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Bambara groundnut landraces response and tolerance to drought stress: A meta-analysis

Authors:
Mosima M. Mabitsela[1]
Ethel E. Phiri[2]
Marthinus J. Booysen[3]
Sydney Mavengahama[4]

Affiliations:
[1]Department of Agronomy, Faculty of AgriSciences, Stellenbosch University, Stellenbosch, South Africa

[2]Faculty of AgriSciences, Stellenbosch University, Stellenbosch, South Africa

[3]Department of Industrial Engineering, Stellenbosch University, Stellenbosch, South Africa

[4]Department of Food Security and Safety Focus Area, Faculty of Natural and Agricultural Sciences, North-West University, Mafikeng, South Africa

Corresponding author:
Ethel Phiri,
ephiri@sun.ac.za

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Background: Drought stress severely limits agricultural productivity. Bambara groundnut, an underutilised legume, shows promise for its resilience to harsh environments, particularly drought. Drought duration and manipulation type have been used to evaluate the response of Bambara groundnut to drought stress. Although studies have explored the effects of drought duration and manipulation on Bambara groundnut, an understanding of the legume's response to drought stress remains inadequate.

Aim: This meta-analysis assessed Bambara groundnut's response to different drought durations (long-term, medium-term, short-term) and manipulation types (constant, dry-and-rewetting, intermittent).

Setting: The study integrates data from multiple independent studies to evaluate how various drought durations and manipulations affect Bambara groundnut.

Methods: A systematic review and meta-analysis of studies examining drought's effects on Bambara groundnut were conducted. Data from qualifying studies were extracted and statistically analysed to quantify drought's impact on various physiological and yield parameters.

Results: Drought stress significantly reduced yield (–10.22), stomatal conductance (–8.04), and pod number (–4.20). Short-term and medium-term droughts had a greater negative impact than long-term droughts. Intermittent drought did not affect biomass, plant height, leaf number, and chlorophyll content, while dry-and-rewetting cycles did not affect seed number.

Conclusion: Based on the meta-analysis, future drought scenarios are predicted to negatively impact Bambara groundnut productivity, surpassing the challenges posed by current drought conditions.

Contribution: This study emphasises the importance of developing strategies to enhance the resilience of indigenous crops, such as Bambara groundnut to drought, crucial for ensuring future food security in the face of changing climate patterns.

Keywords: drought duration; drought manipulation; underutilised crops; *Vigna subterranea*; PRISMA.

Introduction

Underutilised and indigenous crops have gained recognition for their inherent ability to thrive under drought conditions, showcasing impressive drought tolerance (Kunene et al. 2022; Singh, Sreenivasulu & Prasad 2022; Talabi et al. 2022). These crops have evolved in specific regions over generations, adapting to local environmental challenges, including water scarcity (Nhamo et al. 2022; Shembe et al. 2023). Bambara groundnut (*Vigna subterranea* (L.) Verdc.), an indigenous underutilised African legume, is one such crop. This legume demonstrates its adaptability by flourishing in a diverse range of climatic conditions, including both semi-arid and tropical regions (Linus et al. 2023; Olanrewaju et al. 2021; Valombola, Awala & Hove 2021).

The crop reaches its optimal growth and productivity in regions characterised by dry, warm, semi-arid climates, such as those found in Burkina Faso, South Africa, Ghana, Kenya and Nigeria (Majola, Gerrano & Shimelis 2021; Mateva et al. 2020; Zongo et al. 2018). The regions where Bambara groundnut thrives are characterised by their prolonged periods of arid conditions, where rainfall is limited, temperatures can become extreme, and the environment is often harsh (Esan, Oke & Ogunbode 2023; Salazar-Licea et al. 2022). Although drought limits the potential of Bambara groundnut productivity, it is still the third most important legume in sub-Saharan Africa

(Ajilogba, Olanrewaju & Babalola 2022; Maphosa, Jideani & Maphosa 2022).

Research into the impact of drought on Bambara groundnut has revealed a substantial decrease in both seed yields and biomass production under drought conditions (Kundy et al. 2023). Berchie et al. (2016) indicated that Bambara groundnut employs a mechanism to enhance its resilience to drought, which involves maintaining leaf turgor pressure, reducing leaf area, regulating stomatal openings and incorporating osmotic adjustments. This resilience and adaptability make Bambara groundnut a valuable resource for agricultural sustainability in regions where extreme weather conditions, particularly drought, can be a recurring threat to food security and livelihoods (Donkor et al. 2022; Soumare, Diedhiou & Kane 2022). Its ability to thrive in adverse conditions underscores the importance of conserving and promoting the cultivation of this indigenous and underutilised crop (Ayilara et al. 2022; Singh et al. 2022). Therefore, understanding the response and tolerance of Bambara groundnut to drought stress is important, especially because drought is projected to become more extreme in sub-Saharan Africa.

Considering the significant challenges posed by climate change on agricultural production, farmers and researchers are increasingly concerned about the potential rise in extreme changes, changes in critical climatic elements, including severe temperatures and extended periods of drought (Hickman et al. 2021; Stoddard et al. 2021; Weber 2010). The issue of drought is a multifaceted problem as it limits normal plant growth and development by disrupting crucial morphological, physiological and biochemical processes (Jaleel et al. 2008; Lei, Yin & Li et al. 2006; Wahab et al. 2022). Therefore, it is important to understand how plants respond, tolerate and adapt to drought stress conditions.

Several investigations have assessed the impact of drought stress induced at various growth stages on the morphology, physiology and biochemistry of Bambara groundnut (Chai, Massawe & Mayes 2016; Fatimah, Djunaedy & Nurholis 2021; Jorgensen et al. 2011; Mabhaudhi & Modi 2013; Mwale & Azam-Ali 2005; Vurayai, Emongor & Moseki 2011). These studies have demonstrated that the duration and method of drought imposition play a crucial role in determining the intensity of stress on plant growth and development, chlorophyll accumulation, yield and overall plant biomass. It is noteworthy that most of these studies have highlighted the fact that Bambara groundnut landraces exhibit distinct responses to drought stress. Any modifications in plant morphology, physiology and biochemistry, as revealed by these studies, ultimately have negative consequences on crop yield and overall productivity (Mamnabi et al. 2020; Miceli et al. 2023).

A significant number of these studies have examined the impact of drought on Bambara groundnut landraces using non-representative landraces, in diverse growing conditions, in various geographical locations, with a wide array of drought manipulation methods, and often without adhering to a formal naming system. This has made it challenging to identify which landraces exhibit greater tolerance or susceptibility to such stress. Nevertheless, the insights garnered from these studies remain valuable in identifying Bambara groundnut landraces that outperform others in drought conditions. Additionally, these landraces have provided essential information regarding the mechanisms by which Bambara groundnut responds to drought stress.

The complexity and diversity in the responses and tolerance of Bambara groundnut landraces to drought stress make it a challenging subject to comprehend fully. Until now, research efforts to gather information on the effects of drought on Bambara groundnut have largely been based on literature reviews and experimental studies (Hellar et al. 1997; Spreeth et al. 2004). There has not yet been a comprehensive quantitative review that synthesises the available literature through meta-analysis, specifically focussing on the effects of drought on Bambara groundnut. A meta-analysis is a powerful tool that can be used to analyse and consolidate findings from various individual studies that share the common objective of investigating how Bambara groundnut responds to drought. This approach will account for the diversity in experimental factors and variations among these studies (Hedges et al. 1999). Therefore, this study aims to evaluate the morphological, physiological and yield response of Bambara groundnut landraces under drought stress conditions using meta-analysis.

Research methods and design

Literature search and study selection

A systematic literature search was conducted to compile information on the impact of drought on Bambara groundnut. To ensure comprehensive coverage of all relevant articles, multiple databases (i.e. CAB Abstracts, Google Scholar, Scopus, and Web of Science) were searched. In addition to these databases, the reference lists of random articles were also searched in order to capture any additional articles that might not have been retrieved through the initial database searches, thereby enhancing the comprehensiveness of the literature selection process. The literature search string used to retrieve the articles was [(Drought OR 'water stress' OR 'osmotic' OR 'dry periods' OR 'moisture stress' OR 'soil moisture stress') AND ('Effects of drought') AND ('Effects of water stress') AND ('Effects of soil moisture') AND ('Effects of soil moisture stress') AND ('Bambara groundnut' OR '*Vigna subterranea*')]. The search for literature was conducted from 09 November 2022 to 10 November 2023. The meta-analysis adhered to the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analysis) statement (Liberati et al. 2009) as detailed in the results section.

Inclusion criteria

The selection criteria for studies were not constrained by geographic location or publication year. This approach aimed to ensure a comprehensive representation of Bambara groundnut landraces across diverse ecological regions and encompassing various agronomic management practices in the meta-analysis. Consequently, all articles included in this meta-analysis needed to satisfy the following inclusion criteria:

1. Studies were required to focus on the impact of drought on one or more Bambara groundnut landraces.
2. Studies should have incorporated a treatment involving drought duration or drought manipulation, alongside a control group receiving a normal water supply suitable for Bambara groundnut cultivation.
3. Inclusion necessitated the availability of results for at least one of the targeted response variables of Bambara groundnut, encompassing morphological, physiological and yield aspects.
4. Only primary studies were considered, excluding reviews or meeting reports.
5. The language of the studies had to be English.

Data collection and grouping

The impact of drought on Bambara groundnut was evaluated by examining eight response variables identified from the retrieved articles (Table 1). These variables encompassed total plant biomass (t/ha), chlorophyll content (μmol/m^2), stomatal conductance (mmol/m^2/s), plant height (cm), number of leaves, pod number, seed number (number/plant), and yield (t/ha). To systematically gather and organise this information, the means of each response variable were extracted from the articles and compiled in an Excel sheet. This data collection process ensures a comprehensive and structured analysis of the diverse effects of drought on various aspects of Bambara groundnut growth and productivity.

In the process of the meta-analysis, the extraction of means for each response variable was carried out alongside the collection of essential statistical parameters, including standard deviations and the number of replicates for both treatment and control groups. In instances where standard deviations were not directly provided in the retrieved articles, alternative measures of dispersion, such as standard errors, were extracted and subsequently converted to standard deviations.

It is important to highlight that several studies did not provide standard deviations or alternative measures of dispersion. In response to this gap, standard deviations were computed using R software, as detailed in the statistical methods section. This approach was crucial for ensuring the completeness of the dataset and maintaining statistical robustness in the subsequent analyses. Attempts to contact the corresponding authors for missing information were unsuccessful, as none of the contacted authors provided the requested data. Furthermore, for studies presenting results in graphical form, data extraction was facilitated using Web Plot Digitizer (version 4.6, https://automeris.io/WebPlotDigitizer/). This approach ensured the meticulous retrieval of numerical data from graphs, contributing to the comprehensive dataset used for subsequent meta-analysis.

In addition to the aforementioned details, the study also documented the following information: study location (including country and specific study site details); experimental details (comprising study duration specified in seasons, irrigation or rainfed conditions, type of experiment, experimental design, number of replicates, and relevant agronomic practices); characteristics of cultivation media (identifying the planting media type and, for field studies, detailing soil characteristics); drought conditions (specifying the type and induction method, along with the duration of the drought treatment); and crop details (providing information on the specific Bambara groundnut landrace used, including the landrace name or relevant characteristics). In instances where multiple landraces, study locations, experimental types and other relevant information were reported within a single study, these observations were treated as separate studies in the data collection process. This approach was adopted because it was observed that some authors provided only the average of multiple datasets or reported a single set of data typically obtained at the conclusion of a multi-year study (Motsi 2022). By treating each unique set of conditions or data as distinct studies, the meta-analysis ensured a more precise and comprehensive representation of the research findings.

The independent variables comprised of drought duration and manipulation type, while the dependent variables encompassed various crop parameters (Table 1). The categorisation of the independent variables was adapted from a study conducted by He and Dijkstra (2014).

Statistical analysis

The overall effect of drought was computed using the 'standardised mean difference' (SMD) effect size, employing Hedges' *g*, which generated standard deviations, *p*-values, and 95% confidence intervals (CIs) for the selected variables (Hedges & Olkin 1985). The SMD, particularly using Hedges' *g*, is a widely utilised effect size in ecological meta-analyses because of the predominantly continuous nature of variables in ecological studies. Given that most articles did not include standard deviations, the 'esc' package, utilising the 'escalc' function in the *R* statistical software, was employed for

TABLE 1: Independent and dependent variables used in the meta-analysis.

Independent variables	Categories
Drought duration	Short-term (0–30 days)
	Medium-term (31–90 days)
	Long-term (> 90 days)
Drought manipulation type	Constantly stressed (drought stressed throughout the experiment) (Type 1)
	Dry-and-rewetting drought stress (exposed to dry-and-rewetting cycles throughout the experimental period) (Type 2)
	Intermittent drought stress (periods of inducing drought at irregular intervals) (Type 3)
Dependent variables	-
Total plant biomass	-
Chlorophyll content	-
Stomatal conductance	-
Plant height	-
Number of leaves	-
Pod number	-
Seed number	-
Yield	-

standard deviation calculations. The 'esc' package is commonly used when studies do not report standard deviation or any other measure of dispersion.

The random effects model, utilising the residual maximum likelihood (REML) method, was employed under the assumption that the effect size in the dataset is not correlated with the individual studies from which the data were extracted (K). The use of random effects models is advantageous for statistical accuracy as they accommodate the heterogeneity of variance, assuming that effects are normally distributed (Takeshima et al. 2014). Analyses were conducted using the 'rma' function of the 'metafor' package in the R statistical software.

The Higgins and Thompson's I^2 (Higgins & Thompson 2002) and Cochran's Q (Cochran 1954) tests were employed to evaluate the heterogeneity of the effect size. Statistical significance for differences between groups was considered when $p < 0.05$. The effect size serves as an indicator of the relationships that coexist between the selected variables (Kallogjeri & Piccirillo 2023). Negative effect sizes denote a decrease in the selected variables under drought stress, while positive percentages indicate an increase in the selected variables under drought stress conditions. The impact of drought stress categories (drought duration and drought manipulation) on the variables was visualised through forest plots, created using the 'forest' function in the R statistical software package. Drought duration was sub-grouped into long-, medium-, and short-term drought, while drought manipulation was sub-grouped into constant drought stress (Type 1), dry-and-rewetting drought stress (Type 2), and intermittent drought stress (Type 3).

Ethical considerations

This article followed all ethical standards for research without direct contact with human or animal subjects.

Results and discussion

General characteristics of the analysed studies

The literature search, using the search string, initially identified 476 articles from various sources, including CAB Abstracts (105), Scopus (120), Web of Science (245), and others (6) (Figure 1). Following the screening process, 22 articles were deemed suitable for inclusion in this study. The excluded studies were primarily comprised of review articles on Bambara groundnut, studies that did not report on any of the selected variables, and studies from which relevant information could not be obtained even after reaching out to the corresponding author(s).

In terms of geography, South Africa emerged as the dominant contributor with five articles, followed by the United Kingdom and Nigeria, each with four articles. Malaysia had 3 articles, while Botswana, Denmark, and Indonesia had two articles each. Furthermore, India, Ghana and Kenya each contributed one article. The most frequently studied landraces included Swazi-Red, DipC and S19-3. However, it is important to note

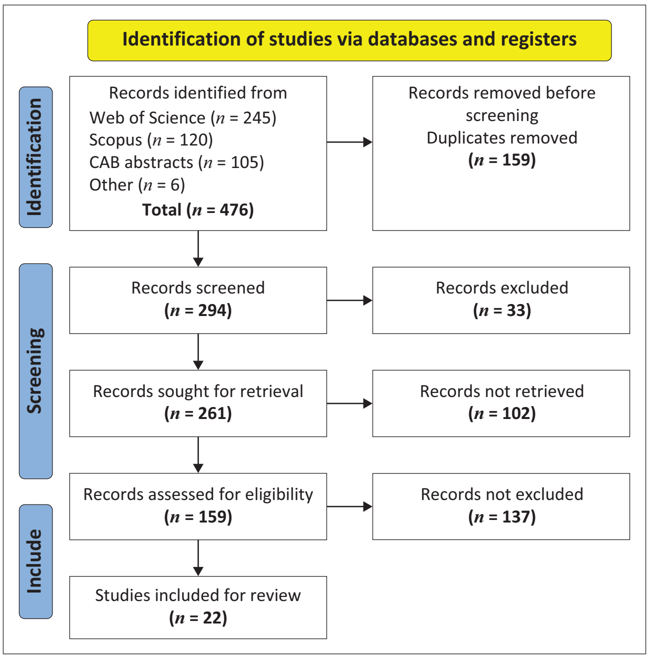

FIGURE 1: The preferred reporting method for systematic reviews and meta-analysis for the effects of drought duration and manipulation on Bambara groundnut landraces.

that these landraces, specifically DipC and S-19-3, have not been described, making some of the studies challenging to replicate. The majority of the studies were conducted in sandy loam soils, with only two studies opting for soilless cultivation systems. Additionally, a few studies reported cultivating Bambara groundnut under protective conditions, while others mentioned planting the crop in open field conditions.

Heterogeneity between the experimental and response variables

Higgins and Thompson's I^2 test revealed values above 90% for biomass, yield, pod number, plant height, leaf number, chlorophyll content and stomatal conductance, contrasting with the 0% heterogeneity observed for seed number (Table 2). However, seed number exhibited low heterogeneity (0%). The high heterogeneity observed among the experimental variables and response variables is a common occurrence in meta-analyses (Motsi 2022). This variance can be attributed to the diverse research approaches employed by different authors in their studies. The primary aim of this meta-analysis was to assess the impact of experimental variables, specifically drought duration and manipulation type, on the response variables. Consequently, the anticipated outcome was a high degree of heterogeneity in the overall effect size across various response variables.

In this meta-analysis, drought duration and manipulation type were categorised into subgroups to comprehensively assess their influence on the response variables. This grouping was crucial because of variations among researchers in terms of: (1) the methods employed to induce drought; (2) the varying durations and manipulation techniques based on study objectives; and (3) the diverse environmental conditions under which the experiments were conducted.

TABLE 2: Statistics for heterogeneity report of effect sizes of experimental variables on response variables.

Parameter	*Q*	*df*	I^2	*p*
Biomass	860.93	103	97.24	< 0.0001
Yield	194.54	24	92.60	< 0.0001
Pod number	620.44	58	96.84	< 0.0001
Seed number	193.75	56	0.00	< 0.0001
Plant height	523.28	77	96.13	< 0.0001
Leaf number	158.77	22	95.70	< 0.0001
Chlorophyll content	489.90	71	94.48	< 0.0001
Stomata conductance	260.44	28	97.09	< 0.0001

df, degrees of freedom.

The overall effect of drought duration and manipulation type on Bambara groundnut

There were significant differences in the morphology (plant height and number of leaves), physiology (chlorophyll content and stomatal conductance), and yield parameters (biomass, yield, pod number, and seed number) in their response to drought stress. On average, drought stress reduced plant height by an effect size (Eff. size) of –4.14 (standard error [SE] = 0.80; CI = –5.70; *K* = 78; *n* = 5; *p* = 0.0001), number of leaves by an effect size of –2.89 (SE = 1.15; CI = –5.16; *K* = 22; *n* = 11; *p* = 0.05), and biomass by an effect size of –3.2 (SE = 0.72; CI = –4.66; *K* = 104; *n* = 15; *p* = 0.0001). The considerable decrease in the yield (Eff. size = –10.22; SE = 1.65; CI = –13.45; *K* = 25; *n* = 6; *p* = 0.0001) of Bambara groundnut may have been influenced by the decrease in pod number (Eff. size = –4.20; SE = 1.13; CI = –6.42; *K* = 59; *n* = 12; *p* = 0.0001) and seed number (Eff. size = –0.55; SE = 0.11; CI = –0.77; *K* = 57; *n* = 7; *p* = 0.00010). Drought also decreased the chlorophyll content by an effect size of –2.04 (SE = 0.53; CI = –3.09; *K* = 72; *n* = 8; *p* = 0.0001) and stomatal conductance by an effect size of –8.04 (SE = 1.57; CI = –4.96; *K* = 29; *n* = 9; *p* = 0.0001).

The effect of drought duration and drought manipulation type on Bambara groundnut

Plant height

Plant height increased significantly under long-term drought duration with an effect size of 1.13 (SE = 1.59; CI= –1.99; *K*= 24; *n* = 3; *p* < 0.0001) and under intermittent drought stress (Eff. size = 4.56; SE = 2.38; CI = –0.18; *K* = 15; *n* = 2; *p* = 0.0554). The slight increase in plant height in Bambara groundnut may be explained by two mechanisms, that is, drought avoidance and tolerance. Drought avoidance is the ability of plants to sustain important physiological and morphological processes under drought stress conditions (Basu et al. 2004). Modification of the root structure including root length, morphology and density is one important strategy used by plants to survive under drought stress conditions. As such, plant height might have increased because of hydrotropism, a process in which plants modify or expand their roots towards the direction of water (Antoni et al. 2016; Dietrich 2018; Gul & Weber 1998). Hydrotropism is an important process during drought stress in which plants modify or expand their roots towards the direction of water in return enhancing growth and ensuring their survival.

Drought tolerance provides plants with the ability to maintain cell turgor through osmotic regulation, cell elasticity and osmo-protectants (Morgan & King 1984). Under drought stress conditions, plants tend to reduce membrane water permeability as a way of conserving water at the cellular level. This is a type of osmoregulation that depends on the synthesis of osmolytes such as sugars, proteins and amino acids (Csonka & Hanson 1991; Ozturk et al. 2021). The synthesis and accumulation of these osmolytes do not interfere with essential plant processes (Darko et al. 2019; Singh et al. 2019). They help plants maintain normal growth enabling them to survive under stress conditions.

Plant height decreased significantly under medium-term drought (Eff. size duration –10.10; SE = 0.79; CI = –11.66; *K* = 33; *n* = 1; *p* < 0.0001). Similar results were reported by Kusaka, Lalusin and Fujimura (2005) in pearl millet. They reported that plant height was inhibited under short-term drought stress conditions. On the other hand, dry-and-rewetting decreased plant height at an effect size of -8.40 (SE = 0.75; CI = –9.88; *K* = 42; *n* = 2; *p* = 0.001).

The development of plants depends on three interlinked cell processes, which are cell division, elongation and differentiation (Beemster & Baskin 1998; Obroucheva 2008). These cell growth and developmental processes are sensitive to drought stress conditions because of their dependency on cell turgor (Ali et al. 2023; Green & Cummins 1974). Cell turgor pressure in plant cells is controlled by osmosis (Rojas & Huang 2018; Zimmermann 1978). As such, maintaining osmotic adjustments during drought stress is important as drought stress affects many biochemical and physiological processes (Ozturk et al. 2021). A decrease in cell turgor pressure inhibits plant growth and development because of disruptions in cell division, elongation and differentiation (Proseus & Boyer 2005).

Number of leaves

No significant differences were observed in the reduction of the number of leaves under medium-term drought duration (Eff. size = –10.12; SE = 2.63; CI = –15.26; *K* = 4; *n* = 1; *p* > 1).

Long-term drought duration had the least impact on the number of leaves (Eff. size = –2.58; SE = 1.15; CI = –4.84; *K* = 21; *n* = 1; *p* < 0.0001). A similar pattern was reported by Sinamo, Hanafi and Wahyuni (2018), who found that *Pueraria javanica*, a drought-tolerant legume, experienced a significant decrease in the number of leaves under long-term drought conditions.

Nutrient imbalances in plants significantly impact crucial physiological processes. Drought stress limits a plants' ability to access essential elements necessary for optimal growth (Da Silva Lobato et al. 2020; Li et al. 2023). Beyond drought's impact on water absorption, the reduction in the number of leaves may have been further influenced by nitrogen deficiency. A meta-analysis conducted by He and Dijkstra (2014) demonstrated that drought stress diminishes nitrogen availability to plants. Nitrogen, a vital macro-element, plays a key role in leaf senescence (Sakuraba et al. 2020; Zakari et al. 2020). Consequently, the deficiency of this nutrient likely contributed to the observed decrease in the number of leaves in the landraces. This interplay between drought-induced nutrient limitations and their effects on plant physiology underscores the complex relationships governing plant responses to environmental stressors.

Furthermore, drought stress hinders the translocation of carbohydrates within leaves (Bunce 1982; Liu, Jensen & Andersen et al. 2004). The resultant reduction in carbohydrate levels can trigger an excessive production of reactive oxygen species (ROS) (Couée et al. 2006; Keunen et al. 2013). These ROS, in turn, inhibit protein synthesis and cause damage to membrane lipids, ultimately amplifying the process of leaf senescence (Bista et al. 2018). The consequential leaf senescence and abscission during plant growth directly influence both the total number of leaves per plant and the overall plant height. This highlights the intricate mechanisms through which drought-induced disruptions in carbohydrate metabolism contribute to broader physiological changes in plants.

Constant drought stress resulted in a significant reduction in the number of leaves, with a mean effect size of –9.04 (SE = 4.01; CI = –16.89; K = 4; n = 4; $p < 0.0243$). In contrast, under intermittent drought stress, there was an increase in the number of leaves, indicated by an effect size of 2.24 (SE = 2.4; CI = –2.44; K = 5; n = 2; $p < 0.0554$).

Kunz, Ra der and Bauhus (2016) also observed a decrease in the number of leaves under the dry-and-rewetting drought manipulation type for *Sorbus torminalis*. Their findings suggested that the loss of leaves in plants may serve as a mechanism of drought tolerance, enabling the plant to allocate available resources to reproductive plant parts. These contrasting responses highlight the diverse strategies employed by plants in coping with different drought stress scenarios and underscore the multifaceted balance between resource allocation and stress adaptation mechanisms.

The timing and duration of drought events are unpredictable (Joshi et al. 2021). During prolonged drought stress, plants undergo adaptive changes in their physiological, morphological and biochemical processes to ensure survival. However, unexpected watering after plants have adapted to drought stress conditions can result in cell swelling and eventual cell death (Bacete & Hamann 2020; Loreti, Van Veen & Perata 2016). Consequently, crucial physiological and metabolic processes essential for plant growth and development are disrupted. In this study, both dry-and-rewetting drought stress and constant drought stress contributed to a reduction in the number of leaves in the landraces. This decline may be attributed to cell death caused by exposure to irregular watering and drying cycles.

Chlorophyll content

Significant decreases in the chlorophyll content were observed under short-term drought duration (Eff. size = –2.49; SE = 0.45; CI = –3.37; K = 39; n = 3; $p < 0.0001$). Conversely, there were no significant reductions in chlorophyll content under medium-term drought conditions (Eff. size = –1.27; SE = 0.81; CI = –2.86; K = 3; n = 1; $p > 0.065$). Similar findings were reported by Hu, Zhang and Guo (2023) who observed a decrease in chlorophyll in yellow horn under short-term drought conditions.

Drought stress has a detrimental impact on the photosynthetic apparatus and the chlorophyll structure within mesophyll cells (Çiçek et al. 2019; LI et al. 2006). This damage limits the plant's ability to harness light, a crucial component of photosynthesis. Light is essential for generating adenosine triphosphate (ATP) and nicotinamide adenine dinucleotide phosphate (NADPH) during photosynthesis (Osborne & Raven 1986; Simkin et al. 2022). In the process of photosynthesis, plants utilise stored energy to convert carbon dioxide and water into glucose. These observed reductions in chlorophyll content and stomatal conductance under short-term drought duration highlight the detrimental impact of this stress on fundamental processes essential for plant growth and metabolism.

In terms of drought manipulation, a significant decrease was observed in chlorophyll content under dry-and-rewetting drought stress, with an effect size of –4.95 (SE = 1.27; CI not provided; K = 42; n = 2; $p < 0.001$).

These findings deviate from those reported by Farooq (2020) in maize, where the author observed a tendency for chlorophyll content to decrease under dry-and-rewetting drought manipulation. Conversely, under intermittent drought stress, the chlorophyll content exhibited an increase (Eff. size = –2.79; SE = 0.41; CI = –0.29; K = 13; n = 2; $p < 0.05$).

These contrasting responses emphasise the variability in plant species' reactions to different drought manipulation types, suggesting that the impact of drought on chlorophyll content is influenced by diverse factors, including the specific characteristics of each plant species and the degrees of the drought manipulation employed. Therefore, the observed increase in chlorophyll content under intermittent drought conditions could be attributed to the intricate interplay between the specific landrace and prevailing environmental conditions.

The degree of this increase appears to be closely linked to the tolerance level of the particular landrace. This correlation underscores the dynamic nature of the plant's response to intermittent drought stress, indicating that certain landraces may exhibit enhanced chlorophyll content as a resilience strategy. Similar findings were reported by Yang et al. (2023) in wheat, where they noted an increase in chlorophyll content under drought stress conditions. This variation was attributed to the diverse levels of drought tolerance among different wheat cultivars, also emphasising the importance of genetic factors in shaping a plant's ability to cope with environmental stressors.

Stomatal conductance

The most substantial decrease in stomatal conductance was observed under short-term drought stress (Eff. size = –22.33; SE = 2.52; CI = –3.37; K = 5; n = 2; p < 0.001) and constant drought stress (Eff. size = –16.62; SE = 1.86; CI = –20.27; K = 11; n = 3; p = 0.001). In contrast, the least reduction in stomatal conductance occurred under long-term drought duration (Eff. size = –2.71; SE = 1.02; CI = –3.37; K = 18; n = 5; p = 0.01) and dry-and-rewetting drought manipulation type showed minimal impact (Eff. size = –0.01; SE = 0.28; CI = –0.57; K = 7; n = 4; p = 0.9639).

Similar findings were reported by Talbi et al. (2020) in their study on the response of *Oudeneya africana* to dry-and-rewetting drought manipulation, where they observed a decrease in stomatal conductance during dry-and-rewetting cycles. These results highlight the varied responses of stomatal conductance to different drought stress conditions and manipulation types, indicating the importance of both duration and management strategies in influencing plant physiological processes.

Stomatal conductance exhibited a similar trend as chlorophyll content, decreasing under the influence of drought stress conditions. The initiation of stomatal closure by stomatal guard cells is a well-documented response to drought stress (Agurla et al. 2018; Buckley 2019). This closure is prompted by a reduction in turgor pressure within the guard cells, leading to the reduction of stomatal pores (Qi et al. 2023). The closure of stomata or alterations in pore sizes have the effect of limiting carbon dioxide intake in leaves, a crucial component in the process of photosynthesis (Chen et al. 2023; Jin et al. 2023). Interestingly, under short-term, medium-term and constant drought conditions, stomatal conductance displayed a more pronounced decrease compared to long-term drought conditions.

This observation suggests a potential avoidance mechanism employed by Bambara groundnut to mitigate further water loss through transpiration. This differential response to drought duration implies that the plant strategically adjusts its stomatal conductance to balance water conservation while still facilitating essential photosynthetic processes under prolonged stress conditions.

Overall yield, pod number and seed number

There were no significant differences in the decrease of the overall yield under short-term drought duration (Eff. size = –22.33; s.e. = 2.51; CI = –27.20; K = 5; n = 1; p > 0.59). The limited availability of studies in the meta-analysis focussing on the effects of short-term drought duration on the yield response of Bambara groundnut may have contributed to this observation. Specifically, the pod number (Eff. size = –5.23; s.e. = 1.30; CI = –7.77; K = 24; n = 4; p < 0.0001) and seed number (Eff. size = –2.72; s.e. = 0.78; CI = –4.25; K = 41; n = 3; p < 0.0001) both exhibited significant decreases under short-term drought conditions.

There were no statistically significant differences in the decrease in the number of seeds under long-term drought conditions (Eff. size = –0.07; s.e. = 0.26; CI = –0.57; K = 16; n = 4; p > 0.1). Similar results were reported by Ru et al. (2022) when evaluating the yield performance of wheat under short-term drought stress. Long-term drought stress leads to a short reproductive phase, which will in turn affect the overall plant performance (Fahad et al. 2017).

The constantly stressed type decreased the yield by an effect size of –13.53 (SE = 2.03; CI = –17.52; K = 7; n = 2; p = 0.0001). The least decrease in yield was observed under intermittent drought stress conditions (Eff. size = –6.55; SE = 1.23; CI = –8.96; K = 5; n = 1; p = 0.0001). The lowest decrease in pod number was observed under intermittent drought, where the pod number decreased by an effect size of –0.93 (SE = 2.40; CI = –5.65; K = 15; n = 3; p = 0.6995). There were no significant differences in the seed number under dry-and-rewetting (Eff. size = 0.0003; SE = 1.84; CI = –3.60; K = 6; n = 2; p = 0.999), and intermittent drought (Eff. size = –0.07; SE = 0.26; CI = –0.58; K = 10; n = 2; p = 0.7848) drought stress conditions.

Similar findings were reported by Nabateregga et al. (2018), who observed that intermittent drought stress conditions led to a reduction in yield and yield components of common beans. Correspondingly, Hamidou, Halilou & Vadez (2013) reported comparable results in peanuts, highlighting that intermittent drought stress conditions resulted in a decreased pod yield across various genotypes included in their study.

Under drought stress conditions, Bambara groundnut normally produces fewer flowers or will have a short flowering period. This will in turn affect pod and seed production (Mateva et al. 2020; Vurayai et al. 2011). Flower formation is one of the important processes that initiates peg formation in Bambara groundnut. This is an important process because peg formation ensures pod formation and provides the pods with an ideal environment for development.

The exposure of plants to drought stress during pod formation increases the chances of poor seed set, shrivelled seeds, delayed pod maturation and ripening, which will eventually lead to decreased number of seeds and the overall total seed weight (Westgate & Peterson 1993). Similarly, the occurrence of dry-and-rewetting cycles at various intervals throughout the growing season and intermittent drought stress happening at irregular intervals pose challenges. The unpredictable nature of droughts makes it difficult to anticipate, and the exposure of Bambara groundnut to drought stress during the flowering stage has a detrimental impact on its yield productivity.

Biomass

Medium term drought duration (Eff. size = –5.77; SE = 1.31; CI = –8.34; K = 43; n = 3; p = 0.0001) and dry-and-rewetting drought manipulation (Eff. size = –4.15; SE = 1.33; CI = –6.74; K = 20; n = 4; p = 0.0001) had a highly significant impact on Bambara groundnut biomass accumulation. However, biomass was significantly increased under intermittent drought stress with an effect size of 0.69 (SE = 1.86; CI = –2.94; $K = 18$; $n = 3$; $p = 0.0001$).

Guasconi, Manzoni and Hugelius (2023), when conducting a meta-analysis on the response of grassland species to drought duration and intensity, observed that the total biomass tends to decrease under long-term drought duration. However, they emphasised that the effects were more dependent on the species and the recovery rate of the plants when exposed to drought stress.

The overall decrease in biomass accumulation might have been influenced by the disruption of crucial physiological processes, that are important in plant growth and development of new leaves. The sensitivity and the tolerance of the landraces to different drought duration and manipulation types influenced the overall biomass accumulation performance under drought stress conditions.

Conclusion

This meta-analysis was conducted to determine the effect of drought duration and manipulation type on Bambara groundnut morphology (plant height and number of leaves), physiology (chlorophyll content and stomatal conductance) and yield parameters (yield, pod number and seed number plant biomass).

Based on the findings from the study, it can be concluded that: (1) the Bambara groundnut landraces differ in their response to drought stress, (2) with time Bambara groundnut landraces are able to adjust their growth as a way of adapting to drought stress and (3) furthermore the effects of drought stress were pronounced with short-term and medium-term drought duration. In addition, constant drought stress and dry-rewetting also showed to have negative effects on most of the measured parameters.

The negative impact of drought on Bambara groundnut may also been influenced by the experiment type; that is, pot experiments are normally conducted under a controlled environment while field experiments are conducted in conditions where it is always impossible to control the weather. It is also important to understand the timing at which Bambara groundnut is exposed to drought stress because the exposure of the crop to drought stress at critical stages might influence the overall performance of the crop during its life cycle. Even though this meta-analysis was centred on drought duration and manipulation type, other drought factors such as the impact of the level of drought on Bambara groundnut need to be evaluated.

Future experimental studies on Bambara groundnut should characterise the landraces or have formal naming system of the landraces used so that better recommendations can be made on the most tolerant and least tolerant landraces. There is also a need to understand and gather information on the early maturing and later maturing landraces as this could help match the landrace to current climatic conditions which can affect crop performance.

In summary, meta-analyses are conducted to summarise findings from different studies in order to come up with conclusions that can encourage future research. As such, researchers need to provide all statistics, that is, standard errors and standard deviations that can strengthen the statistical power of the meta-analysis, as it is often challenging to develop datasets from published literature.

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Competing interests

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Authors' contributions

M.M.M. contributed towards the conceptualisation of the study, methodology, formal analysis and writing of original draft. E.E.P contributed towards the conceptualisation of the study, methodology, formal analysis, supervision, writing-review and editing, and funding acquisition. M.J.B. and S.M. contributed towards the writing-review and editing, formal analysis and supervision.

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Data availability

The data that support the findings of this study are available from the corresponding author, E.E.P., upon reasonable request.

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