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OXIDATIVE STRESS ENZYME ACTIVITIES AND DESICCATION TOLERANCE IN SEEDS OF TWO RAINFOREST SPECIES, *AFZELIA AFRICANA* SM. AND *GAMBEYA ALBIDA* (G. DON) AUBREV. AND PELLEGR.

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Abstract

Plants when exposed to stress generate reactive oxygen species (ROS), which are detoxified through antioxidant defense systems involving enzymatic and non-enzymatic components. This research studied the impact of desiccation on the activities of some oxidative stress enzymes: Peroxidase (POD), Catalase (CAT), Polyphenol oxidase (PPO), and Glucose-6-phosphate dehydrogenase (G6PDH) in seeds of *Afzelia africana* and *Gambeya albida*. Mature seeds were collected directly from parent trees and desiccated under ambient laboratory conditions for 0, 3, 7, 10, 13, 15, 22 and 35 days, after which enzyme activities were assayed. In *A. africana*, maximum germination (90.00%) occurred after 15 days of desiccation at 4.86% moisture content, whereas germinability of *G. albida* declined by more than 50% after 7 days at 9.02% moisture. G6PDH activity in *A. africana* increased appreciably during early desiccation, while *G. albida* showed a momentary peak followed by decline. Peroxidase activity decreased initially in *A. africana* but increased in *G. albida* during early desiccation, whereas catalase activity increased at later stages in both species. PPO activity showed no significant differences between the species. Overall, the orthodox seeds of *A. africana* maintained stronger antioxidant enzyme responses during desiccation while the recalcitrant seeds of *G. albida* exhibited reduced enzymatic activity. These findings highlight the role of antioxidant enzymes in cellular stability during water loss and provide insight into the physiological basis of desiccation tolerance in tropical tree seeds.

Key words: *Antioxidant defense; Enzyme regulation; Moisture deficit; Reactive oxygen species; Seed viability; Tropical trees*

Introduction

Seeds are essential for crop production, used for both direct planting and raising seedlings (Larmaca *et al*., 2016). Most seeds can be stored for long periods and still maintain viability, allowing their use in times other than when they were produced, while others cannot be stored. Responses to desiccation differ between species; while some are sensitive to desiccation, others have more tolerance (Perez *et al*., 2012). Seeds are grouped based on how they react to desiccation as orthodox (desiccation tolerant), recalcitrant (desiccation sensitive) and then the intermediate seeds. Recalcitrant cannot be stored for long and this interfere with their long-term use in propagation and raising of seedlings (Black & Pritchard, 2002; Hay & Probert, 2013; Tchokponhoué *et al*., 2019).

Desiccation tolerance in orthodox seeds is due to a series of a fairly complex protection mechanisms triggered during dehydration (Illing *et al*., 2005). These protective mechanisms, including the rummaging of reactive oxygen species that were activated during desiccation, confer tolerance to desiccation (Berjak *et al*., 2007). Recent studies have further emphasized the central role of ROS metabolism and antioxidant enzymes in determining seed vigor, longevity and tolerance to environmental stresses during germination and seed ageing (Ellouzi *et al*., 2024; Ben Saad *et al*., 2024).

Most times, desiccation sensitive seeds may not have, or do not express the mechanisms that confer desiccation tolerance as obtained in desiccation tolerant seeds. According to Cheng & Song (2008), increased reactive oxygen species accumulation is associated with dehydration and the loss of viability in the desiccation sensitive seeds of *Antiaris toxiacaria*. Also they observed that dehydration accompanied an initial increase, and then reduction in the activity enzymatic antioxidants. Similar observations have been reported in several species where oxidative stress plays a major role in the loss or recovery of desiccation tolerance during seed dehydration and rehydration processes (Bailly *et al*., 2023).

Afzelia africana Sm. and *Gambeya albida* (G. Don) Aubrév. and Pellegr. are economically and ecologically important tropical tree species widely distributed in West and Central Africa (Orwa *et al*., 2009; Balima *et al*., 2018; Houehanou *et al*., 2023). *Afzelia africana* is a valuable hardwood species used extensively for timber, furniture and construction, making it an important component of tropical forest resources (Orwa *et al*., 2009; Balima *et al*., 2018). *Gambeya albida*, commonly known as African star apple, is an indigenous fruit tree valued for its edible fruits, nutritional importance and traditional medicinal uses (Leakey, 2017; Jamnadass *et al*., 2020). Despite their ecological and economic significance, limited information exists on the biochemical mechanisms underlying their seed responses to desiccation. Germination studies indicate

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that seeds of *A. africana* exhibit orthodox storage behaviour, whereas those of *G. albida* show characteristics typical of recalcitrant seeds during desiccation (Tweddle *et al*., 2003; Walters *et al*., 2013; Farnsworth *et al*., 2022).

Therefore, this research investigated the activities of selected oxidative enzymes, peroxidise, catalase and polyphenol oxidase and G6PDH in seeds of two timber species, *Afzelia africana* and *Gambeya albida* during desiccation. The objectives were to compare the antioxidant enzyme responses of the two species and to determine how these responses relate to differences in desiccation tolerance. It was hypothesized that the orthodox seeds of *A. africana* would maintain stronger antioxidant enzyme activity during dehydration than the recalcitrant seeds of *G. albida*, thereby contributing to greater tolerance to desiccation stress.

Materials and Methods

Study area/experimental site: This study was done in Calabar, Cross River State, Nigeria. The laboratory investigations were performed in the Graduate Research Laboratory of the Department of Plant and Ecological Studies (Botany), Faculty of Biological Sciences, University of Calabar.

Seed collection and preparation: Mature fruits of *Afzelia africana* and *Gambeya albida* were obtained directly by harvesting from the parent trees growing within the university campus. Fruits were manually de-pulped to obtain the seeds for the experiment.

Seed desiccation: Seeds were desiccated on a laboratory bench under ambient conditions (temperature 28–30°C and relative humidity 70–85%). The desiccation treatment was undertaken for 0, 3, 7, 10, 13, 15, 22 and 35 days. At each desiccation interval, twenty seeds of each species were randomly picked and weighed to obtain their fresh weight (FW). The weighed seeds were then dried using an oven at 100ºC to a constant weight to obtain the dry weight (DW). The moisture content (MC), in percentage, of the seed lot was calculated following Somrug *et al*., (2024) as:

$$MC\ (\%) = \frac{(\text{Fresh weight} - \text{Fresh weight})}{\text{Fresh weight}} \times 100$$

Biochemical studies on seeds: Seeds of each species, on collection and at each desiccation interval, were used for the extraction and assay of the following enzymes: glucose-6-phosphate dehydrogenase (G6PdH), peroxidise (POD), polyphenol oxidase (PPO) and catalase (CAT). Enzymes were extracted and assayed as reported by Ngele *et al*., (2024), and Nkangand Chandler (1989) with slight modifications.

Enzyme extraction: Enzymes were extracted using a mixed phosphate buffer containing 50 mM potassium phosphate buffer (pH 7.0) and 1% polyvinyl polypyrrolidone (PVPP) as a phenolic absorbent. Cotyledonary seed tissue (0.5 g) was homogenized in 5 ml extraction buffer using a chilled mortar and pestle. The homogenate was centrifuged at 6000 rpm for 10 min, and the supernatant was collected as the crude enzyme extract and kept on ice until analysis.

Enzyme assay: Enzyme activities were determined spectrophotometrically using a Unico S-2150 Series spectrophotometer at 30°C. Changes in absorbance were recorded and used to calculate enzyme activity using the equation:

$$\text{Volume activity (µmol product/L/min)} = \frac{1000 \times V \times Abs.}{v \times d \times \varepsilon \times t}$$

"where:
V = Total assay volume
Abs = Absorbance
v = Volume of enzyme extract
d = Internal diameter of cuvette (1cm)
ε = Extinction coefficient
t = Time in minutes"

The extinction coefficients employed for the calculations correspond to the specific chromogenic products formed in each assay and is widely used for quantifying enzyme activity under similar experimental conditions. These coefficients allow conversion of absorbance changes into enzymatic activity according to the Beer–Lambert law. Control reactions lacking enzyme extract were included in each assay to correct for non-enzymatic substrate oxidation and background absorbance.

Glucose-6-phosphate dehydrogenase assay: G6PDH activity was determined by measuring the formation of NADPH at 340 nm. The reaction mixture contained assay buffer, enzyme extract, glucose-6-phosphate substrate and NADP. Enzyme activity was calculated using an extinction coefficient of 6.22 mM^{-1} cm^{-1} for NADPH (Nkang &Chandler, 1989).

Peroxidase assay: Peroxidase activity was determined using guaiacol as the substrate. The reaction mixture contained assay buffer, enzyme extract, guaiacol and hydrogen peroxide. Formation of tetraguaiacol was monitored at 436 nm, and enzyme activity was calculated using an extinction coefficient of 6.39 mM^{-1} cm^{-1} (Ngele *et al*., 2024).

Polyphenol oxidase assay: PPO activity was determined using phloroglucinol as the substrate. After incubation of the reaction mixture at 30°C for 10 min, absorbance was measured at 475 nm. Enzyme activity was calculated using an extinction coefficient of 1433 mM^{-1} cm^{-1} for the quinone product (Nkang *et al*., 2000; Ngele *et al*., 2024).

Catalase assay: Catalase activity was determined by monitoring the decomposition of hydrogen peroxide at 240 nm. Prior to assay, the crude extract was partially purified by 80% ammonium sulphate precipitation. Enzyme activity was calculated using an extinction coefficient of 43.6 M^{-1} cm^{-1} for hydrogen peroxide (Ngele *et al*., 2024).

Statistical analysis: Germination studies were done using a completely randomized design. Data obtained from moisture

content, germination percentage, enzyme activities were based on three independent replicates and are presented as mean ± standard error of the mean (SEM). Statistical analyses were performed using the Statistical Package for Social Sciences (SPSS) for Windows, version 20.1.

Differences among desiccation intervals and between species were evaluated using one way analysis of variance (ANOVA). When ANOVA indicated significant treatment effects, mean separation was performed using Duncan's Multiple Range Test (DMRT) at a significance level of $p \leq 0.05$. DMRT was selected because of its sensitivity in detecting treatment wise differences across multiple desiccation intervals, allowing effective discrimination of gradual physiological changes associated with progressive drying.

Results

Effect of desiccation on germinability of *Afzelia africana* and *Gambeya albida*: The influence of desiccation on seed germinability of the two species is presented in Table 1. In *A. africana*, germination increased progressively during the early stages of desiccation, reaching a maximum value of 90.00% after 15 days, corresponding to a seed moisture content of 4.86%. However, germination declined significantly ($p \leq 0.05$) during prolonged desiccation periods (22–35 days).

In contrast, *G. albida* exhibited the highest germinability in freshly collected seeds (76.67%). Desiccation caused a rapid decline in viability, with more than 50% reduction in germinability by the 7th day of desiccation. Complete loss of germinability occurred from day 13 onward, indicating strong desiccation sensitivity in this species.

Glucose-6-phosphate dehydrogenase (G6PDH) activity in seeds of *Afzelia africana* and *Gambeya albida* during desiccation: Changes in G6PDH activity in seeds of *A. africana* and *G. albida* during desiccation are shown in Fig. 1.

In *A. africana*, G6PDH activity increased significantly ($p \leq 0.05$) from the time of seed collection to the 7th day of desiccation, after which a decline was observed with significantly lower activity recorded on the 13th day. Enzyme activity increased again significantly ($p \leq 0.05$) by the 35th day, corresponding to very low seed moisture levels (4.03%) (Table 1).

In *G. albida*, G6PDH activity increased significantly ($p \leq 0.05$) during the early desiccation period and reached a peak at 15 days. Thereafter, activity declined significantly ($p \leq 0.05$), with the lowest activity recorded on the 35th day, coinciding with reduced moisture content (9.02%) and loss of seed viability.

Peroxidase (POD) activity in seeds of *Afzelia africana* and *Gambeya albida* following desiccation: Peroxidase activity patterns differed between the two species (Fig. 2).

In *G. albida*, POD activity increased significantly ($p \leq 0.05$) from day 0 to day 10, reaching its maximum value at 10 days of desiccation. Thereafter, enzyme activity declined significantly ($p \leq 0.05$) with continued drying.

In contrast, *A. africana* showed the highest peroxidase activity in freshly collected seeds. Activity decreased significantly ($p \leq 0.05$) during desiccation, reaching the lowest level at 22 days, after which a significant ($p \leq 0.05$) increase was observed towards the 35th day.

Effect of desiccation on polyphenol oxidase (PPO) activity in seeds of *Afzelia africana* and *Gambeya albida*: The effects of desiccation on PPO activity are presented in Fig. 3. PPO activity was initially higher in seeds of *G. albida* at the time of collection. Activity declined gradually and significantly ($p \leq 0.05$) until the 22nd day of desiccation, after which a slight increase was observed.

Although PPO activity trends were broadly similar in both species, no statistically significant differences ($p > 0.05$) were detected between them at comparable desiccation intervals.

Effect of desiccation on catalase (CAT) activity in seeds of *Afzelia africana* and *Gambeya albida*: Catalase activity in seeds of *A. africana* initially increased and then decreased significantly ($p \leq 0.05$) during the early stages of desiccation (Fig. 4). However, enzyme activity increased again between 15 and 35 days, with the highest activity recorded on the 35th day of desiccation.

A similar pattern was observed in *G. albida*, although catalase activity was generally higher than in *A. africana*. The highest activity was recorded on the 22nd day of desiccation, after which a significant decline ($p \leq 0.05$) occurred by the 35th day, corresponding with very low seed moisture content (9.02%) and loss of germinability (Table 1).

Table 1. Effect of desiccation on seed moisture content and germinability (%) in seeds of *Afzelia africana* and *Gambeya albida*.

Desiccation period (days)	*Afzelia africana*		*Gambeya albida*	
	Moisture content (%)	Germinability (%)	Moisture content (%)	Germinability (%)
0	*13.81^{a} ± 0.62	66.28^{bcd} ± 0.23	*40.04^{a} ± 0.34	76.67^{a} ± 3.33
3	8.36^{b} ± 0.24	71.67^{abcd} ±4.41	37.23^{b} ± 0.18	56.67^{b} ± 3.33
7	6.76^{c} ± 0.08	79.67^{ab} ± 5.78	34.77^{c} ± 0.12	15.00^{c} ± 2.89
10	6.36^{c} ± 0.13	77.67^{abc} ± 8.88	32.11^{d} ± 0.19	11.67^{c} ± 3.33
13	5.34^{d} ± 0.15	85.00^{ab} ± 2.89	27.63^{e} ± 0.14	0.00^{d} ± 0.00
15	4.86^{de} ± 0.06	90.00^{a} ± 5.77	25.56^{f} ± 0.30	0.00^{d} ± 0.00
22	4.23^{e} ± 0.05	55.00^{d} ± 8.66	10.31^{g} ± 0.30	0.00^{d} ± 0.00
35	4.03^{e} ± 0.37	60.00^{cd} ± 5.77	9.02^{h} ± 0.07	0.00^{d} ± 0.00

* "Values represent the mean ± standard error of the mean (SEM) of three replicates. Means within each column for a given species followed by different superscript letters are significantly different at $p \leq 0.05$ according to Duncan's Multiple Range Test (DMRT). Means sharing at least one common letter are not significantly different"

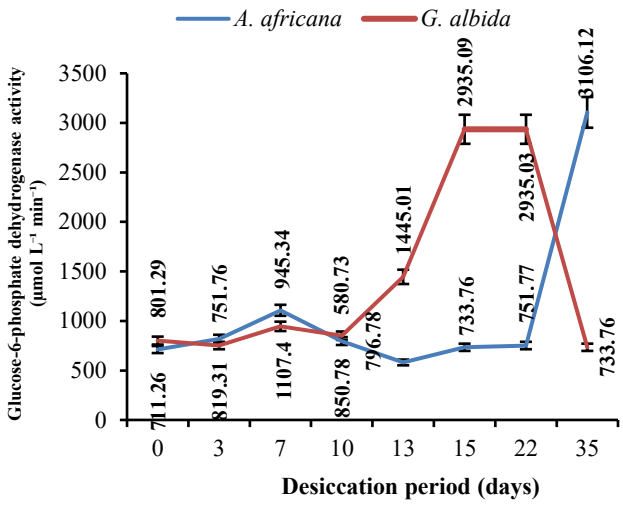

Fig. 1. Glucose-6-phosphate dehydrogenase (G6PDH) activity (µmol L^{-1} min^{-1}) in seeds of *Afzelia africana* and *Gambeya albida* during desiccation. Error bars indicate variability at p≤ 0.05.

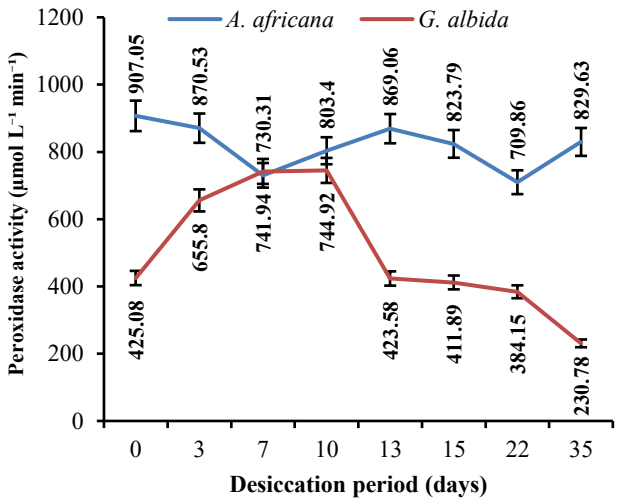

Fig. 2. Peroxidase activity (µmol L^{-1} min^{-1}) in seeds of *Afzelia africana* and *Gambeya albida* during desiccation. Error bars indicate variability at p≤ 0.05.

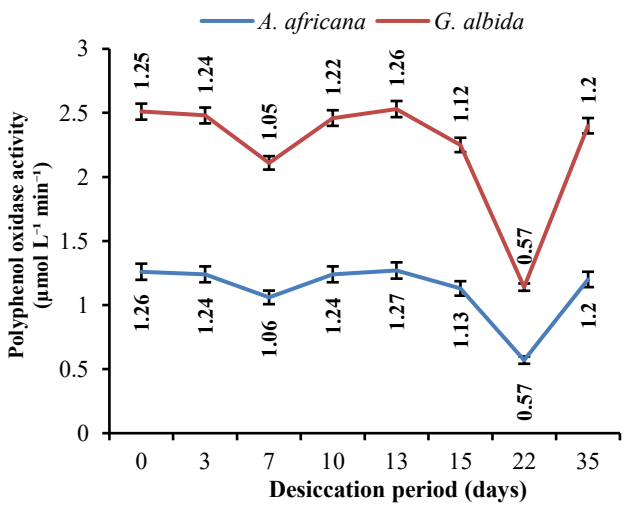

Fig. 3. Polyphenol oxidase activity (µmol L^{-1} min^{-1}) in seeds of *Afzelia africana* and *Gambeya albida* during desiccation. Error bars indicate variability at p≤ 0.05.

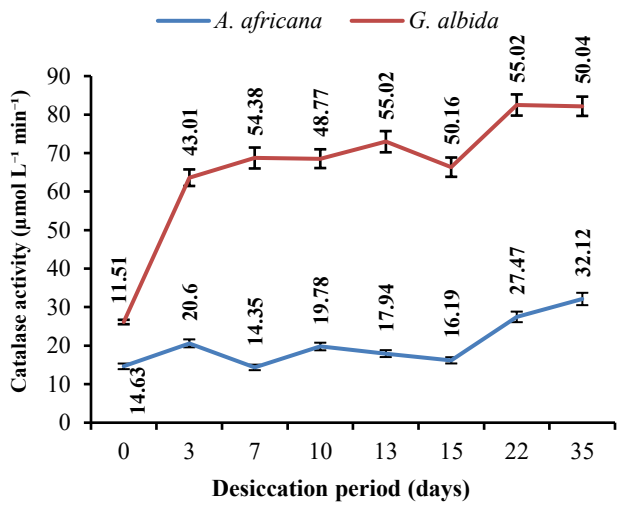

Fig. 4. Catalase activity (µmol L^{-1} min^{-1}) in seeds of *Afzelia africana* and *Gambeya albida* during desiccation. Error bars indicate variability at p≤0.05.

Discussion

Plants exposed to environmental stress frequently experience increased production of reactive oxygen species (ROS), which can cause oxidative damage to cellular components if not effectively neutralized. To mitigate this effect, plants activate antioxidant defense systems that detoxify ROS and maintain cellular homeostasis (Yang *et al*., 2019). The enzymatic antioxidant system represents an important protective mechanism that allows plant tissues, including seeds, to withstand oxidative stress associated with dehydration and other environmental challenges (Baekand Skinner, 2003).

Desiccation has been reported to induce physiological and biochemical adjustments in seeds that may influence germination capacity and metabolic activity. Earlier studies have shown that prolonged drying can distrupt enzyme activities and membrane integrity, ultimately affecting seed viability (Bartels, 2005; Berjak, 2006; Veselovsky &Veselova, 2012). In the present study, the orthodox seeds of *Afzelia africana* maintained relatively higher activities of several oxidative stress enzymes during extended desiccation, whereas enzyme activities in *Gambeya albida* generally declined during the later stages of drying. These contrasting responses are consistent with the well documented differences between orthodox and recalcitrant seeds in their ability to tolerate dehydration.

Glucose-6-phosphate dehydrogenase (G6PDH) is a key regulatory enzyme of the oxidative pentose phosphate pathway and plays an essential role in cellular redox metabolism. Through this pathway, G6PDH generates NADPH, which is required for the regeneration of reduced antioxidants such as glutathione and ascorbate. These molecules are central components of the ascorbate–glutathione cycle that detoxifies hydrogen peroxide and other ROS generated during stress conditions (Sergio, 2016; Yang *et al*., 2019). Consequently, sustained G6PDH activity contributes to the maintenance of cellular redox balance and protects cells from oxidative injury. The relatively higher G6PDH activity observed in *A. africana* during desiccation suggests that the seeds retained the metabolic capacity to generate NADPH required for antioxidant regeneration. In

contrast, the decline in G6PDH activity in *G. albida* during prolonged desiccation may reflect a reduced capacity for redox regulation, which could contribute to increased oxidative damage and loss of viability. Previous studies have similarly reported that changes in G6PDH activity can significantly influence cell survival and stress tolerance (Zhang *et al*., 2000; Stella & Eriyamremu, 2015).

Polyphenol oxidases (PPOs) are widely distributed enzymes in plants and are typically localized in plastids, while their phenolic substrates are stored separately within the cell. Under normal physiological conditions, these enzymes often remain inactive; however, when cellular compartmentalization is disrupted, such as during tissue damage, ageing, or stress, PPO may become activated and catalyze the oxidation of phenolic compounds (Fuerst *et al*., 2014). The physiological significance of PPO activity under stress conditions remains somewhat ambiguous, as the enzyme may contribute either to protective phenolic oxidation processes or to oxidative browning reactions. In the present study, PPO activity showed relatively similar trends in both species and was not strongly influenced by desiccation. This suggests that PPO may play a limited or secondary role in the antioxidant response of these seeds during dehydration, although its activity may still reflect general metabolic changes associated with stress or tissue ageing.

Peroxidase and catalase are important ROS-scavenging enzymes involved in the detoxification of hydrogen peroxide generated during oxidative metabolism. Increased peroxidase activity has frequently been associated with stress adaptation, as the enzyme participates in the removal of hydrogen peroxide and the strengthening of cell walls during stress responses (Sharma *et al*., 2012; Erofeeva, 2015; Pandey *et al*., 2017). Similarly, catalase plays a major role in rapidly decomposing hydrogen peroxide into water and oxygen, thereby preventing oxidative damage to cellular structures (Srivalli *et al*., 2003). When ROS production exceeds the capacity of these scavenging systems, oxidative damage to membranes, proteins, and nucleic acids may occur (Sakihama *et al*., 2002).

The contrasting responses observed between the two species may also be explained by the inherent physiological characteristics of recalcitrant seeds. Recalcitrant seeds, such as those of *G. albida*, generally possess high moisture content at shedding, maintain relatively high metabolic activity, and lack the protective mechanisms required to tolerate extensive dehydration. As a result, drying often leads to membrane destabilization, increased oxidative stress, and rapid loss of viability. These features have been widely reported for recalcitrant tropical tree seeds and are considered major limitations to their long-term storage and conservation (Pukacka &Ratajczak, 2006; Cheng & Song, 2008). The decline in antioxidant enzyme activity observed in *G. albida* during prolonged desiccation may therefore reflect progressive metabolic deterioration and reduced ability to counteract ROS accumulation. Conversely, the maintenance or increase of antioxidant enzyme activity in *A. africana* during drying is consistent with the ability of orthodox seeds to activate protective biochemical mechanisms that support desiccation tolerance.

On the whole, the results of this study suggest that the ability to sustain antioxidant enzyme activity during dehydration may play an important role in determining seed desiccation tolerance. The enhanced enzymatic responses observed in *A. africana* likely contribute to its capacity to withstand water loss, whereas the decline in these protective mechanisms in *G. albida* may cause its recalcitrant behavior and rapid loss of viability during drying.

To our knowledge, this study represents one of the first comparative investigations of oxidative stress enzyme dynamics during desiccation in seeds of *Afzelia africana* and *Gambeya albida*. The findings reveal species-specific differences in antioxidant enzyme responses that help explain their contrasting seed storage behaviours. By linking enzymatic antioxidant activity with desiccation tolerance, this work provides new insights into the biochemical basis of seed viability in tropical tree species and highlights important considerations for seed conservation and germplasm management.

Conclusion

The results of this study revealed clear differences in the desiccation responses of the two rainforest species examined. Seeds of *Afzelia africana*, which exhibit orthodox storage behaviour, showed increased activities of oxidative stress enzymes during the later stages of desiccation, suggesting the activation of antioxidant defense mechanisms that enhance desiccation tolerance. In contrast, seeds of *Gambeya albida*, which display recalcitrant viability characteristics, did not show similar enzymatic responses, indicating a limited capacity to withstand dehydration stress. These findings support earlier reports that enzymatic antioxidant systems play an important protective role in plants by mitigating oxidative damage during dehydration. The observed differences between the two species have important implications for seed conservation and management strategies. While *A. africana* seeds may be suitable for conventional seed banking and long-term germplasm conservation, the recalcitrant nature of *G. albida* seeds suggests that alternative conservation approaches, such as short-term storage, field gene banks, or cryopreservation techniques, may be necessary. Understanding the physiological and biochemical responses of seeds to desiccation is therefore essential for improving conservation strategies for economically and ecologically important tropical tree species.

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Author's Contribution: A.E. Nkang conceived and supervised the study and reviewed the manuscript. B.A. Ngele conducted the research, performed laboratory analyses, collected and interpreted the data, and prepared the original manuscript. E.A. Effa assisted with laboratory work and data collection. O.D. Etim performed the statistical analyses. All authors read and approved the final manuscript.

Conflict of Interest: The authors declare no conflict of interest.

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