

DAVIS EXPEDITION FUND

REPORT ON EXPEDITION / PROJECT

Expedition/Project Title:	Regeneration Strategies of Arid Savannas Trees: Seed Bank Composition and Seed Viability
Travel Dates:	1 st April – 25 th May
Location:	Ongava Game Reserve
Group Members:	Alice Jones, Leena Naftel, Gabriel IK Uusiku and Hilma Amupolo
Aims:	To understand the capacity of woody species to regenerate naturally by examining the composition and viability of the soil seed bank in relation to the standing mature tree community.
Photography consent form attached: (please refer to your award letter)	☐ Yes ☒ No

Regeneration Strategies of Arid Savannas Trees: Seed Bank Composition and Seed Viability



Alice Jones
April – May 2025

DAVIS EXPEDITION FUND

Summary

Spanning one-sixth of the Earth's land surface, savannas are vital ecosystems, contributing 30% of global terrestrial vegetation primary productivity (Grace et al., 2006). Despite their significance, African savanna ecosystem dynamics remain disproportionately understudied. This research investigates the role of the soil seed bank in woody plant regeneration within an arid savanna in northern Namibia, with the aim of identifying potential bottlenecks in the natural regeneration of native woodlands.

Using a plot-based approach, mature woody vegetation was surveyed, and the soil seed bank systematically sampled using quadrats during both the 2024 dry and the 2025 wet seasons, focusing on species composition. Seed viability was evaluated through a germination test.

Results indicate that the soil seed bank is highly localised, with seeds originating only from 8 of the 24 mature tree species present within the plots. Although many woody species were not represented in the soil seed bank, the majority of those that were present occurred in sufficient quantities to potentially support natural regeneration. Only the most abundant seed species (*Colophospermum mopane* and *Terminalia prunioides*) successfully germinated. These findings suggest that although the soil seed bank is not a broad reservoir of potential colonisers, it may still support population stability for certain species. As climate change and land-use pressures intensify, understanding these regeneration mechanisms is essential for effective conservation and restoration in arid savannas.

Background

The natural regeneration of trees is a vital process enabling ecosystems to recover and renew themselves through growth and reproduction (Huss, 2004). Seed germination is essential for maintaining biodiversity and underpins critical ecosystem services and functions, including soil stabilisation, water regulation, food production, habitat creation, nutrient cycling and carbon storage. Natural regeneration enables ecosystems to adapt to changing environments, recover from damage and ensure continued species survival. In dry tropical savannas, the high aridity, fire exposure and megafauna population pressures imposed on trees greatly influences their distribution (Burke, 2006) and ecological strategies. Understanding these strategies and identifying potential regeneration limitations are essential for effective conservation efforts and land management practices that benefit both nature and local communities.

Trees produce seeds to introduce genetic variability, expand distribution and ensure long-term survival (Long et al., 2015). Dormant seeds can accumulate in the soil over several seasons, forming a soil seed bank (Templeton & Levin, 1979). Seed production is influenced by environmental conditions, seed dispersal mechanisms and disruption pressures such as fire, herbivory and frost (Khurana & Singh, 2001). Increasing aridity and greater inter-annual variation in rainfall timing have led to a rise in the number of species producing dormant seeds (Khurana & Singh, 2001). These seeds can remain dormant for years, waiting for the right environmental cues to germinate (Templeton & Levin, 1979). Prolonged droughts and large inter-annual climatic variations may further increase the proportion of dormant seeds, as ideal germination conditions become less frequent. To the best of our knowledge, investigations into the seed bank of natural woodland is yet to be investigated in northern Namibia.

Soil seed banks enable species' persistence through recruitment events (Ooi, 2012), acting as reservoirs of viable seeds in the soil that can germinate under favourable conditions. This mechanism allows plant populations to recover from disturbances such as fire, drought, or grazing, thereby reducing the risk of local extinction. By staggering germination over time and aligning them with optimal conditions, seed banks buffer species against unpredictable

DAVIS EXPEDITION FUND

environmental fluctuations, such as extreme weather events, that might otherwise lead to establishment failures. This strategy enhances long-term population stability and ecosystem resilience and would be highly beneficial in high disturbance environments.

Research into soil seed banks is vital. Soil seed banks act as records of past plant communities (Templeton & Levin, 1979), offering insights into regeneration potential and to future climate change resilience. However, uncertainty remains regarding the long-term viability of seeds under the pressure of anthropogenic climate change. Environmental stresses faced by seeds before germination (Figure 1) are likely to be exacerbated by climate change and the associated extreme weather events (Ooi, 2012). Reduced precipitation, increased soil temperatures, and heightened fire intensity are predicted to threaten seed bank persistence, potentially decreasing seed viability or destroying seed reserves entirely (Ooi, 2012). This highlights the importance of investigating seedbank diversity to understand the current soil seed bank and monitor changes overtime.

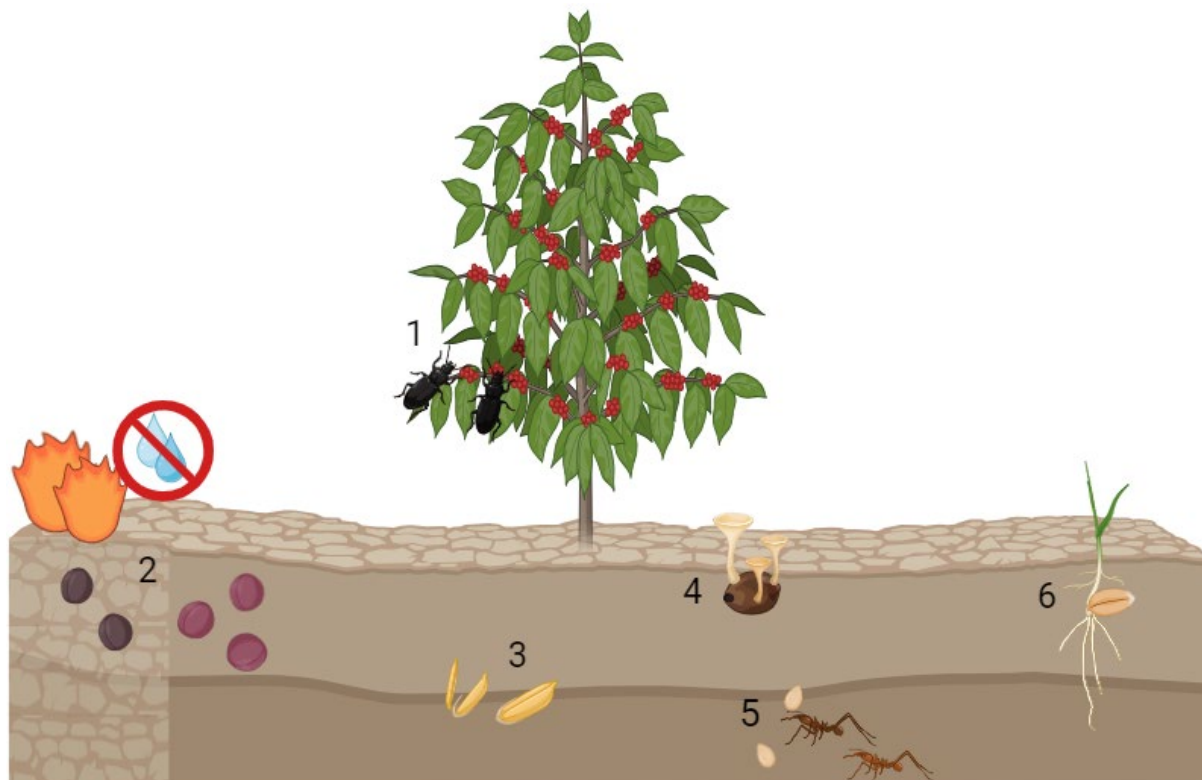


Figure 1: Factors (1-5) that a seed must endure to germinate (6), including pre-dispersal predation (1), decay overtime, sometimes accelerated by unfavourable environmental conditions such as drought and fire events (2), non-viable seed (3), microbial infections (4) and post-dispersal predation (5) Created in BioRender.com.

Understanding the proportion of seeds that are viable is crucial to understand the regenerative potential of plant populations. Gathering species-specific data on seed bank composition and viability is key to understanding the long-term stability of the local tree population. Additionally, sampling the seed bank at multiple points throughout the season captures temporal variations in seed bank composition and viability. Seasonal sampling helps account for fluctuations caused by environmental conditions, seed dispersal timing, and disturbance events, ensuring a more comprehensive understanding of seed bank dynamics and their role in ecosystem stability.

DAVIS EXPEDITION FUND

While grass seed banks have received significant research attention (Ghebrehiwot et al., 2012; Kiss et al., 2018; Snyman, 2005, 2013; van Langevelde et al., 2016), relatively little is known about the dynamics of the tree soil seed bank. In southern Africa, soil seed bank research has primarily focused on bush encroachment (Mndela et al., 2019, 2020; Rabopape, 2021), individual species (Joubert et al., 2013), or the impacts of intense grazing pressures (Dreber & Esler, 2011). In contrast, this study compares the composition of the seed bank to the surrounding mature tree community to assess whether current populations are capable of natural regeneration to maintain stable populations. This work contributes to a broader understanding of tree recruitment potential.

Method

Study Area

Established in the early 1990s, Ongava Game Reserve (OGR), is in northern Namibia on the southern border of Etosha National Park (Figure 2). Renowned for its white and black rhino introductory programs, the 30 000-hectare reserve is home to a rich diversity of wildlife, including other megafauna species, such as elephants (*Loxodonta africana*) and giraffes (*Giraffa camelopardalis*). These species are supported across OGR's diverse landscape, which includes grasslands as well as shrubland and woodland habitats interspersed among the dolomite hills across the reserve. *Colophospermum mopane* dominate large areas of the reserve, with interspersed patches of *Commiphora* and *Terminalia* trees. The reserve transitions from a barren, sparsely vegetated landscape during the dry season to a verdant environment following the onset of seasonal rainfall in early November, with an annual mean rainfall of 370 mm.

DAVIS EXPEDITION FUND

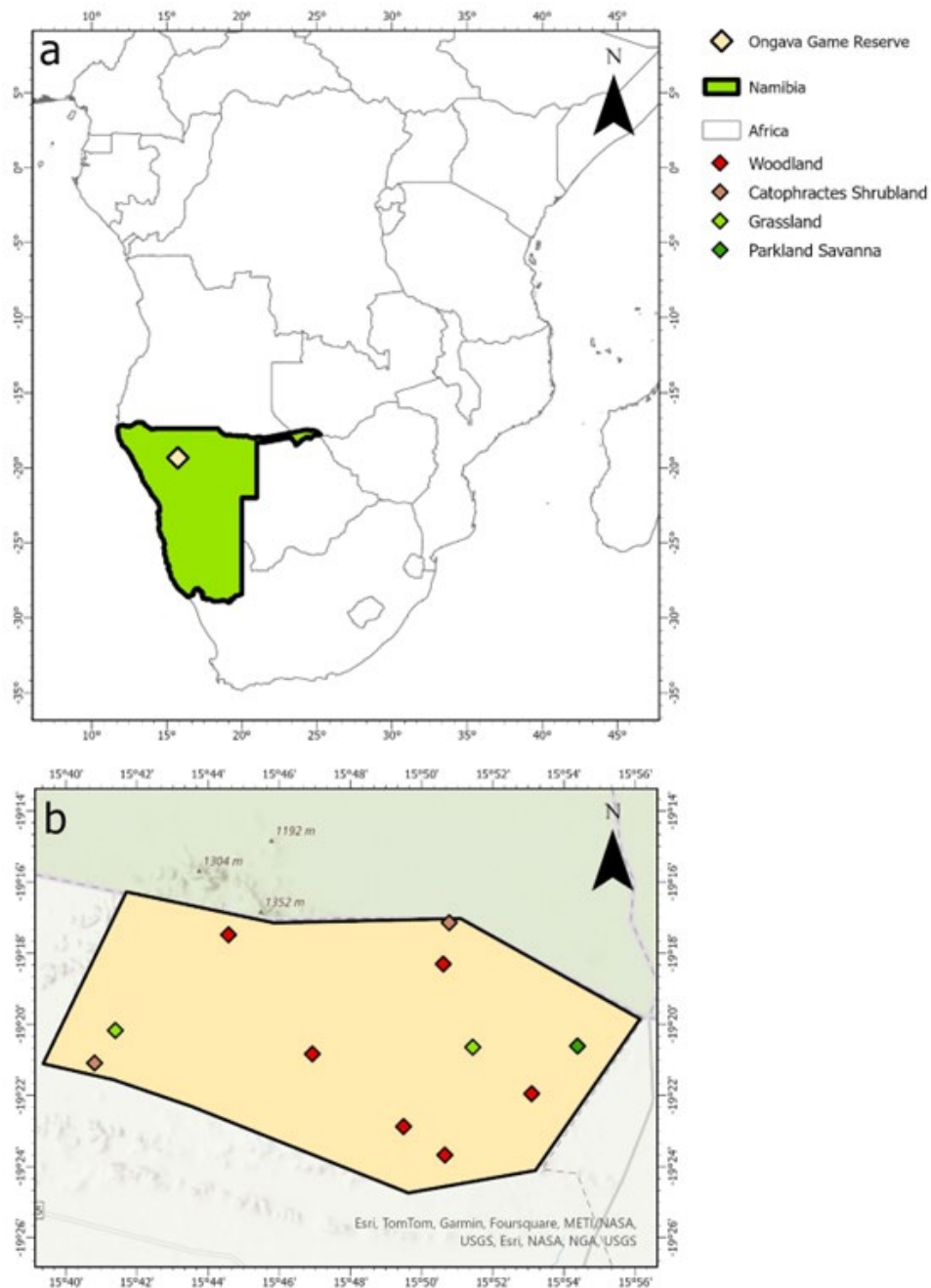


Figure 2: Geographical location of Ongava Game Reserve, Namibia (a) with the 11 plot locations mapped by the dominant vegetation type [woodland, *Catophractes* shrubland, grassland and parkland savanna] (b). The vegetation types are defined in the site-specific sections below.

Mature Tree Sampling

In 2023, 11 one-hectare permanent vegetation monitoring plots were established across the four dominant vegetation types (woodland, *Catophractes* shrubland, grassland and parkland savanna) following the standardised SEOSAW protocol (<https://seosaw.github.io/manuals.html>). Briefly, plots were established in homogenous vegetation types at least 500 metres from roads. All stems with a diameter at breast height (DBH) greater or equal to five cm were tagged, measured and identified to species level. The six woodland plots across the reserve are dominated by *Colophospermum mopane* (n =

DAVIS EXPEDITION FUND

1 029), followed by *Terminalia prunioides* (n = 372), *Commiphora glaucescens* (n = 226) and *Commiphora mollis* (n = 180). In total, 2 049 trees are monitored as part of a global woodland monitoring network. The parkland savanna plot is situated on land historically used for cattle grazing, a practise that has progressively compacted the soil overtime. The compacted soil is thought to inhibit understory growth, resulting in a sparse scattering of large trees, predominantly *C. mopane*. The two *Catophractes* plots are dominated by *Catophractes alexandri*, a spiny shrub that can reach three metres tall. Finally, the two grassland plots are located in natural grassland grazing lawns devoid of trees and, to the best of our knowledge, where there has been no historic removal of trees. These 11 plots were re-censused during this fieldwork trip and the abundance of live individuals was used to quantify the mature tree counts in this study.

Seed Sampling

At the end of the November 2024 dry season, seeds were collected using 12 x 400 cm² quadrats, covering a surface area of 0.48 m² per one-hectare plot (Figure 3). The results from this study indicated that seed presence within the soil layer was rare and never below 5 cm, therefore at the end of the April 2025 wet season, seeds were only collected on the surface and in the top 5 cm of soil. In April 2025, the surface sampling area was increased to 5.25 m², using 21 x 2 500 cm² quadrats. In the laboratory seeds were identified, weighed and information regarding seed predation and colouring were recorded. Subsequently, seed viability was tested by monitoring germination over several weeks on moist kitchen roll, a method that enables gradual water uptake and minimises the risk of cotyledon cracking.

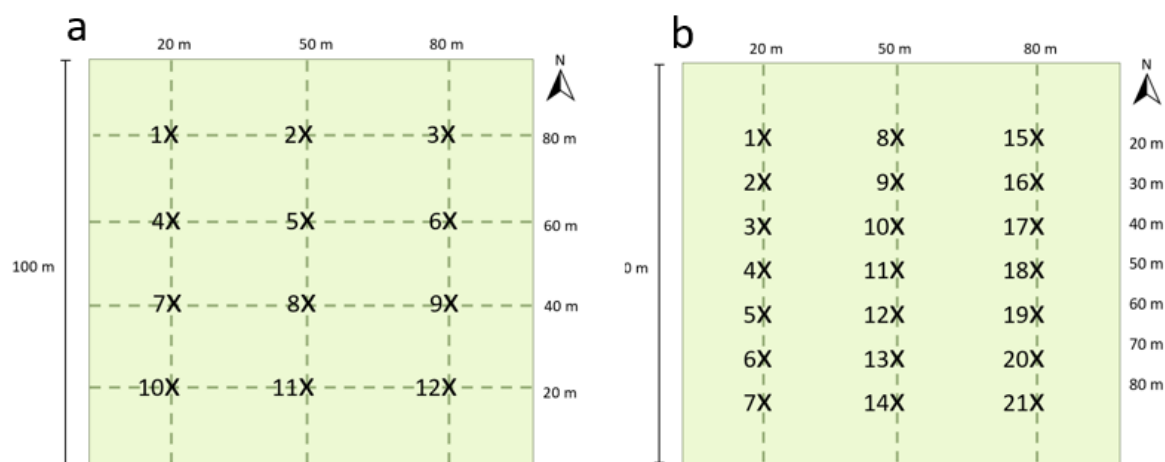


Figure 3: Sampling strategy within each of the 11 one-hectare plots during the 2024 dry season (a) and the 2025 wet season (b), with sampling locations indicated (X).

Results

A total of 355 of the 378 seeds collected from the soil seed bank, were identified to species level, representing six families. The eight species identified were *Colophospermum mopane* (n = 148), *Terminalia prunioides* (n = 96), *Kirkia acuminata* (n = 52), *Commiphora glaucescens* (n = 42), *Ozoroa crassinervia* (n = 10), *Commiphora mollis* (n = 4), *Combretum apiculatum* (n = 2), and *Berchemia discolor* (n = 1) (Figure 4). The soil seed bank was dominated by *C. mopane* (39.2%) and *T. prunioides* (25.4%). The majority of seeds were collected at the end of the 2024 dry season, with seed abundance per hectare nearly 11 times greater than at the end of the 2025 wet season. For all species recorded in both seasons, their seeds abundance per hectare was consistently greater following the dry season than the wet season.

DAVIS EXPEDITION FUND

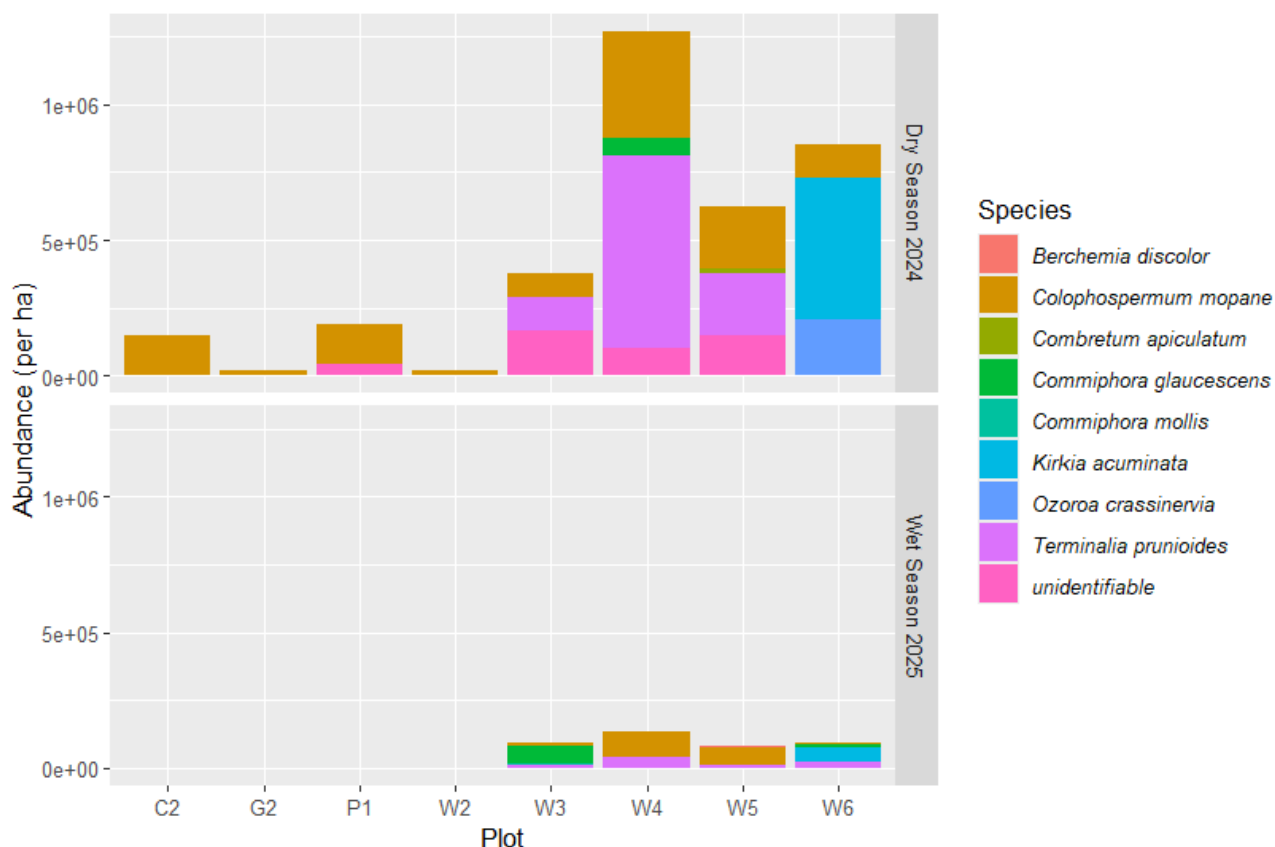


Figure 4: Seed abundance per hectare across the 11 one-hectare plots at the end of the 2024 dry season and 2025 wet season.

Although species richness was similar at both sample points (dry season = 6 species, wet season = 7 species), species composition varied seasonally. *Ozoroa crassinervium* was only detected at the end of the dry season, while *Berchemia discolor* and *Commiphora mollis* were only present at the end of the wet season. *Commiphora glaucescens* was the only species recorded at similar abundances per hectare across both sampling periods. All remaining species showed higher per hectare abundances at the end of the dry season. Among vegetation types, the woodland plots supported the highest seed abundance and species richness, followed by parkland savanna and *Catophractes* shrubland, with grassland exhibiting the lowest species diversity. Notably, three plots (W1, C1 and G1) yielded no seeds.

In total there are 2 049 mature trees across the 11 plots, representing 24 different species. The two most abundant mature trees, *C. mopane* and *T. prunioides*, accounted for the majority of seeds in the soil seed bank (Figure 5). Despite the high abundance of mature *Senegalia* or *Vachellia* trees, no seeds from these genera were found in the soil seed bank.

DAVIS EXPEDITION FUND

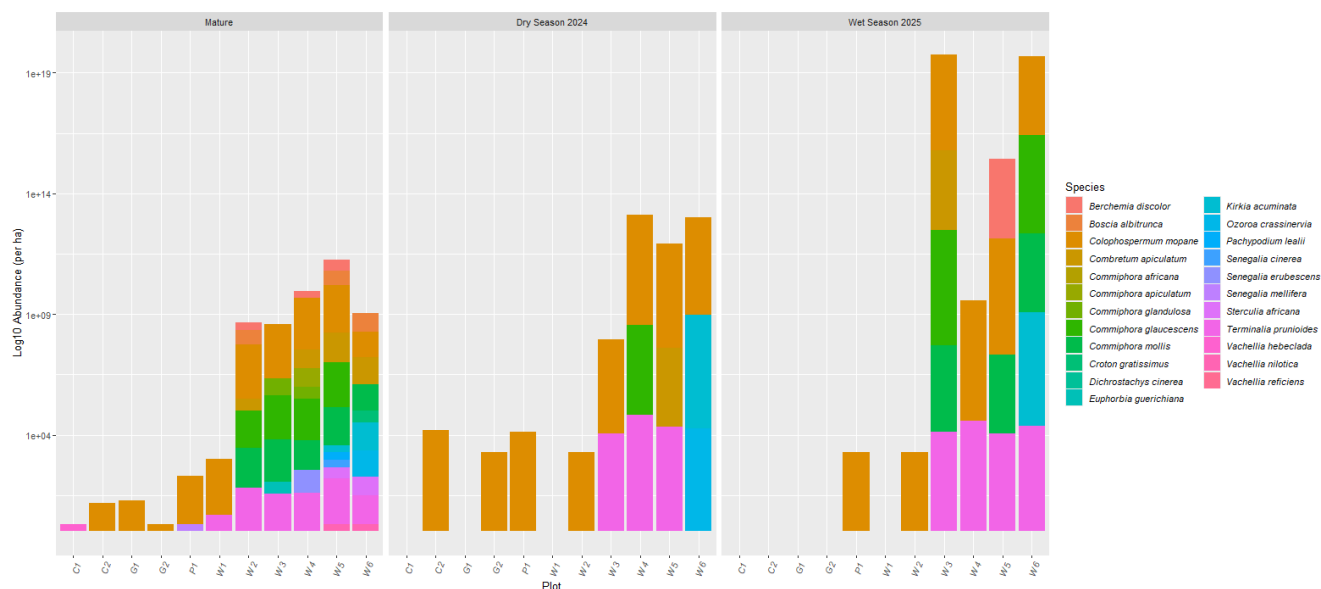


Figure 5: The density of mature trees and seeds per hectare across the 11 one-hectare plots on a logarithmic scale.

Overall, germination rates were low (8.7%), with seeds from only two of the eight species successfully germinating (Figure 6). The highest germination rates were observed in the two most abundant species, *T. prunioides* (17.7%), followed by *C. mopane* (10.8%). Germination success peaked following the dry season, with *C. mopane* seeds germinative exclusively at its end. Similarly, *T. prunioides* germination success was substantially higher at the end of the 2024 dry season (27.5%) than at the end of the 2025 wet season (6.7%).

DAVIS EXPEDITION FUND

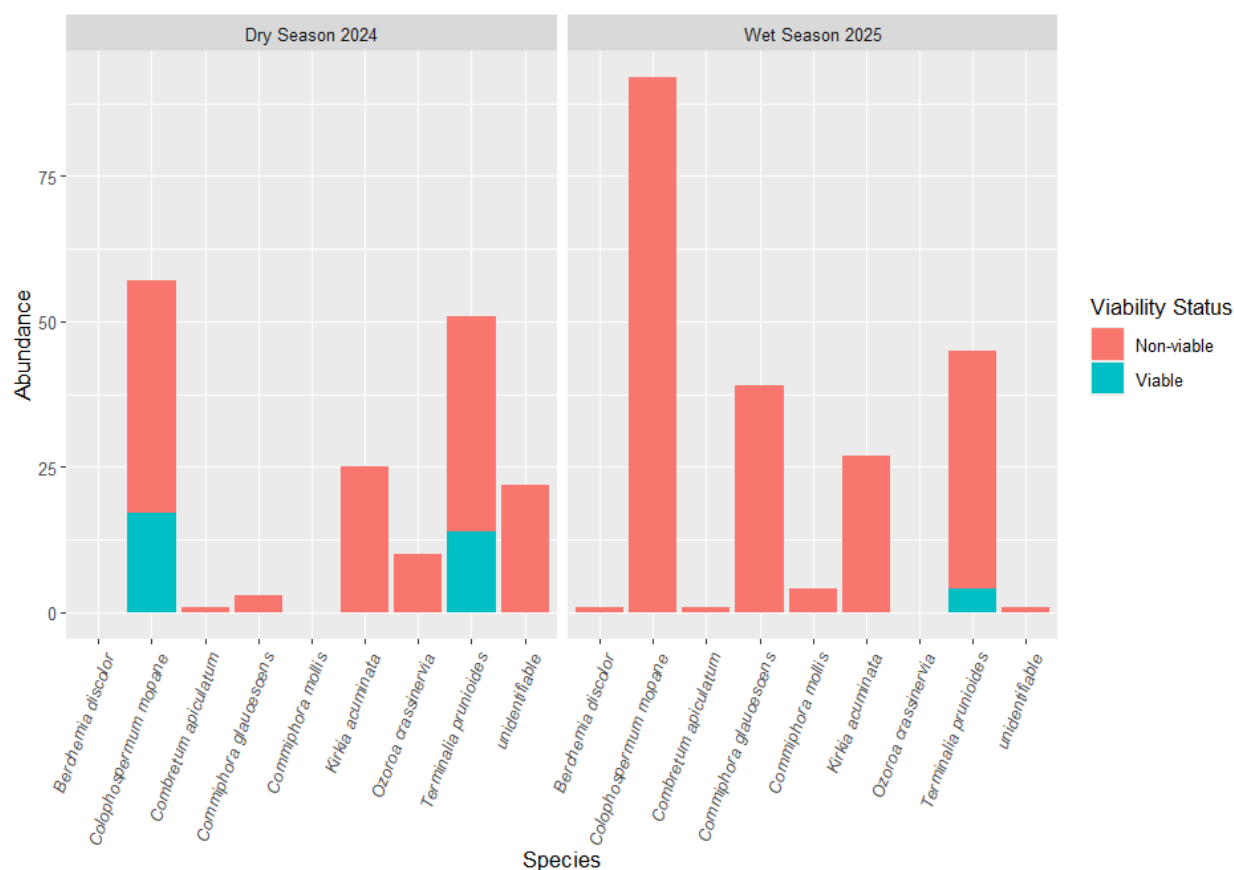


Figure 6: Viability of seeds collected at the end of the dry season in 2024 and at the end of the rainy season in 2025, assessed through a germination test.

Discussion

This study found that seed abundance in the soil seed bank was higher at the end of the dry season compared to the end of the wet season. A similar pattern was reported in the Caatinga dry forest, where seed dispersal occurs throughout the season, but seed rain abundance and richness peaks during the dry season (Souza de Paula et al., 2023). This may reflect a strategy whereby seeds are dispersed during the dry season to ensure seed germination occurs with the first rains of the following wet season, maximising growth during the more favourable conditions. This would be particularly advantageous in arid savanna like Ongava Game Reserve, where annual rainfall is extremely low and every millimetre of precipitation must be used efficiently.

The lack of seeds found in three plots (C1, G1 and W1) can be explained by the mature tree composition within the plots. The *Catophractes* shrubland (C1 and C2) and the grassland plots (G1 and G2) are comprised of very few mature trees. Additionally, W1 is a transition plot, established to monitor the boundary of the woodland area. This differs to the other woodland plots, which were established in homogenous vegetation cover containing an abundance of mature trees.

No seeds were found from mature tree species absent from the plot, indicating that the soil seed bank is composed exclusively of species currently present. This suggests that the soil seed bank does not preserve evidence of past communities, nor does it indicate potential for colonisation from outside of the plot. Instead, it reflects only recent, local seed inputs and

DAVIS EXPEDITION FUND

appears compositionally stable. Furthermore, for species with seeds detected in the soil seed bank, their higher per-hectare abundance compared to the mature trees implies that the community is capable of self-renewal and may be resilient to future disturbances.

However, the substantial difference in soil seed abundance between the two sampling points, suggests that seed survival is short lived, with seeds either perishing or germinating soon after dispersal. This limited persistence likely prevents long-term seeds accumulation in the soil, further supporting the conclusion that the seed bank reflects current vegetation rather than serving as a reservoir for future colonisation. Consequently, the conservation of mature trees is crucial, as once lost perhaps the soil seed bank alone will be insufficient for natural regeneration.

Germination was only successful in the two most abundant species (*C. mopane* and *T. prunioides*). This may suggest that overall germination rates are low across all species and that a large sample of seeds may be required to accurately assess germination rates. However, as the germination test occurred outside of a controlled facility, suboptimal conditions, such as inappropriate temperature and light exposure, may have inhibited germination in the remaining six species. Additionally, the seed count included all collected seeds regardless of their condition, meaning that deformed, partially predated or decayed seeds were included in the total. This likely lowered the observed proportion of viable seeds, further complicating interpretation of germination success.

Berchemia discolor and *Commiphora mollis* were only detected at the end of the wet season. However, this may be due to the smaller sampling area used during the 2024 dry season, which likely limited the detection of low-abundance species. To improve the accuracy of temporal comparisons and better capture the composition of the soil seed bank, sampling during the 2025 dry season should occur and match the sampling area used in the 2025 wet season.

Ideally, this study would be complemented with seed traps to monitor seed rainfall throughout the dispersal season. However, at Ongava Game Reserve, the presence of high densities of megafauna and inquisitive *Papio ursinus* (baboons) limits the feasibility of deploying the infrastructure required for such traps. Future efforts could explore alternative or more robust trap designs that can withstand wildlife disturbance, or consider short-term deployments during peak seed dispersal periods when supervision is possible.

References

- Burke, A. (2006). Savanna trees in Namibia - Factors controlling their distribution at the arid end of the spectrum. *Flora: Morphology, Distribution, Functional Ecology of Plants*, 201(3), 189–201. <https://doi.org/10.1016/j.flora.2005.06.011>
- Dreber, N., & Esler, K. J. (2011). Spatio-temporal variation in soil seed banks under contrasting grazing regimes following low and high seasonal rainfall in arid Namibia. *Journal of Arid Environments*, 75(2), 174–184. <https://doi.org/10.1016/j.jaridenv.2010.09.007>
- Ghebrehiwot, H. M., Kulkarni, M. G., Kirkman, K. P., & van Staden, J. (2012). Smoke and heat: Influence on seedling emergence from the germinable soil seed bank of mesic grassland in South Africa. *Plant Growth Regulation*, 66(2), 119–127. <https://doi.org/10.1007/s10725-011-9635-5>
- Grace, J., José, J. S., Meir, P., Miranda, H. S., & Montes, R. A. (2006). Productivity and carbon fluxes of tropical savannas. *Journal of Biogeography*, 33(3), 387–400. <https://doi.org/10.1111/j.1365-2699.2005.01448.x>
- Huss, J. (2004). Natural Stand Regeneration. *Encyclopedia of Forest Sciences*.
- Joubert, D. F., Smit, G. N., & Hoffman, M. T. (2013). The influence of rainfall, competition and predation on seed production, germination and establishment of an encroaching

DAVIS EXPEDITION FUND

- Acacia in an arid Namibian savanna. *Journal of Arid Environments*, 91, 7–13.
<https://doi.org/10.1016/j.jaridenv.2012.11.001>
- Khurana, E., & Singh, J. S. (2001). *Ecology of tree seed and seedlings: Implications for tropical forest conservation and restoration* (Vol. 80, Issue 6).
<https://about.jstor.org/terms>
- Kiss, R., Deák, B., Török, P., Tóthmérész, B., & Valkó, O. (2018). Grassland seed bank and community resilience in a changing climate. In *Restoration Ecology* (Vol. 26, pp. S141–S150). Blackwell Publishing Inc. <https://doi.org/10.1111/rec.12694>
- Long, R. L., Gorecki, M. J., Renton, M., Scott, J. K., Colville, L., Goggin, D. E., Commander, L. E., Westcott, D. A., Cherry, H., & Finch-Savage, W. E. (2015). The ecophysiology of seed persistence: A mechanistic view of the journey to germination or demise. *Biological Reviews*, 90(1), 31–59. <https://doi.org/10.1111/brv.12095>
- Mndela, M., Madakadze, C. I., Nherera-Chokuda, F., & Dube, S. (2020). Is the soil seed bank a reliable source for passive restoration of bush-cleared semi-arid rangelands of South Africa? *Ecological Processes*, 9(1). <https://doi.org/10.1186/s13717-019-0204-6>
- Mndela, M., Madakadze, I. C., Nherera-Chokuda, F., & Dube, S. (2019). Dynamics of the soil seed bank over the short-term after bush clearing in a semi-arid shrubland in Springbokvlakte thornveld of South Africa. *South African Journal of Botany*, 125, 298–309. <https://doi.org/10.1016/j.sajb.2019.07.033>
- Ooi, M. K. J. (2012). Seed bank persistence and climate change. In *Seed Science Research* (Vol. 22, Issue SUPPL. 1). <https://doi.org/10.1017/S0960258511000407>
- Rabopape, M. C. (2021). *Assessing Soil Seed Bank Diversity in Bush Enchroached Savanna Rangeland, Limpopo Province, South Africa*. University of Limpopo.
- Snyman, H. A. (2005). The effect of fire on the soil seed bank of a semi-arid grassland in South Africa. *South African Journal of Botany*, 71(1), 53–60.
- Snyman, H. A. (2013). Disturbances impact on longevity of grass seeds, semi-arid South African Rangeland. *Rangeland Ecology & Management*, 66(2), 143–156.
- Souza de Paula, A., Sfair, J. C., Trindade, D. P. F., Rito, K. F., Tabarelli, M., & Barros, M. F. (2023). The role of seed rain and soil seed bank in the regeneration of a Caatinga dry forest following slash-and-burn agriculture. *Journal of Arid Environments*, 211. <https://doi.org/10.1016/j.jaridenv.2023.104948>
- Templeton, A. R., & Levin, D. A. (1979). EVOLUTIONARY CONSEQUENCES OF SEED POOLS. In *Am. Nat* (Vol. 114, Issue 2).
- van Langevelde, F., Tessedema, Z. K., de Boer, W. F., & Prins, H. H. T. (2016). Soil seed bank dynamics under the influence of grazing as alternative explanation for herbaceous vegetation transitions in semi-arid rangelands. *Ecological Modelling*, 337, 253–261. <https://doi.org/10.1016/j.ecolmodel.2016.07.013>