavior, it is essential to study the effect of different temperatures on drying rate, desiccation sensitivity and seed storage behavior for facilitating *ex situ* conservation. Ecologically, these seed characteristics are important as they regulate a number of regeneration strategies such as synchronization of seed germination timing with onset of monsoon season. They also maintain seed viability until the wet season so that particular seed moisture content coincides with temperatures needed for successful establishment of seedlings at an appropriate time.

Material and methods

Mature yellow fruits were collected during the monsoon season in July–August 2005 from Somwarpet, Coorg district, Karnataka, India from 21 trees. Fruits were de-pulped and seeds were separated. The cleaned seeds from all the trees were bulked and surface dried at room temperature (25 ± 2 °C) by spreading them in a single layer on a laboratory bench for two days. Samples were drawn from the bulked seeds, and initial moisture content and germination were determined. Moisture content was calculated on a fresh weight basis (ISTA 1993). The fresh weight of five replicates of 10 seeds each with an intact seed coat was taken. The seeds were then dried at 103 ± 2 °C for 17 hours and dry weights were recorded. To determine germination percentages, four replicates of 100 de-coated seeds were germinated on paper towels in a growth chamber at 30 ± 2 °C. Seeds had an initial MC of 43% and had 100% germination.

Effect of seed coat on water uptake

To determine whether seeds have a water-impermeable seed coat, *i.e.*, seeds have PY or not, water uptake (imbibition) was monitored in intact seeds (with seed coat) and de-coated seeds. Twenty-five seeds each with (a) intact seed coat as a control and (b) de-coated seeds were placed on filter paper moistened with distilled water in 9 cm diameter petri dishes and kept on a laboratory bench at room temperature (c. 25 ± 5 °C). After 0, 4, and 11 days, each of the 25 seeds per treatment were blotted dry, weighed to the nearest 0.1 mg and returned to the moistened filter paper. The amount of water uptake by each of the 25 seeds was calculated using the following equation (Baskin *et al.* 2004):

$$\%W_i = [(W_i - W_d)/W_d] \times 100,$$

Where W_i and W_d = mass of imbibed and dry seeds, respectively. Student's t-test was used to quantify differences in imbibition rates between seed with/without seed coats.

Phenology of seedling emergence

To test for PD in seeds of *G. gummi-gutta*, on 1st September 2005, four replicates of 100 seeds each with intact seed coats and de-coated seeds were sown on nursery trays placed in a non-temperature-controlled poly-house at the Institute of Wood Science and Technology, Bangalore, Karnataka, India, until the first week of March 2006. Nursery beds were watered as required and daily maximum and minimum temperatures were recorded. Seedlings that emerged above the soil surface were counted and removed initially at 3–4 day intervals and later at two-week intervals.

Seed desiccation at different temperatures

Intact seeds (with 43% MC and 100% viability) were desiccated in glass desiccators using silica gel at 15, 25 and 35 °C temperature maintained in BOD incubators. The desiccators were sealed using petroleum jelly and the silica gel was changed at periodic intervals as the color changed from blue to white. Changes in MC and germination percentage were recorded at 24, 48, 72, 96, 120, 168, 240, 336 and 504 hours. For recording change in MC, 10 replicates of a single seed each were taken from the desiccators and for germination, four replicates of 25 seeds each were taken. The seeds were de-coated and germinated on paper towels in a growth chamber at 30 ± 2 °C and germination was monitored. The change in germination percentage for seed desiccated at different temperatures and time period was compared for significance using ANOVA.

Seed storage

Samples were drawn from the processed seed lot with initial MC of 43%, for storage at six different storage temperatures, *i.e.* –10, 5, 15, 25, 35 °C and room temperature (25 ± 10 °C). The remaining seeds were further dried by spreading on a laboratory bench at room temperature (25 ± 3 °C) and MC was periodically checked. By the end of two weeks the seeds had attained 34% MC. The seeds with these two different MCs (43 and 34%) were stored at six different storage temperatures for 18 months in plastic boxes with sealed lids.

Viability of stored seeds was tested at bimonthly intervals for 18 months. For viability testing, three replicates of 50 de-coated seeds per replicate were taken and germinated on paper towels in a growth chamber at 30 ± 2 °C. The viability of seed stored in different combinations of temperature and seed moisture content was compared for significance using ANOVA prior to Probit analysis. To determine the optimum conditions for long-term storage, Probit analysis of germination percentage vs. storage time was performed, and the time taken for viability to decline to 50% of the original, or the half viability period (P_{50}), was calculated according to Roberts (1973). To assess the trend of change in germination, survival curves were drawn by plotting expected germination (calculated through Probit analysis) against storage period in months. Probit analysis was performed using SPSS v.12.0.

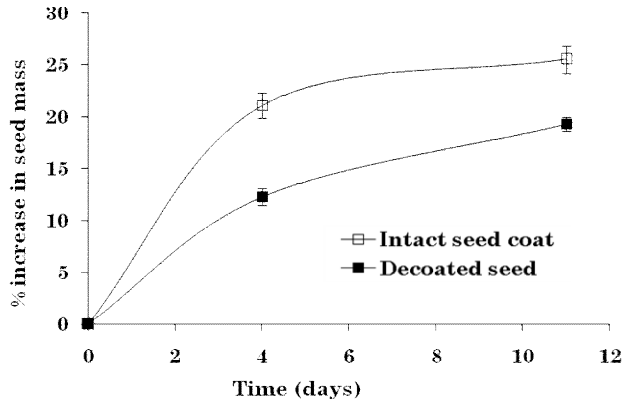

Fig. 1. Time course for water uptake in *G. gummi-gutta* seeds on moist filter paper at ambient laboratory temperature (c. 25 °C) (t - value$_{(df)}$ = 4.01$_{(24)}$; P = 0.01). Data are mean ± SE.

Results

Effect of seed coat on water uptake

Imbibition rates for intact and de-coated seeds significantly differed (Fig. 1). The weight of seeds with intact seed coats increased by 21% in 4 days and by 25% in 11 days, whereas the weight of de-coated seeds increased by 12 and 19% in 4 and 11 days, respectively (Fig. 1).

Phenology of seedling emergence

Seedlings emerged within four weeks from > 90% of the de-coated seeds sown on 1st September 2005. The mean daily minimum and maximum temperatures were 21 and 30 °C, respectively. By the first week of October 2005, seedlings had emerged from 94% of the seeds (Fig. 2). Seedlings did not emerge from seeds with intact seed coats even after 17 weeks from sowing (December 2005). Seedling emergence was initiated in the first week of January 2006 and by 1st March 2006 seedlings had emerged from 92% of the intact seeds, when mean daily minimum and maximum temperatures were 21 and 34 °C, respectively. Thus, seeds with an intact seed coat required 26 weeks for > 90% seedling emergence (Fig. 2).

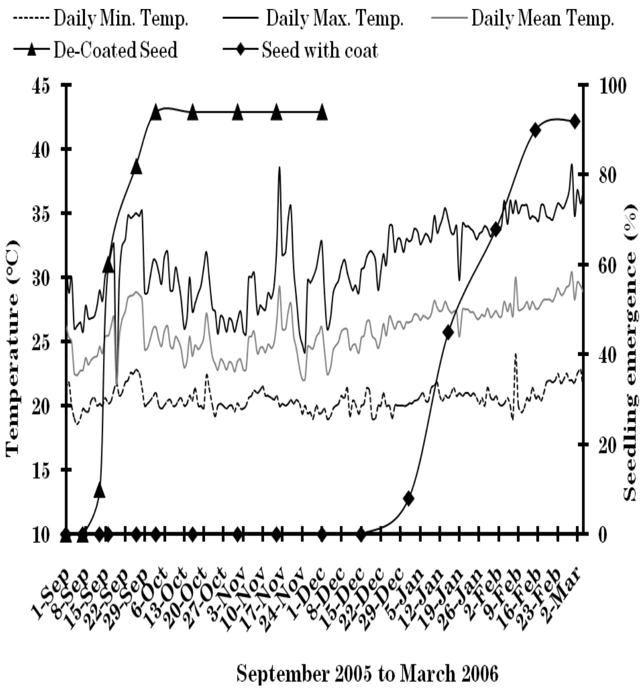

Fig. 2. Daily maximum, minimum and mean temperatures and phenology of seedling emergence in *G. gummi-gutta* seeds sown in nursery beds.

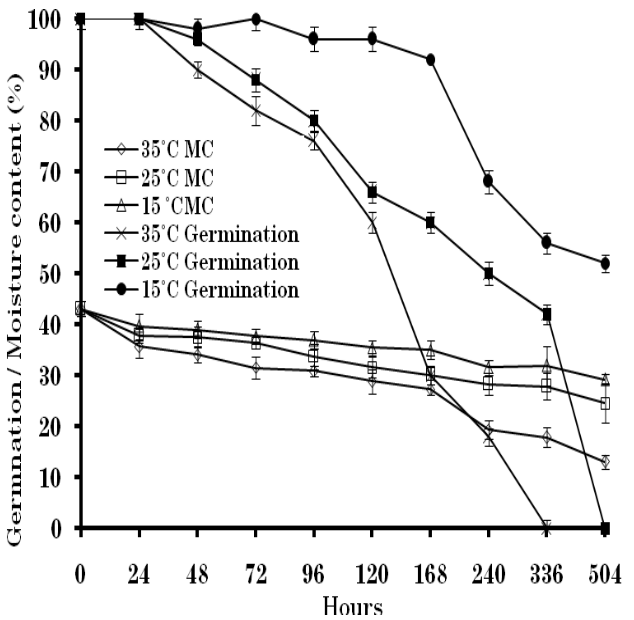

Fig. 3. Effect of drying with silica gel on moisture content (MC) and germination percentage of *G. gummi-gutta* seeds at 15, 25 and 35 ºC temperatures (F - value$_{(df)}$ = 12.64$_{(2,119)}$; P = 0.0003). Data are mean ± SE.

Seed desiccation at different temperatures

Drying by silica gel at different temperatures resulted in significantly different drying rates (Fig. 3). It was observed that ~34% MC was attained in 48, 72 and 168 hours at 35, 25, and 15 ºC, respectively, with ~90% germination. At all the temperatures, even though they have a different drying rates, germination percentage at 34% moisture was about 90%. However, on reduction of moisture content below ~34%, the rate of drying as well as germination percentage varied with the temperature. MC of 31% was attained in 72, 120 and 336 hours with the corresponding germination of 84, 69 and 56% at 35, 25, and 15 ºC, respectively. The rate of loss of germination was rapid below 29% MC at 35 ºC and 28% at 25 ºC. Germination was 50% for the seeds desiccated at 15 and 25ºC for 504 and 240 hours with 29 to 28% MC, respectively (Fig. 3). Complete loss of viability was observed at 17% MC by 336 hours at 35 ºC and at 24% MC by 504 hours at 25 ºC (Fig. 3).

Seed storage

The mean germination percentage was significantly different among temperature ($F_{5,240}$ = 1868; P < 0.01), moisture content ($F_{1,\ 240}$ = 273.7; P < 0.01) and the interaction of moisture content and temperature ($F_{5,240}$ = 90.63; P < 0.01) and moisture content, temperature and months of storage ($F_{45,\ 240}$ = 26.61; P < 0.01) (Figs. 4 and 5). When seeds were stored at -10 and 5 ºC complete loss of viability was observed by 2 months. Viability of seeds was also lost within 4 months when seeds were stored at high temperature (35 ºC). The seeds are thus sensitive to low as well as high temperatures. Survival curves showed that reductions in germination were faster at 43% MC as compared to reduced MC of 34% (Fig. 4). At room temperature the seeds with 43 and 34% MC had zero and 5% viable seeds, respectively, by 18 months. Maximum viability of 90% was retained by seeds stored at 15 ºC at both the MCs. Probit analysis revealed that seeds stored at 15 ºC with 34% MC would take 336 months to reach the half viability period (Fig. 5).

Discussion

Mature seeds of *G. gummi-gutta* with an intact seed coat did not germinate within four weeks, indicating some kind of dormancy. Earlier reports

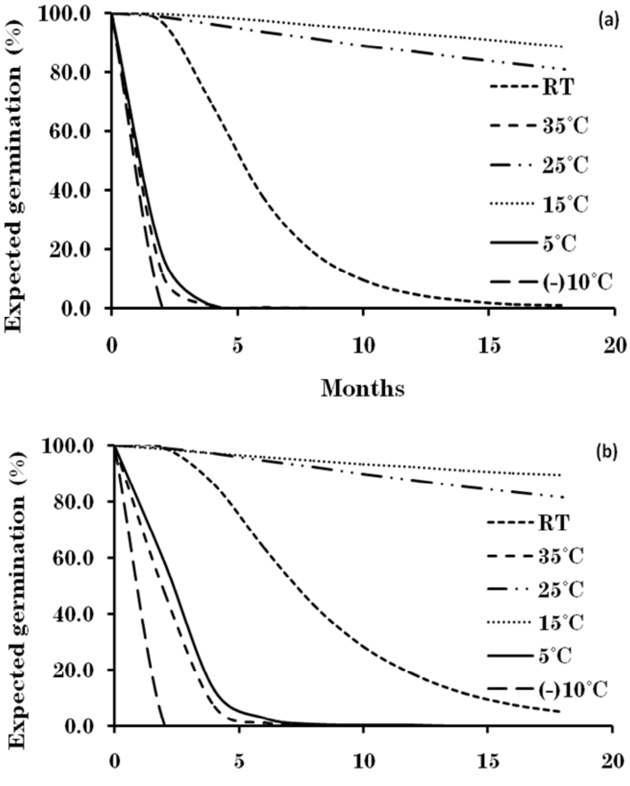

Fig. 4. Survival curves for the seeds of *G. gummi-gutta* with (a) 43% and (b) 34% moisture content stored at –10, 5, 15, 25, 35 °C and at ambient laboratory temperature (25 ± 10 °C). By Probit analysis of germination data, expected germination was calculated and plotted against months to get survival curves.

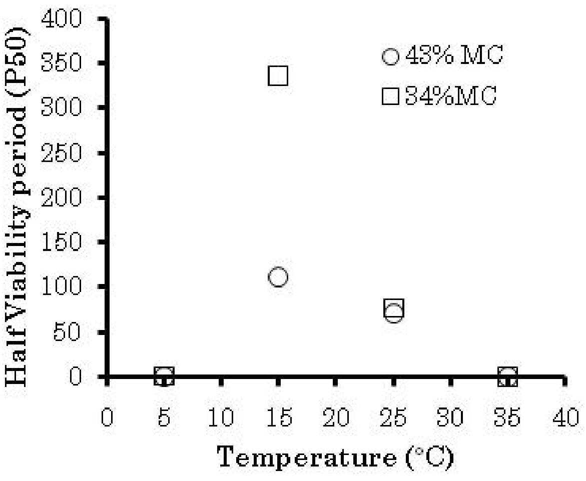

Fig. 5. Half viability period (P_{50}) of seeds with 43 and 34% moisture content (MC) stored at 5, 15, 25, 35 °C and at ambient laboratory temperature (25 ± 10 °C) extrapolated by Probit analysis of germination data.

of PY in this species (Chacko & Pillai 1997; Joshi *et al.* 2006; Mathew & George 1995) imply that the seed coat is water impermeable. However, in our study, both untreated (intact seed coat) and treated (without seed coat) seeds imbibed 25 and 19% water at different rates within 11 days of incubation on wet substrate (Fig. 1). Similarly, in *Garcinia cowa,* intact seeds imbibed more water than de-coated seeds (Liu *et al.* 2005). The fibrous seed coat surface and presence of gum resin (called Gamboge) sandwiched in the seed coat may be the reason for the high percentage of water uptake by intact seeds. Generally, seeds with PY need to dry to < 20% MC for the seeds or fruit coat to become water impermeable (Qu *et al.* 2010). In case of *G. gummi-gutta* the seeds had 43% moisture content, so it is not surprising that seeds of this species do not have PY.

Although seeds of *G. gummi-gutta* with an intact seed coat absorbed water, they failed to germinate within a four-week period of incubation. This indicates that the seed coat acts as a mechanical barrier, which is corroborated by the fact that when the seed coat was removed, a high percentage of seeds germinated within four weeks (Fig. 2). Nikolaeva (1977) previously recognized this type of dormancy as a mechanical dormancy. However, the new classification scheme proposed by Baskin & Baskin (2004) views mechanical dormancy as a component of PD. Therefore, we also recognize mechanical resistance by the seed coat in *G. gummi-gutta* as a component of PD, similar to seeds of *Calophyllum longifolium* (Garwood 1983), *Garcinia nigrolineata* (Ng 1973, 1980), *G. opaca* (Ng 1978), *G. parvifolia* (Ng 1978, 1980), *G. scortechinii* (Ng & Asri 1979), and *G. cowa* (Liu *et al.* 2005) of the Clusiaceae family, as inferred by Baskin and Baskin (1998). Further, Baskin & Baskin (2004) recognized three levels of PD: deep, intermediate and non-deep. The phenology of seedling emergence in *G. gummi-gutta* revealed that seeds were exposed to about 21–31 °C temperature throughout the experimental period. Thus, it revealed that *G. gummi-gutta* seeds require warm stratification to overcome PD. In addition, Joshi *et al.* (2006) highlighted that excised embryos produce normal seedlings and scarification promotes germination in this species. Based on these characteristics, it can be concluded that *G. gummi-gutta* seeds have non-deep PD.

In this study the effect of temperature on drying rate and desiccation tolerance was critically examined. It was found that at 35 °C, drying rate was faster compared to 15 and 25 °C. This is similar to findings for *Eugenia involucrata*, where the rate of drying was faster at 50 °C than at 40 and 30 ºC (Maluf *et al.* 2003). We also found that desiccation tolerance was higher on drying at 35 ºC as compared to 15 ºC. At 35 ºC, 29% moisture content was attained in 72 hours with 60% germination; however at 15 ºC the same moisture content was attained by seeds in 504 hours with only 52% germination. Earlier reports also suggest that rapid drying of whole seeds allows lower water content to be attained whilst still retaining viability (Farrant *et al.* 1986; Pammenter *et al.* 1998). This is because at slow drying, seed tissue spends a longer time at intermediate water content at which deleterious processes occur due to unregulated metabolism (Pammenter & Berjak 1999; Walters *et al.* 2001).

Recalcitrant seeds show differential responses to dehydration at different drying rates, therefore it is not possible to define unequivocally a critical moisture content (i.e., the moisture content below which there is a rapid reduction in viability; CMC) for viability loss (Pammenter *et al.* 1998). However, in this study, we found that up to ~34% MC, the rate of drying had no effect on seed viability and below this there was a rapid reduction in viability, and desiccation tolerance was dependent on drying rate. Therefore it can be concluded that ~34% is the CMC for this species. According to Vertucci & Farrant (1995) CMC in general is near 30% and dependent on membrane integrity and metabolic activity. Similarly, in *Garcinia kola* CMC is 30% (Asomaning *et al.* 2011). In *G. gummi-gutta* viability was completely lost at 17 and 24% MC at 35 and 25 ºC, respectively, and cannot be sustained at a temperature below 15 ºC. Bedi & Basra (1993) have reported that storage temperatures below 15 ºC are lethal for most tropical recalcitrant seeds. Chilling sensitivity in *G. gummi-gutta* has also been reported by Malik *et al.* (2005). Due to their low tolerance to desiccation and chilling sensitivity, *G. gummi-gutta* can be classified as recalcitrant. The recalcitrant nature of this species is in accordance with the other members of Clusiaceae family. Storage behavior of nine of the 11 *Garcinia* species in the Seed Information Database (Royal Botanic Gardens Kew, 2008) have been classified or provisionally classified as recalcitrant seeds. Seeds of *G. livingstonii* (Hong *et al.* 1998), *G. cowa* (Liu *et al.* 2005), *G. indica, G. cambogia* (syn. *G. gummi-gutta*), *G. xanthochymus* (Malik *et al.* 2005) and *G. kola* (Asomaning *et al.* 2011) have also been reported to be desiccation sensitive.

The seeds stored at ambient temperature (25 + 5 ºC) with 43% MC had 27% viability at month eight and those stored with 34% MC had 21% viability at month 12. However, Malik *et al.* (2005) reported that under ambient conditions, seeds of *G. cambogia* (syn. *G. gummi-gutta*) retain viability only for 30 days. This is in contrast to the survival mechanism of *G. gummi-gutta* under natural conditions. The seeds remain dormant for eight months under natural conditions and germinate at the onset of the monsoon (Rai 2003). This substantiates our results of 8 to 12 months of seed viability under ambient conditions.

The species can be stored for 18 months at 15 ºC at both the moisture contents with 90% viability. This contradicts the results by Malik *et al.* (2005), as they reported that viability was completely lost by 60 days at 15 ºC. Our results suggest that optimum conditions for long-term seed storage *of G. gummi-gutta* is 15 ºC at 34% seed moisture content.

Dormancy in recalcitrant seed is not a common phenomenon but has been reported from both temperate and tropical species like *Beilschmiedia kweo, Ocotea usambarenses* (Msang 1998), *Garcinia livingstonii* (Hong *et al.* 1998), *G. cowa* (Liu *et al.* 2005), *Cryptocarya floribunda* (Thapliyal *et al.* 2004), *Humboldtia laurifolia* (Jayasuriya *et al.* 2010), *Browenea coccinea* and *Cynometra cauliflora* (Jayasuriya *et al.* 2012). *G. gummi-gutta,* in spite of being desiccation sensitive, can sustain viability for a long time, even under natural conditions due to PD. According to Debeaujon *et al.* (2000) and Liu *et al.* (2005), dormancy often confers greater seed longevity and it is easier to store recalcitrant seed with dormancy. It could be an adaptation to overcome the prevailing unfavorable dry conditions during the time of fruit maturity, thereby facilitating germination at the onset of the more favorable monsoon season. The information about the nature of seed dormancy and desiccation sensitivity would also help in devising strategies for the *ex situ* conservation of the species.

Conclusion

We show that seeds of *G. gummi-gutta* have non-deep physiological dormancy and are sensitive to desiccation and low temperatures. The critical MC of these seeds is ~34% and the optimum conditions for long-term seed storage are 15 ºC with 34% MC. The seeds are classified as a tropical dormant recalcitrant. This has ecological significance as it helps seeds to survive dry conditions and leads to germination of seeds in the subsequent monsoon season.

References

Adelina, E., L. B. Sutopo, B. Guritno & Kuswanto. 2014. Mutual effect of drying on jackfruit (*Artocarpus heterophyllus* Lamk.) seed viability to water critical level for storage indicator. *Scholars Academic Journal of Biosciences* **2**: 909–912.

Asomaning, M. J., N. S. Olympio & M. Sacande. 2011. Desiccation sensitivity and germination of recalcitrant *Garcinia kola* Heckel seeds. *Research Journal of Seed Science* **4**: 12–27.

Baskin, C. C. & J. M. Baskin (eds.). 1998. *Seeds Ecology, Biogeography, and Evolution of Dormancy and Germination*. Academic Press, New York.

Baskin, C. C. & J. M. Baskin (eds.) 2014. *Seeds Ecology, Biogeography, and Evolution of Dormancy and Germination*. Second Edition, Academic Press, New York.

Baskin, J. M. & C. C. Baskin. 2004. A classification system for seed dormancy. *Seed Science Research* **14**: 1–16.

Baskin, C. C. & J. M. Baskin. 2005. Seed dormancy in trees of climax tropical vegetation types. *Tropical Ecology* **46**: 17–28.

Baskin, J. M., B. H. Davis, C. C. Baskin, S. M. Gleason & S. Cordell. 2004. Physical dormancy in seeds of *Dodonaea viscosa* (Sapindales, Sapindaceae) from Hawaii. *Seed Science Research* **14**: 81–90.

Bedi, S. & A. S. Basra. 1993. Chilling injury in germinating seed: basic mechanism and agricultural implications. *Seed Science Research* **3**: 219–229.

Berjak, P. & N. M. Pammenter. 1997. Progress in the understanding and manipulation of desiccation sensitive (recalcitrant) seeds. pp. 689–703. *In:* R. M. Ellis, M. Black, A. J. Murdoch & T. D. Hong (eds.) *Basic and Applied Aspects of Seed Biology: Proceedings of Fifth International Workshop on Seeds*. Kluwer Academic Publishers, London.

Berjak, P. & N. W. Pammenter. 2013. Implications of the lack of desiccation tolerance in recalcitrant seeds. *Frontiers in Plant Science* **4**: 478. doi: 10.3389/fpls.2013.00478

Berjak, P., C. W. Vertucci & N. W. Pammenter. 1993. Effect of developmental status and dehydration rate on characteristics of water and desiccation sensitivity in recalcitrant seeds of *Camellia sinensis*. *Seed Science Research* **3:** 155–166.

Chacko, K. C. & P. K. C. Pillai. 1997. Seed characteristics and germination of *Garcinia gummi-gutta* (L.) Robs. *Indian Forester* **123**: 123–126.

Chomitz, K. M. 2007. *At Loggerheads?: Agricultural Expansion, Poverty Reduction, and Environment in the Tropical Forests*. World Bank, Washington, DC.

Debeaujon, I., K. M. Leon-Kloosterziel & M. Koornneef. 2000. Influence of the testa on seed dormancy, germination and longevity in *Arabidopsis*. *Plant Physiology* **122**: 403–413.

Farrant, J. M., N. W. Pammenter & P. Berjak. 1986. The increasing desiccation sensitivity of recalcitrant *Avicennia marina* seed with storage time. *Physiologia Plantarum* **67:** 291–298.

Farrant, J. M., N. W. Pammenter & P. Berjak. 1988. Recalcitrance: A current assessment. *Seed Science and Technology* **16**: 155–166.

Finch-Savage, W. E. 1992. Seed development in the recalcitrant species *Quercus robur* L. germinability and desiccation tolerance. *Seed Science Research* **2**: 17–22.

Finch-Savage, W. E., S. K. Pramanik & J. D. Bewley. 1994. The expression of dehydrin proteins in desiccation-sensitive (recalcitrant) seeds of temperate trees. *Planta* **193**: 478–485.

Garwood, N. C. 1983. Seed germination in a seasonal tropical forest in Panama: A community study. *Ecological Monographs* **53**: 159–181.

Hill, J. P., W. Edwards & P. J. Franks. 2012. Size is not everything for desiccation sensitive seeds. *Journal of Ecology* **100**: 1131–1140.

Hong, T. D. & R. H. Ellis. 1990. A comparison of maturation drying, germination and desiccation tolerance between developing seeds of *Acer pseudoplatanus* L. and *Acer platanoides* L. *New Phytologist* **116***:* 589–596.

Hong, T. D., S. Linington & R. H. Ellis. 1998. *Compendium of Information on Seed Storage Behaviour*. Royal Botanic Gardens, Kew, UK.

ISTA (International Seed Testing Association). 1993. International rules for seed testing. Rules 1993. *Seed Science and Technology* **21**: 1–75.

Jayasuriya, K. M. G. G., A. S. T. B. Wijetunga, J. M. Baskin & C. C. Baskin. 2010**.** Recalcitrancy and a new kind of epicotyl dormancy in seeds of the understory tropical rainforest tree *Humboldtia laurifolia* (Fabaceae, Caesalpinioideae). *American Journal of Botany* **97**: 15–26.

Jayasuriya, K. M. G. G., A. S. T. B. Wijetunga, J. M. Baskin & C. C. Baskin. 2012**.** Physiological epicotyls dormancy and recalcitrant storage behaviour in seeds of two tropical Fabaceae (subfamily Caesalpinioideae) species. *AoB PLANTS* **2012**: pls044;doi:10.1093/aobpla/pls044.

Joshi, G., A. N. Arunkumar, B. Gowda & Y. B. Srinivasa. 2006. Production of supernumerary plants from seed fragments in *Garcinia gummi-gutta*: Evolutionary implications of mammalian frugivory. *Current Science* **91**: 372–376.

Lamb, D., D. P. Erskine & A. J. Parrottam. 2005. Restoration of degraded tropical forest landscapes. *Science* **310**: 1628–1632.

Liu, Y., Y. P. Qiu, L. Zhang & J. Chen. 2005. Dormancy breaking and storage behaviour of *Garcinia cowa* Roxb. (Guttiferae) seeds: Implications for ecological function and germplasm conservation. *Journal of Integrative Plant Biology* **47**: 38–49.

Malik, S. K., R. Chaudhury & Z. Abraham. 2005. Desiccation-freezing sensitivity and longevity in seeds of *Garcinia indica, G. cambogia* and *G. xanthochymus*. *Seed Science and Technology* **33**: 723–732.

Maluf, A. M., D. A. C. Bilia & C. J. Barbedo. 2003. Drying and storage of *Eugenia involucrata* DC. seeds. *Scientia Agricola* **60**: 471–475.

Mathew, K. L. & S. T. George. 1995. Dormancy and storage of seeds in *Garcinia cambogia* Desr. (Kodampuli). *Journal of Tropical Agriculture* **33**: 77–79.

McDonald, M. B. 1999. Seed deterioration: physiology, repair and assessment. *Seed Science Technology* **27**: 177–237.

Ming-Yue, J., Z. Nan, Y. Qi, & W. Bin. 2015. Storage behavior characteristics of recalcitrant *Podocarpus nagi* seeds. *Plant Diversity and Resources* **37**: 63–70.

Msanga, H. P. 1998. *Seed Germination of Indigenous Trees in Tanzania: Including Notes on Seed Processing, Storage and Plant Uses*. Canadian Forest Service, Northern Forestry Centre, Edmonton, Canada.

Ng, F. S. P. 1973. Germination of fresh seeds of Malaysian trees. *Malaysian Forester* **36**: 54–65.

Ng, F. S. P. 1978. Strategies of establishment in Malayan forest trees. pp. 129–162. *In*: P. B. Tomlinson & M. H. Zimmermann (eds.) *Tropical Trees as Living Systems*. Cambridge University Press, UK.

Ng, F. S. P. 1980. Germination ecology of Malaysian woody plants. *Malaysian Forester* **43**: 406–438.

Ng, F. S. P. & N. S. Asri. 1979. Germination of fresh seeds of Malaysian trees IV. *Malaysian Forester* **42**: 221–224.

Nikolaeva, M. G. 1977. Factors controlling the seed dormancy pattern. pp. 51–74. *In*: A. A. Khan (ed.) *The Physiology and Biochemistry of Seed Dormancy and Germination*. North-Holland Publishing Company, Amsterdam.

Normah, M. N., S. D. Ramiya & M. Gintangga. 1997. Desiccation sensitivity of recalcitrant seeds - a study on tropical fruit species. *Seed Science Research* **7**: 179–183.

Oboho, E. G. & E. L. Ngalum. 2014. Germination response of *Treculia africana* (Dacne) seeds in relation to moisture content, storage method and its duration. *Journal of Applied and Natural Science* **6**: 88–94.

Orwa, C., A. Mutua, R. Kindt, R. Jamnadass & A. Simons. 2009. Agroforestree Database: A tree reference and selection guide version 4.0 (World Agroforestry Centre, Kenya) Available at http://www.worldagroforestry.org/af/treedb [accessed on 27 March 2013]

Pammenter, N. W. & P. Berjak. 1999. A review of recalcitrant seed physiology in relation to desiccation-tolerance mechanisms. *Seed Science Research* **9**: 13–37.

Pammenter, N. W., V. Greggain, J. L. Kioko, J. Wesley Smith, P. Berjak & W. E. Finch Savage. 1998. Effects of differential drying rates on viability retention of recalcitrant seeds of *Ekebergia capensis*. *Seed Science Research* **8**: 463–471.

Pritchard, H. W. 1991. Water potential and embryonic axis viability in recalcitrant seeds of *Quercus rubra*. *Annals of Botany* **67**: 43–49.

Qu, X., J. M. Baskin & C. C. Baskin. 2010. Whole-seed development in *Sicyos angulatus* (Cucurbitaceae, Sicyeae) and a comparison with the development of water-impermeable seeds in five other families. *Plant Species Biology* **25**: 185–192.

Rai, N. 2003. *Human Use, Reproductive Ecology, and Life History of Garcinia gummi-gutta, a Non Timber Forest Product in the Western Ghats, India*. Ph.D. Thesis, Pennsylvania University. (http://www.libraries.psu.edu/theses/approved/WorldWide Index/ETD-352).

Rai, N. D. 2004. The socio-economic and ecological impact of *Garcinia gummi-gutta* fruit harvest in the Western Ghats. pp. 23–42. *In*: K. Kusters & B. Belcher (eds.) *Forest Products, Livelihoods and Conservation. Case Studies of Non-Timber Forest Product Systems*. Volume 1 - Asia. Center for International Forestry Research, Indonesia.

Roberts, E. H. 1973. Predicting the storage life of seeds. *Seed Science and Technology* **1**: 499–514.

Rosa, S. D. V. F., D. S. Brandão Junior, E. V. R. von Pinho, A. D. Veiga & L. H. C. Silva. 2005. Effects of different drying rates on the physiological quality of *Coffea canephora* Pierre seeds. *Brazilian Journal of Plant Physiology* **17**: 199–205.

Royal Botanic Gardens Kew. 2008. Seed Information

Database (SID). Version 7.1. Available from: http://data.kew.org/sid/ (May 2008) (accessed on 31 Dec. 2013).

Sautu, A., J. M. Baskin, C. C. Baskin, J. Deago & R. Condit. 2007. Classification and ecological relationships of seed dormancy in a seasonal moist tropical forest, Panama, Central America. *Seed Science Research* **17**: 127–140.

Thapliyal, R. C., S. S. Phartyal & J. Nayal. 2004. Germination, desiccation tolerance and storage of seed of a tropical evergreen tree - *Cryptocarya floribunda* Nees (Lauraceae). *Seed Science and Technology* **32**: 537–545.

Tompsett, P. B. & H. W. Pritchard. 1998. The effect of chilling and moisture status on the germination, desiccation tolerance and longevity of *Aesculus hippocastanum* L. seed. *Annals of Botany* **82:** 249–261.

Tweddle, J. C., J. Dickie, C. C. Baskin & J. M. Baskin. 2003. Ecological aspects of seed desiccation sensitivity. *Journal of Ecology* **91**: 294–304.

USDA, ARS**,** National Genetic Resources Program. ´Germplasm Resources Information Network - (GRIN)´ [Online Database]. (National Germplasm Resources Laboratory, Beltsville, Maryland) Available at http://www.ars-grin.gov/cgi-bin/npgs/html/taxon.pl?420224 [accessed 27 March 2013]

Varghese, B., Sershen, P. Berjak, D. Varghese & N. W. Pammenter. 2011. Differential drying rates of recalcitrant *Trichilia dregeana* embryonic axes: a study of survival and oxidative stress metabolism. *Physiologia Plantarum* **142**: 326–338.

Vertucci, C. W. & J. N. Farrant. 1995. Acquisition and loss of desiccation tolerance. pp. 237-271. *In*: J. Kigel & G. Galili (eds.) *Seed Development and Germination*. Marcel Dekker Inc., New York.

Walters, C., N. W. Pammenter, P. Berjak & J. Crane. 2001. Desiccation damage: Accelerated aging and metabolism in desiccation tolerant and sensitive seeds. *Seed Science and Research* **11**: 135–148.

Wright, J. S. 2005. Tropical forests in a changing environment. *Trends in Ecology and Evolution* **20**: 553–560.

(Received on 31.08.2015 and accepted after revisions, on 18.02.2016)