Trees, Forests and People 26 (2026) 101336

Contents lists available at ScienceDirect

Trees, Forests and People

journal homepage: www.sciencedirect.com/journal/trees-forests-and-people

Exploring assisted tree regeneration to support sustainable forest management in the Mopane and Baikiaea woodlands of Southern Africa

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ARTICLE INFO

Keywords:
Bio-inoculant
Forest degradation
Germination responses
Nursery practices

ABSTRACT

Dry tropical woodlands are ecologically and socio-economically important but increasingly affected by climate change and unsustainable land use. Natural regeneration is constrained by seed predation, poor seed germination, seedling browsing, and harsh environmental conditions, which limit seedling recruitment and survival. Assisted regeneration may enhance dryland carbon sequestration, but its success depends on species-specific ecological knowledge. This study evaluated germination, seedling development, and survival of seven socio-economically important tree species native to Southern Africa: *Pterocarpus angolensis, Guibourtia coleosperma, Baikiaea plurijuga, Burkea africana, Colophospermum mopane, Sterculia africana* and *Terminalia prunioides*. The experimental treatments were evaluated across various seed ages, soil media, sowing depths, seasons, and microbial inoculation levels at Mopane and Baikiaea woodland sites in Namibia. Soil media had no significant effect on germination across species, whereas seeding depth influenced germination, with *B. plurijuga* and *T. prunioides* showing higher germination when sown at shallow depths. Seed age had species-specific effects. Older seeds germinated better in *C. mopane*, whereas freshly collected seeds performed better in *G. coleosperma, B. plurijuga*, and *P. angolensis*. Seasons also affected *T. prunioides* and *G. coleosperma*, with higher germination during the rainy season, while *B. plurijuga, P. angolensis*, and *S. africana* germinated under dry season conditions. Although microbial inoculation did not significantly enhance seedling growth, it significantly improved seedling survival in *B. africana*. Overall, these findings highlight species-specific requirements for nursery protocols, seed storage, and scalable assisted regeneration strategies, contributing to effective dryland forest management, restoration and carbon sequestration initiatives.

1. Introduction

Dry forests and woodlands play a vital role in the socio-economic and ecological fabric of Southern Africa (Hoffman et al., 2010; Moura et al., 2017). These ecosystems support rural livelihoods by providing timber, food, medicine, fuelwood, and construction materials (Maquia et al., 2019; Ribeiro et al., 2015), while also contributing to biodiversity conservation, water regulation and nutrient cycling. However, woodland structure and regeneration are increasingly influenced by both natural and human pressures (Boyle, 2017; Lyly et al., 2014; Ribeiro et al., 2015).

Dry woodlands such as Miombo and Mopane occur predominantly in rural and remote areas where infrastructure, market access and formal employment opportunities are limited (Shackleton et al., 2008). As a result, local communities rely heavily on woodland resources, yet often face persistent socio-economic challenges, including poverty and limited livelihood opportunities (King et al., 2000; Nikodemus and Hajek, 2015). Over the past two to three decades, rapid population growth in Southern Africa has further intensified pressure on these ecosystems through agricultural expansion, fuelwood extraction and timber harvesting (Chidumayo, 2010; Moura et al., 2017). Population projections indicate that sub-Saharan Africa is expected to experience substantial population growth by 2050, increasing demand for land and forest resources and contributing to woodland degradation and deforestation (Alemu and Alebachew, 2018).

Among the dominant woodland systems in the region are Mopane

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https://doi.org/10.1016/j.tfp.2026.101336

Available online 2 June 2026

and Baikiaea woodlands, which occur across southeastern Southern Africa, including northern Namibia at the southern margin of the Miombo region (Fig. 1). Mopane woodlands are shaped by frequent veldfires and herbivory, particularly by elephants, which influence stand structure and regeneration dynamics (Amutenya, 2020; Chidumayo, 2010; Ribeiro et al., 2008). Baikiaea woodlands are strongly affected by selective timber harvesting, agricultural expansion and fire, often associated with shifting cultivation and fallow cycles (Chidumayo and Gumbo, 2010; Moura et al., 2017).

Fallow land is defined as land left uncultivated for a period to restore soil fertility (Haas et al., 1974). However, regeneration in fallow systems may be limited. For example, a study in northern Namibia reported low densities of woody seeds in fallow soils (0.04 seeds m^{-2}), with soil seed banks containing fewer woody species than the above-ground vegetation (Hilukwa, 2018). This reduced representation of woodland species has been linked to previous cultivation, limited seed dispersal, and the dominance of isolated or ageing seed sources (Alelign et al., 2007; Eilu and Obua, 2005).

Although dry woodlands are often assumed to regenerate naturally, tree recruitment is frequently low and spatially variable, particularly in degraded and drought-prone landscapes (Chidumayo, 2010; Zenebe, 2020). Several ecological factors constrain regeneration, including seed predation, browsing, competition, drought and temperature extremes (Caro et al., 2005). Selective logging of the most vigorous trees further limits seed availability and weakens genetic diversity by leaving behind senescent or poorly formed individuals (Sebbenn et al., 2008). Consequently, assisted regeneration techniques such as direct seeding, protection measures and the planting of nursery-grown seedlings are increasingly important for woodland restoration.

Seed germination and early seedling establishment are bottlenecks in tree regeneration in dry woodlands and savanna (Chidumayo and Gumbo, 2010; Shackleton et al., 2008). These ecosystems are characterised by nutrient-poor soils and erratic rainfall, which limit seedling survival (Clark et al., 1999; James et al., 2011; Margherita et al., 2022). Several factors influence germination success, including sowing depth, soil type, seasonal timing and seed age. Shallow sowing can increase desiccation and predation, while deeper placement may restrict oxygen and hinder emergence (Masilamani et al., 2013). Soil properties affect moisture and nutrient availability, and seed storage conditions can influence viability and seedling vigour (Pahla et al. 2014; Dada et al. 2019; Buitink and Leprince, 2024; De Vitis et al., 2020). Understanding these factors is therefore essential for developing effective species-specific propagation protocols (Chamshama et al., 2009).

In addition, soil microbial interactions may further influence seedling establishment (Ayomide and Yisau, 2022; Mridha et al., 2016; Wunderlin, 1982). Plant growth–promoting (PGP) microorganisms are beneficial soil microbes that enhance plant growth through mechanisms such as nutrient mobilisation, phytohormone production, and improved tolerance to environmental stress (Grönemeyer and Reinhold-Hurek, 2018). In tree nurseries, microbial inoculation has been proposed as a sustainable alternative to chemical fertilisation and can improve seedling growth and survival (Dobo et al., 2016; Grönemeyer and Reinhold-Hurek, 2018; Haiyambo and Chimwamurombe, 2018; Jordaan et al., 2000; Pule-Meulenberg, 2014). However, despite their promising role in nursery management, species-specific responses to microbes remain poorly understood.

Previous studies on woodland species in Southern Africa have focused on seed pre-treatment methods to improve germination, while the ecological factors influencing germination and early seedling establishment remain less explored (De Cauwer et al., 2018; De Cauwer and Younan, 2015; Heita et al., 2019; Melusi et al., 2021; Mojeremane et al., 2018). Moreover, ecologically important but less-studied species such as *Sterculia africana* and *Terminalia prunioides* remain underrepresented in the literature despite their roles in woodland dynamics (Table 1).

This study addresses these knowledge gaps by examining how germination and early seedling growth of seven indigenous Southern African tree species (*Pterocarpus angolensis, Guibourtia coleosperma, Baikiaea plurijuga, Burkea africana, Colophospermum mopane, Sterculia africana*, and *Terminalia prunioides*) respond to key ecological and

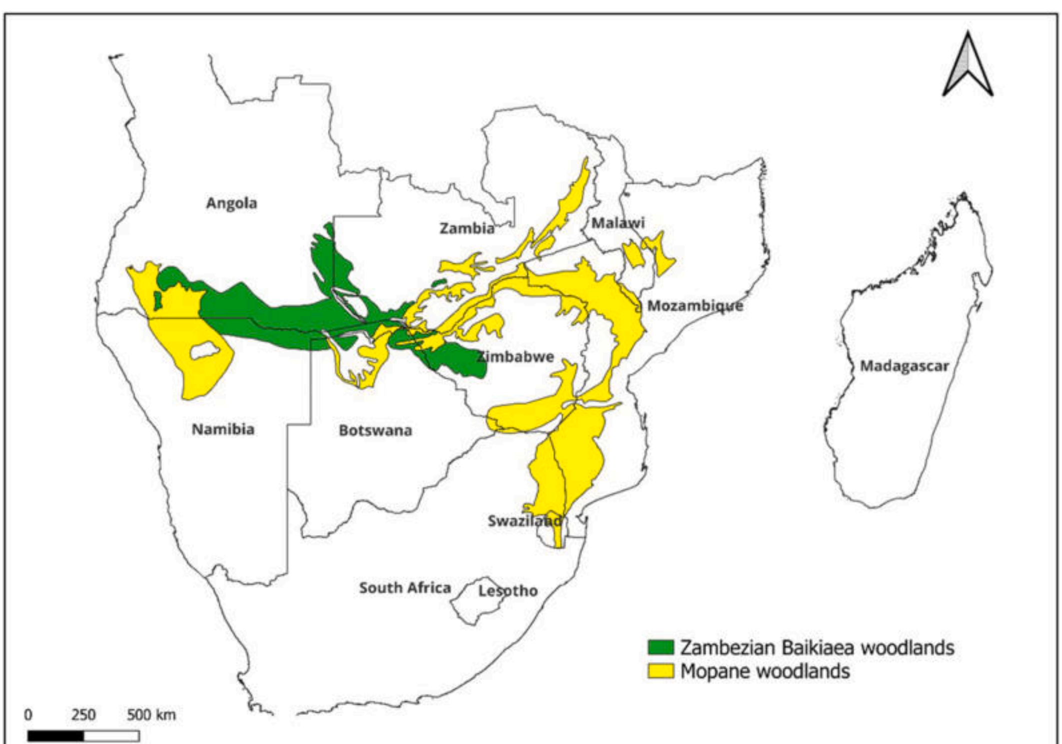

Fig. 1. Distribution of Zambezian Baikiaea woodlands and Mopane woodlands in Southern Africa, based on the Terrestrial Ecoregions of the World (Olson et al., 2001).

Table 1
Summary of tree species studied.

Species	Seed pre-treatment	Ecological and economic values	Challenges
Mopane woodland species, Ongava Research Centre (ORC)			
Colophospermum mopane	Soak in cold water for 12 hours (Mojeremane and Kgati, 2005).	Browsed by livestock and wildlife, timber, firewood, charcoal, edible mopane worm habitat (Makhado et al., 2014; Maupare, 1994).	Low sapling survival, poor regeneration in dry years (Mashabane et al., 2001; Voorthuizen, 2009).
Sterculia africana	Nicked and soaked in lukewarm water for 24 hours (www.worldagroforestry.org, 2007).	Heavily browsed by elephants and rhinos (Personal observation, 2024), self-medication by baboons and humans (Kirabo et al., 2018).	High susceptibility to seed predation, lacks regeneration data (www.worldagroforestry.org, 2007).
Terminalia prunioides	Nicked and soaked in lukewarm water for 24 hours (Orwa et al., 2009).	Traditional medicine, firewood, fencing, nurse tree (Cock, 2015).	Lack of information on regeneration, undervalued due to preference for more commonly used species like mopane (Orwa et al., 2009).
Baikiaea woodland species, Mashare Irrigation Training Centre (MITC)			
Pterocarpus angolensis	Nicked and soaked in lukewarm water for 24 hours (Mojeremane and Lumbile, 2016).	High-value timber (Mojeremane and Lumbile, 2016), traditional medicine (Chipinga et al., 2018; Ndamba et al., 1994).	Poor natural seedling establishment and sapling survival make it difficult to grow in nurseries (De Cauwer, 2020; Van Daalen, 1991). Seeds easily predate, medium growth (radial stem growth of 5.5 mm per year), but a long suffrutex period (repeated shoot die-back) (De Cauwer, 2016).
Guibourtia coleosperma	Nicked and soaked in water for 24 hours (De Cauwer and Younan, 2015; Heita et al., 2019).	High-value timber, shade tree, traditional beer and oil production (Curtis and Mannheimer, 2009).	Slow growth (radial stem growth of 3 mm per year) (Goncalves et al., 2017).
Burkea africana	Nicked and soaked in water for 24 hours (Nemadodzi et al., 2020).	Traditional medicine, timber and construction (Gerhardt and Nemarundwe, 2006).	Seeds easily predated, with low seedling survival in the nursery (Neya et al., 2004).
Baikiaea plurijuga	Nicked and soaked in water for 24 hours (De Cauwer and Younan, 2015).	High-value timber (Curtis and Mannheimer, 2009).	Sensitive to logging pressure, limited natural regeneration (Gambiza et al., 2005) and difficult to grow in the nursery due to fast root growth (Ngoma et al., 2017).

management factors: soil type, sowing depth, seed age, germination season, and bacterial inoculation. The findings aim to support the production of vigorous seedlings for reforestation, woodland enrichment, and climate-resilient land restoration, while informing species-specific nursery protocols for sustainable forest management in Southern Africa.

2. Materials and methods

2.1. Tree species studied

Seven native tree species were selected to represent Mopane and Baikiaea woodland zones in Southern Africa based on their ecological importance, socio-economic value, and lack of regeneration in natural woodlands. Table 1 summarises key characteristics that guided their selection.

2.2. Study area

The research was conducted between 2023 and 2024 in Namibia, a semi-arid country in Southern Africa (Fig. 1). To reflect climatic conditions in the natural distribution of the study species, propagation experiments were conducted in nurseries located within their respective woodland types. The Mopane woodland site was the Ongava Research Centre (ORC) (19°20′37.0″ S, 15°53′55.7″ E), situated within the 30,000-ha Ongava Game Reserve in northern Namibia along the southern boundary of Etosha National Park. The second site was the Mashare Irrigation Training Centre (MITC) (17°53′21.48″ S, 20°10′12.93″ E) in Zambezian Baikiaea woodland, located in the Mashare Constituency near Rundu in the Kavango East Region (Fig. 2).

Each site was equipped with local tree nurseries consisting of shade-net structures with minimal environmental regulation, which are commonly used for tree propagation in Namibia and other semi-arid regions of Southern Africa (FAO, 2012). This differs from temperate regions, where nurseries are commonly enclosed in glasshouses with controlled temperature, humidity and light.

2.3. Climate, geology, soil and flora

ORC is located in a semi-arid region of northern Namibia, receiving a mean annual rainfall of approximately 380 mm with high interannual variability (Stratford and Stratford, 2011). The climate has a distinct wet season from December to March and a prolonged dry season from May to November (Adam et al., 2024). The site lies within the Karstveld geological region, characterised by dolomitic bedrock and shallow stony soils, including grey calcisols and red regosols. Vegetation is dominated by *Colophospermum mopane* woodland with associated species such as *Terminalia prunioides* and *Combretum apiculatum* (De Cauwer et al., 2024).

MITC is located within the Forest and Woodland Savanna biome of northeastern Namibia and experiences a wetter subtropical climate with mean annual rainfall of 550–650 mm and a mean annual temperature of about 22.3°C (Adam et al., 2024). The area forms part of the Kalahari Basin and is characterised by deep aeolian sands with predominantly sandy loam soils (Vushe et al., 2014). Vegetation consists of mixed woodland dominated by species such as *Burkea africana, Baikiaea plurijuga* and *Terminalia sericea* (De Cauwer et al., 2016).

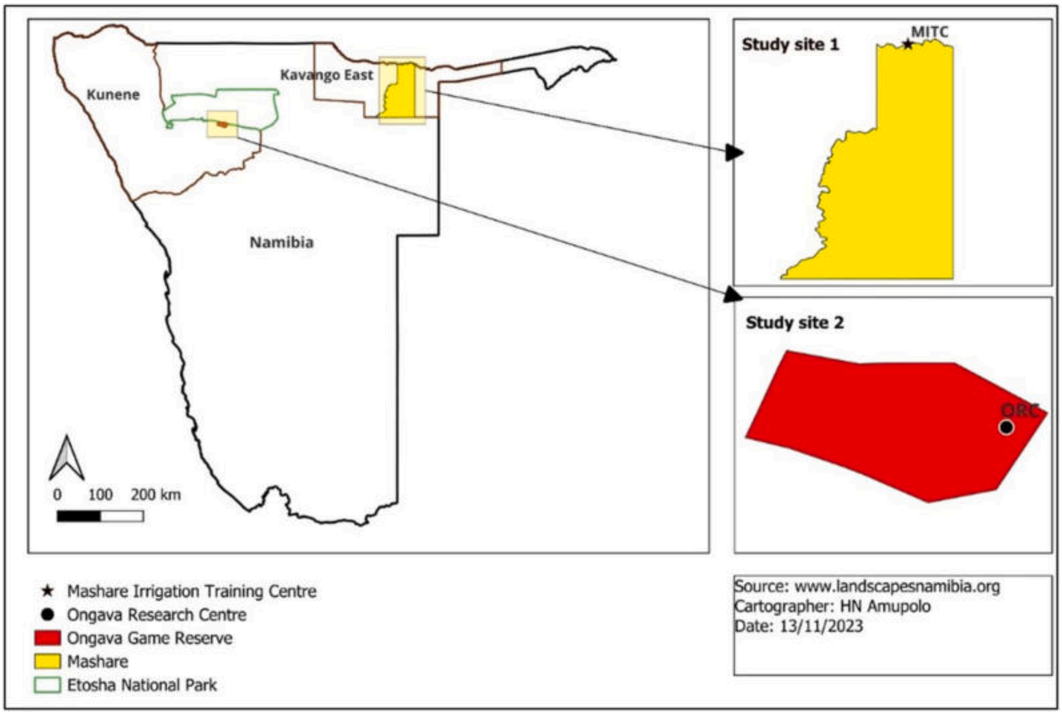

Fig. 2. Location of Ongava Research Centre (Mopane woodland) and Mashare Irrigation Training Centre (Baikiaea woodland) in Namibia.

2.4. *Experimental design and treatment*

This study assessed two stages of regeneration: (i) seed germination, and (ii) seedling growth. Each stage was subjected to treatments designed to assess the response of native woodland species to potentially crucial environmental factors. At each site, treatments were arranged in a factorial design to enable comparison among treatment combinations.

Germination experiments included seeding depth × soil media × seed age, which was repeated for two seasons. One seed was sown per polybag, representing a replicate. The number of replicates per treatment ranged from 10 to 30, depending on species and seed availability. Seed age was not uniformly represented across species and seasons, resulting in an unbalanced design due to differences in seed availability among species and treatments. The total number of replicates per species ranged from 144 to 288 (Table 2). Full details of the distribution of seeds across treatments are provided in Supplementary Table S3. Seedling growth experiments assessed microbial inoculation (inoculated vs control) × soil media effects on surviving seedlings from the germination experiment, available at the time of inoculation. Replication, therefore, varied among species and was based on the number of surviving seedlings and the soil in which the seedlings germinated (Supplementary Table S2).

2.4.1. *Treatments assessed during the germination stage*

Seeds were germinated after applying commonly used pre-treatments (nicking or soaking seeds in warm water (Kumar et al., 2024) (Table 1). Seed viability was assessed using a flotation test, where floating seeds were discarded and sinking seeds were considered viable (International Seed Testing Association, 2010). Seed germination was recorded daily for three consecutive weeks after sowing, with seeds considered germinated when the radicles were clearly visible (Dayamba et al., 2014). Germination capacity was calculated as the proportion of seeds (%) that germinated after three weeks.

Four experimental factors were tested:

Seeding depth: Seeds were sown at either once or twice their diameter (1 × or 2 × seed diameter), representing shallow and moderately deep sowing treatments, respectively. Seed diameter was measured using a representative subset of uniform seeds per species. These measurements determined the depth applied to all seeds of a species. Sowing depths were marked on a pencil using a ruler to ensure accurate seeding depth during planting (Anjah and Mbogue, 2020).

Soil media: Soil type was included as a treatment because differences in physical properties, such as water retention, aeration, and drainage, can influence seed germination and early seedling establishment (FAO, 2006). Three soil media were used as growth substrates: clay, loamy, and sandy soils. At Ongava, red regosols were classified as clay soil, grey calcisols as loamy soil, and a compost–river sand mixture,

Table 2
Number of seeds sown, average seed size, germination percentage, and mean germination time for each species at the two study sites (ORC = Mopane woodland, MITC = Baikiaea woodland).

Species name	Study site	Seeds sown (n)	Seed size (cm)	Germination capacity (%)	Mean germination time (days)	Seedling survival (%)
Colophospermum mopane	ORC	240	1.1	44	8.0	19
Terminalia prunioides	ORC	168	0.5	20	10.6	8
Sterculia africana	ORC	144	0.4	39	8.6	8
Guibourtia coleosperma	MITC	288	0.4	53	19.5	48
Baikiaea plurijuga	MITC	288	1.0	63	16.0	60
Pterocarpus angolensis	MITC	240	0.35	23	10.4	20
Burkea africana	MITC	240	0.25	53	9.0	39

commonly used in nursery propagation, as sandy soil (Hartmann et al., 2011). At Mashare, soils were classified in the field using the texture-by-feel method and similarly grouped as clay, loamy, or sandy soils (Schoeneberger et al., 1998).

Seed age: Two seed-age classes were tested. Fresh seeds (new) were collected in 2023 from the respective study sites during the fruiting season, while older seeds (old) were obtained from the National Tree Seed Collection (NTSC) at the National Forestry Research Centre of Namibia. These older seeds, collected between 2000 and 2020 (Supplementary Table 1), were stored under controlled conditions in a cold room at 0 to 3°C and sealed in ventilated plastic bags to allow air circulation. No old seed lots were available for *T. prunioides* and *S. africana*; these species were excluded from the seed-age analysis.

Season: Germination trials were conducted during the rainy and dry seasons (March and October, respectively) to assess the effect of seasonal variation on seed germination.

2.4.2. Treatments assessed during the seedling growth stage

The impact of bio-inoculation and soil medium on seedling growth was tested. The bio-inoculant, consisting of potentially beneficial bacteria in peat (see 2.5), was applied to the soil when the seedlings were three months old. Seedlings were monitored for six months, and height was measured from the soil surface to the apex of the tallest shoot. The experiment was conducted in two replicates: one during the rainy season (March) and another during the dry season (October).

2.5. Bacteria used and inoculation procedure

The following bacteria were isolated at the University of Bremen, Germany, from plants grown in study areas in Northern Namibia or from soils collected there. They were chosen for their potential to enhance early root development, fix nitrogen in root nodule symbiosis and improve plant performance in nutrient-limited soils (Burbano et al., 2015). *Azospirillum sp.* R111 was applied to *G. coleosperma, B. plurijuga, B. africana, S. africana,* and *T. prunioides* seedlings. The strain had been isolated as an endophyte from a root nodule of Bambara groundnut (*Vigna subterranea*) grown in the facilities of the University of Bremen in a soil mixture collected in 2013 in the constituencies of Mashare and Mupampa from dryland agriculture fields, bushveld and forest (Grönemeyer and Reinhold-Hurek, unpublished). *Azospirillum* spp. is a metabolically versatile, free-living nitrogen-fixing bacterium known to promote root development through phytohormone production, thereby enhancing water and nutrient uptake and improving seedling growth (Cassan et al., 2009; Lucy et al., 2004).

Enterobacter sp. Mop1-1 was applied to *C. mopane* seedlings. The strain had been isolated from surface-sterilised roots of *C. mopane* seedlings collected from the Kunene Region of Namibia (and is highly related to *Enterobacter cloacae* with 99% of 16S rRNA gene identity) (Burbano *et al.*, 2015). Mopane, which grows in nitrogen-deficient soils, does not form traditional root nodules but hosts endophytes. The isolate showed plant-growth-promoting characteristics, including IAA (indole-3-acetic acid) and siderophore production (Burbano et al., 2015).

Bradyrhizobium sp. WR93 was isolated from a root nodule of the wild legume *Chamaecrista* sp. in Kavango West, Namibia, and is closely related to *B. ripae* and forms effective nitrogen-fixing nodules on *P. angolensis* but induces ineffective nodules on *Macroptilium atropurpureum* and *Arachis hypogaea* (Bünger et al., 2021). *B. ripae* was chosen as a nodule symbiont of *P. angolensis* for the provision of fixed nitrogen, and because it shows plant-growth-promoting characteristics such as IAA (Bünger et al., 2021).

The inoculants were prepared with peat carrier at the University of Bremen, as outlined previously for *Bradyrhizobium* (Sarkar et al., 2023). *Bradyrhizobium* cultures were grown in MAG medium, whereas *Azospirillum* sp. and *Enterobacter* sp. were grown in R2A medium (Reasoner and Geldreich, 1985). Approximately 6.5×10^8 cells were added per sachet. Inoculant bags were transported to Namibia and stored for no longer than 3 months at 4°C.

Seedling inoculation: Inoculation was performed following an adapted version of the seed inoculation protocol (see Supplementary File S1). Each inoculant sachet was mixed with 13 ml of sterile water to form a uniform slurry. Seedlings were inoculated at three months of age to ensure sufficient root development. Approximately 2.5 ml of the slurry was applied to the soil around the seedling roots using a sterile syringe.

2.6. Statistical analysis

All statistical analyses were conducted in the R software (R Core Team, 2023) with the packages: ggplot2, Tidyr, Dplyr, ARTool, and MultiComp (Hothorn et al., 2008; Kay et al., 2023; Wickham, 2016; Wickham et al., 2023a; Wickham et al., 2023b).

Generalised linear models (GLMs) with a binomial structure were used to analyse the simultaneous effects of the treatments and their interactions on germination status (germinated vs non-germinated and alive vs dead) in relation to explanatory variables. For continuous variables, data distributions were assessed using residual plots, histograms and the Shapiro–Wilk normality test. As the data did not meet normality assumptions, non-parametric tests were applied.

Differences between two groups were tested using the Wilcoxon rank-sum test, while comparisons among more than two groups were analysed using the Kruskal–Wallis test. P-values were adjusted for multiple comparisons across species using the Benjamini–Hochberg false discovery rate (FDR) procedure (Benjamini and Hochberg, 1995). Statistical significance was set at $p < 0.05$.

3. Results

3.1. Germination performance across species

Germination capacity and mean germination time varied among the seven species tested. *B. plurijuga* exhibited the highest germination of 63%, while *T. prunioides* had the lowest germination rate of 20%. On average, seeds took between one and three weeks to germinate, with noticeable variation across species (Table 2).

3.1.1. Germination across species and treatments

Season had a significant effect on the germination of most species ($p < 0.05$; Table 3), with *G. coleosperma* and *T. prunioides* showing higher germination rates during the rainy season, while *B. plurijuga, P. angolensis*, and *S. africana* performed better under the dry season (Fig. 3a). Seed age also significantly affected germination ($p < 0.05$). Fresh seeds of *B. plurijuga, G. coleosperma*, and *P. angolensis* showed higher germination compared to older seeds, whereas *C. mopane* germinated better with older seeds (Fig. 3b). In contrast, *B. africana* showed no significant difference in germination between seeds collected in October 2007 and those collected in October 2023 (Supplementary Table S1). Notably, *P. angolensis* seeds stored for 23 years showed 13.4% decrease in viability.

Table 3
Effect of soil media on seedling survival (%) across seven woodland tree species. Significance was tested using binomial generalised linear models. Asterisks indicate significant effects of soil media (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; ns = not significant).

Species name	Loamy	Clay	Sandy	Significant effect
Baikiaea plurijuga	96%	95%	99%	ns
Burkea africana	68%	77%	77%	ns
Colophospermum mopane	65%	50%	88%	**
Guibourtia coleosperma	90%	93%	89%	ns
Pterocarpus angolensis	94%	80%	87%	ns
Sterculia africana	100%	100%	100%	ns
Terminalia prunioides	100%	100%	75%	ns

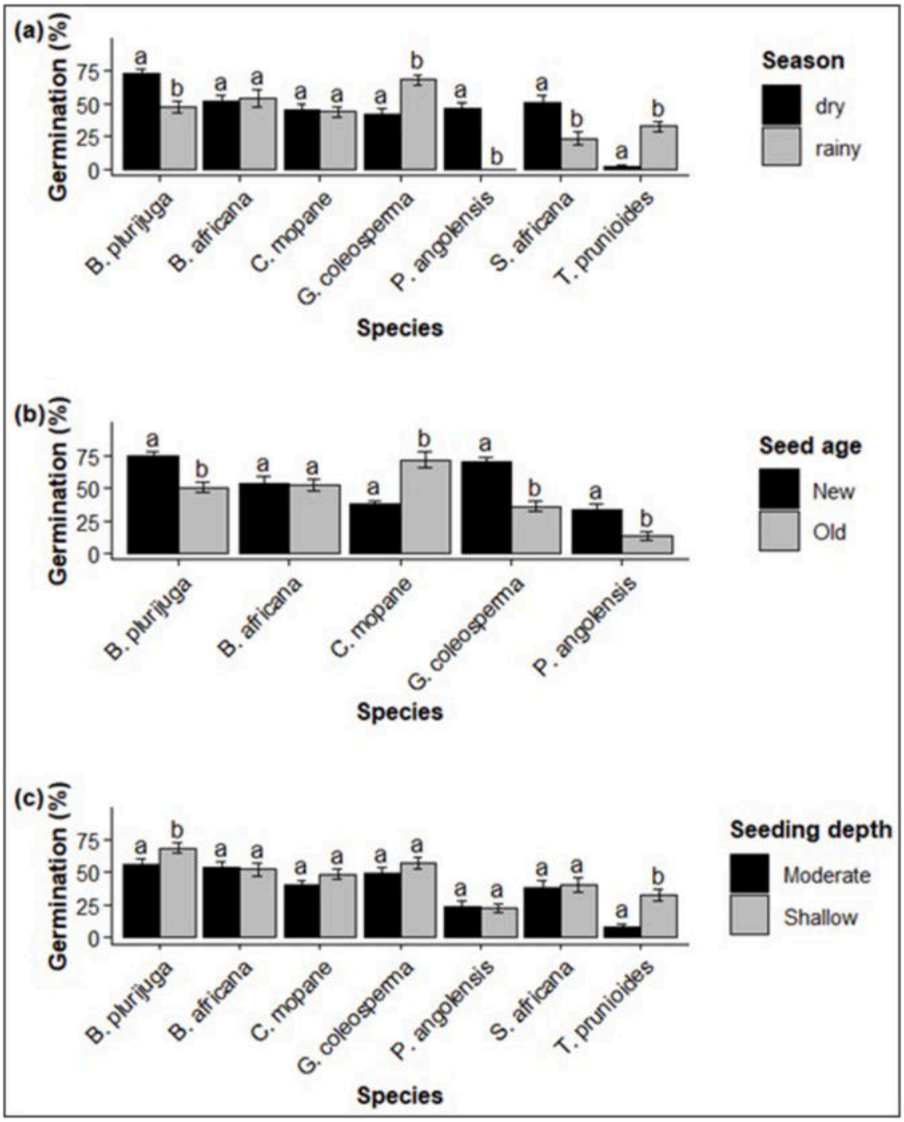

Fig. 3. Germination percentage across treatments: (a) season: dry: October vs. rainy: March, (b) seed age: new seeds < 1 year vs. old seeds > 3 years, and (c) seeding depth effects: shallow vs. moderate. Bars represent mean germination percentages ± standard error. Different letters indicate statistically significant differences between treatment groups within each species ($p < 0.05$). Species abbreviations: *B. plurijuga = Baikiaea plurijuga; B. africana = Burkea africana; C. mopane = Colophospermum mopane; G. coleosperma = Guibourtia coleosperma; P. angolensis = Pterocarpus angolensis; S. africana = Sterculia africana; T. prunioides = Terminalia prunioides.*

Seeding depth influenced germination in some species, particularly *B. plurijuga* and *T. prunioides* ($p < 0.05$), with shallow sowing resulting in higher germination than deeper sowing (Fig. 3c).

3.1.2. Post-emergence seedling survival

Soil media had no significant effect on seed germination across species (Table 3). However, it significantly influenced seedling survival after emergence at the ORC site, with higher survival in sandy soil than in clay and loamy soils. In contrast, no significant effect of soil media on seedling survival was detected at the MITC site ($p > 0.05$).

3.2. Seedling growth and survival

Overall, inoculation did not significantly affect seedling growth across all species. However, the interaction effect of inoculation and soil media indicated that seedling height responses were soil-dependent in some species. For example, *B. plurijuga* showed a significant difference in height following inoculation with *Azospirillum* sp. R111 in sandy soil (Fig. 4a). In contrast, *G. coleosperma* showed a significant difference in seedling height with higher values observed in the uninoculated treatment in loamy soil (Fig. 4c). *C. mopane* showed higher height following inoculation with *Enterobacter* sp. Mop1-1 in sandy soil; however, this difference was not statistically significant (Fig. 4b).

In terms of seedling survival, the inoculation with Azospirillum sp. had a significantly positive effect on *B. africana* ($p < 0.05$). Survival rates were significantly higher in B. africana (85% in inoculated vs. 67% in non-inoculated soils; Fig. 5). A positive trend was observed for C. mopane inoculated with Enterobacter sp. (73% vs. 65%) and T. prunioides inoculated with Azospirillum sp. (100% vs. 70%; Fig. 5). However, these differences were not statistically significant.

4. Discussion

This study demonstrates that germination and early seedling development of woodland species are influenced by interacting environmental factors, particularly season, seed age, and sowing depth, while soil conditions play a more prominent role during post-emergence survival. These findings highlight the importance of species-specific

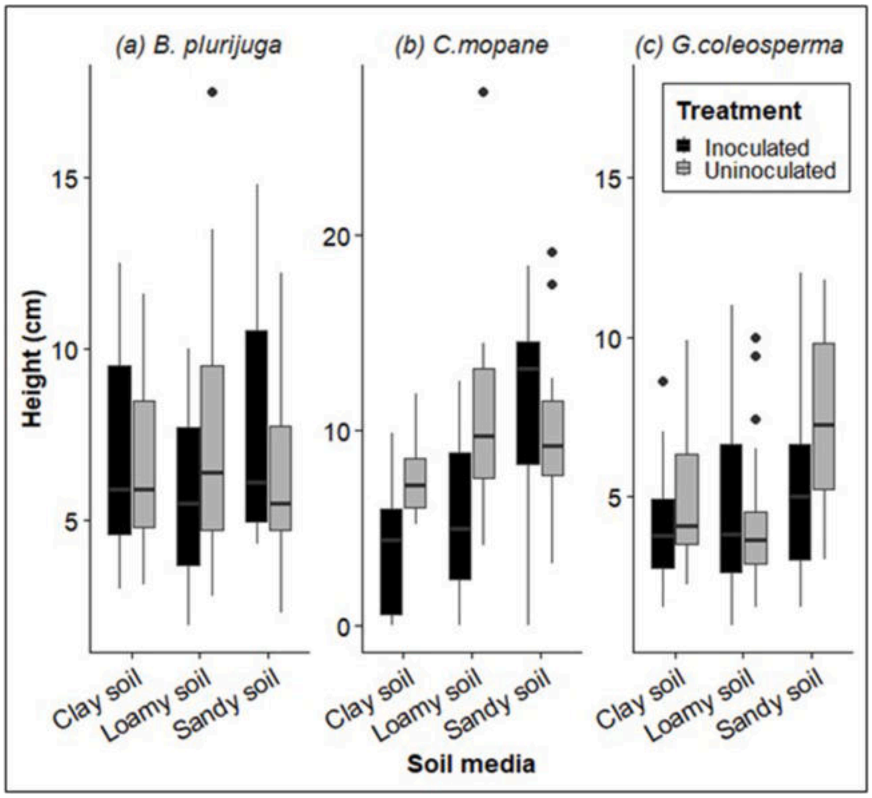

Fig. 4. Effects of microbial inoculation on seedling height across soil media. (a) Height of *Baikiaea plurijuga* (*B. plurijuga*) following inoculation with *Azospirillum* sp. R111, (b) height of *Guibourtia coleosperma* (*G. coleosperma*) following inoculation with *Azospirillum* sp. R111, and (c) height of *Colophospermum mopane* (*C. mopane*) following inoculation with *Enterobacter* sp. Mop1-1. Seedlings were grown in clay, loamy, and sandy soils. Boxplots represent the distribution of seedling height, with whiskers indicating minimum and maximum values and outliers shown as dots.

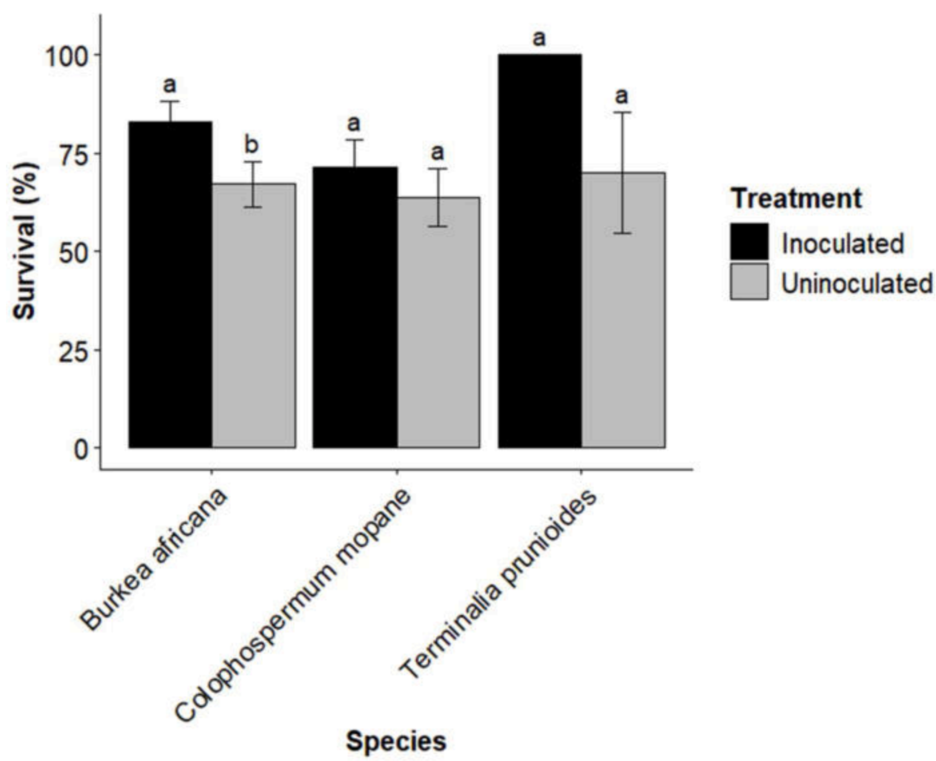

Fig. 5. Survival of inoculated and uninoculated seedlings of *Burkea africana, Colophospermum mopane*, and *Terminalia prunioides*, three months after inoculation. Error bars represent standard errors. Different letters show statistically significant differences between groups ($p < 0.05$).

responses in determining successful regeneration outcomes.

4.1. Germination response to treatments

Seasons influenced germination responses, although patterns varied among species. Most species showed higher germination under dry-season conditions, while a few germinated better during the rainy season. Notably, *S. africana* germinated well during the dry season but experienced complete seedling mortality shortly after emergence. This suggests that successful germination does not necessarily translate into successful establishment, particularly under conditions of limited soil moisture or unfavourable microclimates. Early seedling survival, therefore, represents a critical bottleneck, highlighting the importance of adequate post-germination care in nursery systems (Yisau et al., 2023).

In addition to seasonal effects, germination was influenced by seeding depth in some species, particularly *B. plurijuga* and *T. prunioides,* where higher germination was observed under shallow depth (Fig. 3c). Seeding depth determines the physical environment experienced by the seed, including moisture availability and resistance to emergence. As such, seed size often provides a useful guide for optimal sowing depth, with appropriate placement enhancing not only germination success but also early seedling establishment and growth (Ali and Idris, 2015; Fredrick et al., 2018; Ren et al., 2002).

The timing of seed collection and seed provenance can influence physiological maturity and dormancy status (Thapliyal et al., 2025). In this study, the timing of seed collection affected viability in some species (Fig. 3b). For example, *C. mopane* seeds collected in March of the experimental year showed lower germination rates than those collected in August (Supplementary Table S1). Additionally, older *C. mopane* seeds collected in 2015 were sourced from Endola, in north-eastern Namibia, within the North-Eastern Kalahari Woodland vegetation zone. The relatively humid microclimate in this area may have contributed to improved seed development and viability.

In contrast, soil conditions showed a different pattern. Soil medium did not influence seed germination across species. This suggests that germination in these species is driven more by seed traits and climate than by soil type. This contrasts with findings from other dryland studies, where soil properties influenced germination success (Dada et al., 2019; Pahla et al., 2014; Valdes-Rodriguez et al., 2013). However, soil media significantly affected *C. mopane* seedling survival, with higher survival observed in sandy soil (Table 3). Sandy soils are typically well-drained and aerated, which may facilitate root development and reduce the risk of waterlogging during early growth (Chidumayo and Gumbo, 2010; Mlambo et al., 2005). This suggests that although soil conditions may not directly control germination, they interact with plant physiological processes during early development, thereby influencing seedling survival (Chidumayo and Gumbo, 2010; Fenner and Thompson, 2005).

4.2. Germination differences among species

Differences in germination timing among species were observed and are likely associated with seed coat thickness and seed size, which together influence water uptake, dormancy release, and emergence dynamics (Baskin and Baskin, 1989; Fenner and Thompson, 2005). Hard-coated species such as *B. plurijuga* and *G. coleosperma* required more than two weeks to germinate, whereas soft-coated seeds, such as *C. mopane* and *B. africana*, germinated within approximately one week (Table 2). Similar patterns have been reported in other dry woodland species, where germination varies due to differences in seed coat properties and internal seed structure. For example, in *Sterculia urens*, variation in dormancy among seeds results in delayed or failed germination (Bhuva et al., 2019), while in *Terminalia ivorensis*, hard, impermeable seed coats limit water uptake and slow germination (Ibe et al., 2015). In *Pterocarpus indicus*, germination depends on sufficient water uptake and embryo development before radicle emergence (Capiltan et al., 2022). In addition to these seed traits, the timing of seedling emergence after germination may also influence early survival. Although not directly assessed in this study, species with epigeal germination may be more exposed to desiccation and temperature stress, whereas hypogeal species may benefit from protected cotyledons during early growth (Fenner and Thompson, 2005; Kitajima, 1992). Together, these factors help explain the differences in germination and early seedling survival observed among species in this study.

4.3. Bio-inoculant on seedling growth and survival

On seedling survival and growth, the primary intervention tested was inoculation with potential PGP bacteria, which was applied to the root zones three months after germination. Azospirillum sp. significantly improved survival rates in *B. africana*. For growth responses, increased height was observed in *B. plurijuga* in sandy soil following inoculation with Azospirillum sp., and in *C. mopane* following inoculation with *Enterobacter* sp.; however, the latter was not statistically significant. This indicates that the effectiveness of microbial inoculation under nursery conditions may be limited or highly context-dependent, varying with species-specific compatibility and soil conditions. This aligns with findings from Narula et al. (2000), who reported that soil texture significantly influences the performance of inoculants by affecting microbial mobility, colonisation, and root interactions.

The effectiveness of microbial inoculants is often species-specific. A study conducted in Botswana demonstrated contrasting responses to inoculation with *Bradyrhizobium ripae* during seed germination of two woodland species. In that study, inoculation increased the germination of *Baikiaea plurijuga*, whereas it reduced germination in *Pterocarpus angolensis* (Makgobota et al., 2026). In the present study, the response to inoculation also depended on both species and soil type, indicating interactions among species, soil, and inoculant. The interactions between the host plant, microbial strain, and environmental conditions influence the effectiveness of microbial inoculation (Bashan et al., 2014; Riaz et al., 2021). Host specificity is one of the key factors, as plant species differ in their ability to form beneficial associations with inoculated microbes (Smith and Read, 2008). This may explain why some species in this study showed positive responses to inoculation, while others did not. In addition, soil characteristics such as texture, moisture, and nutrient availability can affect microbial survival, mobility, and root colonisation (Rillig and Mummey, 2006). These findings indicate that the effectiveness of microbial inoculation is context-dependent and governed by interactions between host plant compatibility, microbial traits, and soil conditions, rather than by inoculation alone.

4.4. Ecological and management implications

Beyond physiological responses, ecological interactions and species roles within woodland systems should also be considered when evaluating regeneration strategies. In this study, *S. africana* and *T. prunioides* showed relatively low germination and seedling survival (Table 1). Nevertheless, both species play important ecological roles in woodland ecosystems. *S. africana* is an important browse species for elephants during the dry season. Similarly, *T. prunioides* frequently acts as a nurse tree for *C. mopane*, facilitating mixed-species woodland dynamics in arid environments (De Cauwer et al., 2024; Siebert et al., 2003). Although both species are currently listed as of least concern, their ecological functions highlight the importance of proactive conservation and restoration measures.

From a forest management perspective, promoting the sustainable use of underutilised species such as *T. prunioides* could help reduce harvesting pressure on heavily exploited species such as *C. mopane*. Diversifying the range of species used for fuelwood or restoration could enhance both ecological resilience and local livelihoods (Shackleton and Shackleton, 2004). Enrichment planting of *T. prunioides* could further support *C. mopane* regeneration while expanding available fuelwood and non-timber resource options for local communities.

Few studies have evaluated the long-term performance of nursery-grown seedlings after transplantation into natural environments (Chamshama et al., 2009; Hongwane et al., 2017; Ilunga-Mulala et al., 2024; Vyamana and Chamshama, 2007). Successful regeneration requires attention to the entire process, from seed collection and storage to germination, nursery management, and early seedling growth. By examining several key stages of this process, the present study provides practical insights for improving nursery practices for woodland restoration. In addition, this study serves as a baseline for future monitoring of the survival and establishment of nursery-raised seedlings after reintroduction into their natural habitats. Overall, the results highlight that successful assisted regeneration in dry woodlands requires species-specific protocols that account for both germination conditions and early seedling survival, which together determine restoration success.

5. Conclusion

Trees of southern African savannas and open woodlands respond differently to environmental conditions from germination through early seedling growth. The most critical stage occurs immediately after germination, when many seedlings fail to establish successfully. This highlights the importance of appropriate post-germination care in nurseries, including practices such as microbial inoculation, to improve seedling survival, health, and growth. These results provide a basis for developing species-specific nursery protocols and other assisted regeneration techniques to support restoration and sustainable management of native tree species in dry forest and woodland ecosystems.

Funding

This study was conducted as part of the “SASSCAL 2.0 – SUSTAIN Subproject NUST Forestry” under the Southern African Science Service Centre for Climate Change and Adaptive Land Management (Sustain 2.0), funded by the German Federal Ministry of Research, Technology and Space (BMFTR) to VDC. In the same framework, a grant SUSTAIN from BMFTR was awarded to BRH (no. 01LG2051A).

Ethics approval and consent to participate

Not applicable.

CRediT authorship contribution statement

Hilma N. Amupolo: Writing – original draft, Investigation, Formal analysis, Data curation, Conceptualization. **Vera De Cauwer:** Writing – review & editing, Validation, Supervision, Project administration, Funding acquisition, Conceptualization. **Barbara Reinhold-Hurek:** Writing – review & editing, Funding acquisition, Conceptualization. **Judith E. Giel:** Writing – review & editing. **Rolf W. Becker:** Writing – review & editing, Investigation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors would like to thank the Okahandja Seed Centre, under the National Tree Seed Collection (NTSC) program, for providing the seeds essential to this research. Sincere appreciation is extended to the nursery assistants at both Ongava Research Centre (ORC) and Mashare Irrigation Training Centre (MITC), as well as to all individuals involved in the collection of seeds and soil samples. We would like to thank Alice Jones for proofreading the initial manuscript. The lead author gratefully acknowledges the financial support provided by the Namibia Chamber of Environment (NCE) through a tuition bursary, which facilitated her academic enrolment and contributed to the successful completion of this research.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.tfp.2026.101336.

Data availability

Data will be made available on request.

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