NAMIBIA UNIVERSITY OF SCIENCE AND TECHNOLOGY

Photosynthetic Pathways and Functional Traits of Namibian Dryland Flora: Implications for Dryland Restoration

Paulina Ndinelago Naupu

221123792

Thesis submitted in fulfillment of the requirements for the Doctorate in Natural Resource Sciences at the Namibia University of Science and Technology

Supervisor:

Professor Theo Wassenaar: Namibia University of Science and Technology

Co-Supervisors:

Professor Rolf Becker: Ongava Research Centre

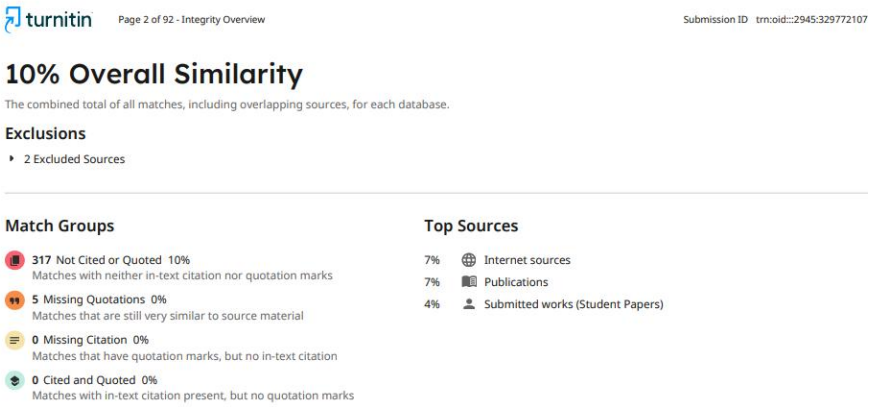
Professor Ezekeil Kwembeya: University of Namibia

Professor Andrew Smith: Oxford University

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Declaration

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List of Acronyms

Acronyms	**Meaning**
AFR100	African Forest Landscape Restoration Initiative
CAM	Crassulacean Acid Metabolism
CHIRPS	Climate Hazards Group InfraRed Precipitation with Stations
C_3	Calvin Cycle Photosynthetic Pathway
C_4	Hatch–Slack Photosynthetic Pathway
$\delta^{13}C$	Stable Carbon Isotope Ratio (delta carbon-13)
ET	Evapotranspiration
ESI	Evaporative Stress Index
GDP	Gross Domestic Product
GEE	Google Earth Engine
GGW	Great Green Wall
GGWI	Great Green Wall Initiative
IEK	Indigenous Ecological Knowledge
KBDI	Keetch–Byram Drought Index
LDMC	Leaf Dry Matter Content
MODIS	Moderate Resolution Imaging Spectroradiometer
NILALEG	Namibia Integrated Landscape Approach for Enhancing Livelihoods and Environmental Governance
NUST	Namibia University of Science and Technology
PDSI	Palmer Drought Severity Index
PET	Potential Evapotranspiration
PTAI	Priestley–Taylor Alpha Index
PWD	Potential Water Deficit
QGIS	Quantum Geographic Information System
REST	Restoring Ecosystem Services Tool
RWC	Relative Water Content
SD	Stomatal Density
SLA	Specific Leaf Area
SPI	Standardised Precipitation Index
SPSS	Statistical Package for the Social Sciences
TBR	Trait-Based Restoration
Tmax	Maximum Temperature
Tmin	Minimum Temperature
TrN	Transect North
TrS	Transect South
UN	United Nations
UNCCD	United Nations Convention to Combat Desertification
UNEP	United Nations Environment Programme
VPD	Vapour Pressure Deficit
WUE	Water-Use Efficiency
WWF	Worldwide Fund for Nature

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Dedication

To the firstborn child in the forgotten villages of Namibia

With nothing but a dream. No support, no roadmap, only courage and quite a hope that life will be different one day. You may be the first in your family to receive a formal education, the first to step into a university lecture hall, and the first to rewrite your family's story. This thesis is proof that it is POSSIBLE. I had nothing but a dream, and this work is the evidence that dreams do come true. As they say, "God does not call the qualified; He qualifies those He calls.

And to my mothers: Mee Paulina Katchinatcha Athingo, Mee Alina Nangula Amoonga, and Mee Johanna Naambo Athingo

I show up the way I do every day because I stand on the shoulders of GREAT women. Women who never had the opportunity to walk through the doors of a university, yet moved mountains to ensure I did. For your strengths, sacrifices, and your unwavering beliefs in me, even when there was little to give, you each gave everything you had. This is our victory! And like Mee Nangula would say, "*Inadi tulamo okoola tchili, ashike Kandina na Newman aye hi tulamo*", I scored Mama, I did.

But God!

Note on thesis structure and duplication:

This thesis is presented as a collection of standalone manuscripts (Chapters 2, 3, and 4), each formatted as an individual chapter intended for publication in peer-reviewed journals. As a result, some duplication of background information, methods, and references across chapters is unavoidable. As these manuscripts are intended for publication in different journals, variations in formatting, referencing style, and presentation may be observed across chapters. These differences reflect the respective requirements of each journal and do not affect the overall coherence of the thesis.

Specifically, the following referencing styles were used:

- Chapter 2: Uses the Council of Science Editors (CSE) Name-Year (N-Y) system, tailored specifically for the *Restoration Ecology* journal.
- Chapter 3: Uses the Harvard reference style (Author-Date) system, tailored by *Frontiers* journals.
- Chapter 4 and General Chapters (Introduction 1 /Synthesis 5): Use the American Psychological Association (APA) 7th Edition style.

To ensure coherence, the thesis includes a general introduction (Chapter 1) that outlines the overarching aims and context of the research, as well as a final synthesis chapter (Chapter 5) that integrates the main findings and discusses their broader significance.

All supervisors on the thesis are acknowledged here as co-authors of the manuscripts, with their respective contributions to each manuscript detailed below. Chapter 3 includes two additional co-authors who were not part of the supervision team. The specific author contributions for each chapter are outlined below:

Chapter 2

Title: Trait-based restoration to improve outcomes in African dryland restoration projects: Overcoming systemic and scientific barriers for a viable future

Author Contributions:

- Paulina N. Naupu led the conceptualisation and development of the central argument, designed the manuscript structure and layout, and was responsible for the full manuscript drafting and writing.
- Rolf W. Becker contributed to concept discussions, provided critical feedback on the narrative, and reviewed the manuscript.
- Ezekeil Kwembeya contributed to conceptual guidance and review of the scientific framing of the paper.
- Theo Wassenaar provided overall supervision, strategic guidance, and conceptual input throughout the writing process, and critically reviewed and edited the final version.

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Chapter 3

Title: Identification of New CAM Species in Southern African Succulent Plants

Author Contributions:

- Paulina N. Naupu designed and conceptualized the study, conducted the analysis and investigation, interpreted the results, and led the writing of the manuscript.
- Theo Wassenaar, Rolf W. Becker, Ezekeil Kwembeya, and Andrew Smith were responsible for overseeing the overall study design, conceptualization, funding acquisition, and supervision; Andrew Smith additionally served as the subject-matter expert on CAM physiology.
- Vera De Cauwer and Aune Angobe contributed to manuscript review and editing.

This manuscript is prepared for submission to *Frontiers in Plant Science*.

Chapter 4

Title: Functional trait responses to aridity gradients in three Namibian woody forage species

Author Contributions:

- Paulina N. Naupu: Collected data, analysed the data and interpreted results, and wrote the manuscript.
- Rolf W. Becker, Ezekeil Kwembeya, and Theo Wassenaar: Provided study design guidance, conceptual input, supervision, and critical manuscript review.

This manuscript was prepared for submission to the *Journal of Arid Environments.*

Research Permits

Field sampling, access, phytosanitary clearance, and export of plant material were conducted under the following authorisations: The National Commission on Research, Science and Technology (NCRST), Authorisation Nos. 202302010 and AN202202008; Ministry of Water, Agriculture and Forestry, Phytosanitary Certificate No. 80246; Ministry of Environment, Forestry and Tourism, Access Permit No. ABS-0057CHM1022; Ministry of Environment and Tourism, Export Permit Nos. 133094, 131624, and 140916. (Ministry names and numbers reproduced exactly as they appear on the permits.)

Thesis abstract

Land degradation and desertification affect over 45% of Africa's land surface, particularly in sub-Saharan drylands, driven by climatic variability, historical land-use changes, and contemporary pressures. These processes are most severe in arid and semi-arid zones such as the Sahel, Horn of Africa, and southwestern Africa, where erratic rainfall and soil nutrient depletion undermine ecosystem resilience and rural livelihoods. Restoration in these landscapes is urgently needed to recover ecosystem functions and services such as food and water. Current global frameworks advocate ecological restoration, emphasising approaches that enhance adaptive capacity under increasing aridity. Effective ecological restoration in these environments requires species–site matching based on strategies/traits that ensure survival under water limitation. However, this trait-based restoration (TBR) approach remains constrained by limited regionally grounded trait data and an incomplete understanding of drought-adaptive strategies. Namibia, one of the driest countries in sub-Saharan Africa and a global centre of floral diversity, provides an ideal system for addressing this gap. This study integrated conceptual analysis, physiological screening, and empirical trait measurements to build an evidence base for trait-informed restoration in Namibian drylands and beyond.

Chapter 2 critically reviewed TBR in African drylands. The review showed that ecological restoration across the continent remains largely disconnected from functional ecology because of limited trait datasets, among others. This highlighted the need for regionally grounded trait and drought tolerance research to guide species–site matching under water limitation.

Chapter 3 assessed Crassulacean Acid Metabolism (CAM) in Namibia's succulents. As a key metabolic pathway conferring drought tolerance, CAM plays an essential role in dryland persistence. Carbon-isotope analysis ($\delta^{13}C$) of 273 species, supported by titratable acidity, revealed a far richer terrestrial CAM flora than previously documented, with CAM newly confirmed in 26 genera. Based on the study dataset and previously published CAM records, Namibia's CAM flora constitutes approximately 12% of its vascular plant variety. CAM represents an important drought-adaptive functional strategy in Namibian flora, and identifying CAM species expanded the pool of water-efficient candidates available for restoration planning.

The third component (Chapter 4) presented the first systematic measurement of selected leaf functional traits along aridity gradients in northwest Namibia. Focusing on three dominant woody species: *Colophospermum mopane* (J. Kirk ex Benth.) J. Kirk ex J. Léonard, *Catophractes alexandri D. Don*, and *Terminalia prunioides* M.A. Lawson. The results showed contrasting drought-response strategies. *Terminalia prunioides* exhibited strong phenotypic plasticity, *C. alexandri* relied on structural drought tolerance, and *C. mopane* showed trait stability. These strategies offered mechanistic insights into species performance under different aridity intensities and informed species choice for restoration contexts.

Together, these findings produced a novel database of functionally important CAM species and mechanistic trait data that enable practitioners to select species based on drought-tolerance strategies. This study advanced theoretical understanding of dryland plant adaptation and substantially strengthened the foundation for trait-informed restoration in Namibia and sub-Saharan Africa.

These findings provide practical guidance for improving dryland restoration under Namibia's arid conditions. Restoration planning should prioritise species–site matching informed by functional traits such as specific leaf area (SLA), leaf dry matter content (LDMC), stomatal characteristics, and relative water content (RWC), together with the local aridity context. This approach helps ensure that species with acquisitive or conservative strategies are placed in environments where they can perform optimally. In the most arid zones, CAM succulents identified in Chapter 3 can be incorporated as early soil stabilisers and micro-site facilitators, while rock-crevice *stapeliads* may be used on slopes and inselbergs to create nurse shade and trap organic matter. For woody forage species, the trait–environment relationships observed in this study suggested that *T. prunioides* is suitable where plasticity to changing moisture conditions is required, while *C. alexandri* where strong structural drought tolerance is advantageous. Furthermore, *C. mopane* may be suitable where trait stability across variable aridity is beneficial. Restoration efforts should further prioritise small-scale planting in favourable microsites such as run-on patches, soil cracks, and sheltered areas rather than relying on uniform seeding. Framework shrubs such as *Aloe* and *Euphorbia* may also be introduced at low densities to minimise water competition. These are evidence-informed recommendations based on $\delta^{13}C$ signals, succulence, functional traits, and habitat association from this study. Hence, field trials are required for final species–site matching, a necessary next step that fell outside the scope of this study. In addition, integrating Indigenous and local ecological knowledge with trait-based data can strengthen restoration planning. Restoration programmes should incorporate long-term monitoring of plant survival and trait performance so that species selection and management approaches can be refined over time.

Chapter 1: General introduction



Arid landscapes like this one remind us how finely tuned dryland species must be to survive under extreme water limitations (photograph P.N. Naupu).

1.1 Background

1.1.1 Land degradation in dryland ecosystems

Land degradation is one of the most pressing ecological challenges of the 21st century, threatening food security, rural livelihoods, and biodiversity across much of the globe (Wang et al., 2012; Gupta, 2019). It affects more than 25% of the world's land area and continues to expand, particularly in developing regions where it erodes soil fertility, reduces crop productivity, and diminishes household incomes (Sterk & Stoorvogel, 2020; Mahata & Vishwambhar, 2021). The main drivers include intensive agricultural practices, historical land-use, overgrazing, deforestation, and the compounding effects of climate change (Gupta, 2019). Over the past 6-7 decades, these pressures have contributed to the degradation of nearly 35% of the world's arable land (Gupta, 2019). Drylands are defined as all regions with an aridity index (AI) below 0.65, encompassing hyper-arid, arid, semi-arid, and dry sub-humid zones (Zomer et al., 2022). These regions are disproportionately affected because of their chronic water scarcity, fragile soils, and high climatic variability (Wang et al., 2012; Prăvălie, 2016). Globally, these ecosystems cover about 40–41% of the Earth's terrestrial surface and support roughly two billion people (Feng et al., 2020; Martinez-Valderrama et al., 2023). They also sustain nearly 50% of the global livestock, 44% of croplands, and are home to 36% carbon stores and 30% forest areas (Martinez-Valderrama et al., 2023). Their ecological and socio-economic importance underscores the urgency of protecting and restoring them in the face of accelerating degradation.

Approximately 65% of Sub-Saharan Africa is classified as degraded, with about 350 million hectares (20-25% of total land areas) affected by severe degradation (Vlek et al., 2008; Zingore et al., 2015). In dryland systems, land degradation refers to a decline in the land's capacity to sustain ecological functions and livelihoods (Zingore et al., 2015). It is typically reflected in indicators such as soil erosion, bush encroachment, declining vegetation productivity, and losses in soil fertility and ecosystem services. Although the severity and drivers vary across regions, these processes collectively reduce land productivity and threaten rural livelihoods across much of Sub-Saharan Africa. This widespread degradation poses a critical challenge to the region's agricultural sustainability. In Sub-Saharan Africa, dryland degradation has significant economic and environmental impacts on rural communities. It leads to reduced livestock productivity, decreased household income, and increased food insecurity (Slayi et al., 2024a). It is estimated that dryland degradation costs Sub-Saharan Africa about $68 billion annually, reducing the region's agricultural gross domestic product (GDP) by 3% (Zingore et al., 2015). Across rural communities, degradation is consistently linked with lower crop yields, declining livestock productivity, and greater food insecurity (World Bank, 2017; UNCCD, 2022).

Often referred to as the "land between two deserts", Namibia is the driest country south of the Sahara (Ejikeme, 2011; Mupambwa et al., 2021). According to the global classification of drylands, Namibia's entire land area qualifies as dryland (Zomer et al., 2022). This ecological context makes it very sensitive to climatic variability and land degradation. Land degradation in the country has led to reduced agricultural activity, loss of biodiversity, and food insecurity, with up to 70% of food now being imported (Mupambwa et al., 2019). The main drivers of degradation in the country include overgrazing, deforestation, and overexploitation of natural resources (Seely & Klintenberg, 2011). These pressures are exacerbated by high population growth, limited water availability, and restricted livestock mobility (Ward et al., 2000).

Traditional pastoral systems in Namibia have historically maintained rangeland condition through flexible, mobility-based management, including seasonal transhumance, opportunistic grazing, and adaptive herd redistribution in response to rainfall variability (Müller et al., 2007; Schwieger & Mbidzo, 2020). These strategies functioned as a social-ecological buffer, allowing vegetation recovery across large landscapes and reducing grazing pressure on drought-sensitive patches. However, this adaptive system was progressively undermined by colonial and post-colonial interventions that promoted sedentarisation, individual land tenure, borehole expansion, and modernisation of livestock production (Haller et al., 2016; Samuels et al., 2021). Such policies constrained herd mobility, encouraged permanent settlement around water points, and facilitated higher continuous stocking rates—conditions that accelerate soil compaction, reduce grass cover, and intensify bush encroachment in arid rangelands. The cumulative effect has been a shift from a historically resilient pastoral system toward a more ecologically brittle, management-driven degradation pathway, where reduced mobility magnifies the sensitivity of rangelands to climatic variability (Schwieger & Mbidzo, 2020; Samuels et al., 2021). This historical context underscores the need for restoration strategies aligned with drought-adaptive ecological processes, including the functional-trait approaches advanced in this study.

Climate change is further fundamentally reshaping agricultural and pastoral systems globally through intensifying water scarcity, reducing vegetation productivity, and heightened climatic variability (Stanimirova et al., 2019). However, the magnitude and expression of these impacts vary regionally, reflecting differences in ecosystem sensitivity and adaptive capacity. Globally, approximately 14.5% of pasturelands have experienced statistically significant vegetation changes, with arid ecosystems showing up to 69% variation in productivity linked to precipitation fluctuations (Stanimirova et al., 2019). These shifts underscore the high dependency of rangeland productivity on rainfall distribution and highlight the vulnerability of drylands to even marginal climatic perturbations. In Australia, for instance, projected increases in drought frequency are expected to drive substantial declines in pasture productivity and forage quality, compounding feed deficits and threatening the viability of extensive rangeland systems (Stokes et al., 2008). Similarly, (Nefzaoui et al., 2012) estimate a 20% reduction in precipitation accompanied by a 0.2°C temperature rise per decade in semi-arid regions. This is an alarming trend that further destabilises pastoral livelihoods.

Nowhere are these pressures more acute than in Africa, where the coupling of rising temperatures, erratic rainfall, and recurrent droughts is severely constraining agricultural and livestock systems. Climate projections indicate that under mid-range emission pathways, global warming is likely to reach around 2 °C by 2100, with African land areas warming faster than the global average, intensifying evapotranspiration and water stress and, in many regions, increasing the likelihood of heavy rainfall events and flooding (IPCC, 2023). Southern Africa is particularly vulnerable, with agricultural productivity projected to decline by 15–50%, with the most severe impacts expected in arid and semi-arid zones (Nhemachena et al., 2020). Such climatic disruptions not only threaten crop and forage yields but also undermine the adaptive capacity of small-scale, rain-fed livestock systems that depend heavily on indigenous genetic resources for resilience (Assan, 2022). Collectively, these findings illustrate a cascading pattern of systemic stress, where both droughts and damaging floods interact to reduce ecosystem functionality, accelerate soil erosion, and degrade rangeland quality across the continent (IPCC, 2023). Therefore, addressing land degradation is crucial for regional and global food security. This requires education, policy changes, and technical innovations to restore degraded land and prevent further deterioration (Gupta, 2019).

1.1.2 The need for ecosystem restoration in drylands

Ecosystem restoration has become a global imperative, recognised as essential for achieving biodiversity conservation, climate resilience, and sustainable livelihoods. In response to widespread environmental degradation, the United Nations (UN) declared 2021–2030 as the UN Decade on Ecosystem Restoration, calling for coordinated global action to prevent, halt, and reverse ecosystem loss (UNEP & FAO, 2021). This initiative underscores the urgency of restoring degraded landscapes and mobilising governments, research institutions, and communities toward large-scale rehabilitation efforts. Within this global framework, numerous projects have been implemented to restore ecological functioning and rehabilitate degraded ecosystems in arid and semi-arid regions across Africa. These include the Great Green Wall, the Bonn Challenge, the African Forest Landscape Restoration Initiative (AFR100), and Namibia's Integrated Landscape Approach for Enhancing Livelihoods and Environmental Governance to Eradicate Poverty (NILALEG) project, among others (Sacande & Muir, 2022; Sacande et al., 2021). Yet despite large-scale investments and global attention, restoration success in drylands remains disappointingly low (Chambers, 2000; Carrick & Krüger, 2007; Valladares & Gianoli, 2007; James et al., 2011; Larson et al., 2015; Hardegree et al., 2016). Harsh environmental conditions characterised by high temperatures, recurrent droughts, and nutrient-poor soils continue to constrain plant establishment and survival (Stroosnijder et al., 2012; Svejcar & Kildisheva, 2017a; Jarrar & El-Keblawy, 2022; Stapleton et al., 2024). Even well-funded projects often achieve only limited recovery (James et al., 2013a), highlighting a persistent mismatch between the species selected for restoration and the environmental constraints they encounter.

1.1.3 Plant trait frameworks informing ecological restoration

1.1.3.1 Response–effect trait framework

Trait-based ecology provides a framework for linking plant characteristics to both their responses to environmental conditions and their influence on ecosystem functioning. The response–effect trait framework is central to this approach because it distinguishes between traits that determine how plants respond to environmental constraints and those that influence ecosystem processes once plants are established (Lavorel & Garnier, 2002). Response traits describe how plants pass environmental filters such as drought, soil nutrient limitation, and temperature variability. These include characteristics such as rooting depth, drought tolerance, and physiological traits related to water-use efficiency (Bardgett et al., 2014). In contrast, effect traits determine how plants influence ecosystem processes after establishment, for example, through canopy structure, litter quality, and biomass production (Pakeman, 2011), which can affect soil stability, nutrient cycling, and overall ecosystem productivity (Suding et al., 2008).

Importantly, the response–effect framework provides a conceptual bridge between plant functional ecology and ecological restoration. In restoration planning, response traits help identify species capable of establishing under specific environmental conditions, while effect traits help determine which species can contribute to desired ecosystem functions such as soil stabilisation, vegetation recovery, and improved ecosystem resilience (Zirbel et al., 2017; Fu et al., 2023). By integrating both types of traits, restoration practitioners can improve species–site matching and increase the likelihood that selected species will not only survive in degraded environments but also contribute to the recovery of ecosystem structure and function.

1.1.3.2 Trait-based restoration (TBR) models

Building on the response–effect framework, trait-based restoration (TBR) provides a practical approach for translating ecological theory into restoration planning. Rather than selecting species solely based on availability or traditional species lists, TBR focuses on identifying functional targets that reflect the ecological requirements and restoration goals of a particular site (Laughlin et al., 2014). These targets may include traits associated with conservative water use, drought tolerance, soil stabilisation, or structural vegetation cover. Species are then selected based on whether their trait values collectively meet these functional targets.

Trait-based restoration models, therefore, emphasise the role of community-weighted trait values, where the overall functional characteristics of a plant community are shaped by the dominant traits of the species present (Garnier & Navas, 2012). These models draw on ecological theories such as environmental filtering, which determines which species can establish under specific environmental conditions; limiting similarity, which promotes functional diversity by reducing competition among species with similar traits; and mass-ratio and niche-complementarity effects, which explain how dominant traits and trait diversity influence ecosystem functioning (Mokany et al., 2008; Laughlin et al., 2014; Lhotsky et al., 2016; Cadotte, 2017). TBR models integrate these ecological principles to provide a structured method for designing plant communities that are better suited to site conditions and capable of delivering desired ecosystem functions. This approach makes functional traits directly applicable to species–site matching and restoration planning, particularly under changing climatic conditions (Laughlin, 2014).

1.1.4 Functional traits relevant for dryland restoration

Plant growth in drylands faces three main challenges: an increasing scarcity of water; difficulties in utilising the available water due to various growth-limiting factors such as soil salinity and poor soil structure, and limited soil nutrient availability (Stroosnijder et al., 2012). Hence, plant species selection and adaptation strategies are crucial for successful restoration in arid regions. Studies have shown that species with effective water-use efficiency (WUE) strategies, such as maintaining high stomatal conductance or efficient water uptake in drying soils, have a greater survival rate in restoration projects (Butterfield et al., 2023a). Selecting plant species with traits that enable them to establish and persist under both current and projected future conditions in arid regions is essential for ensuring long-term dryland restoration success (Bainbridge, 2007; Cho et al., 2019; Stroosnijder et al., 2012; Stavi et al., 2024).

One of the main challenges in species selection for dryland restoration is the scarcity of functional trait data for native African species (Merchant et al., 2023). Functional traits are the measurable morphological, physiological, or phenological features of plants that influence their performance and ecological roles (Violle et al., 2007). In plant functional ecology, traits are broadly classified as response traits and effect traits (Suding et al., 2008). Response traits determine how plants react to environmental conditions such as drought, temperature, or nutrient availability and therefore influence fitness and survival. Effect traits, in contrast, shape ecosystem processes such as carbon cycling, productivity, and water dynamics, often independent of individual fitness (Suding et al., 2008). Many traits and strategies, however, serve both functions.

Photosynthetic pathways illustrate the dual role that functional attributes can play in shaping plant performance and ecosystem processes. Both photosynthetic rate and pathway type act as response

and effect attributes, mediating plant tolerance to environmental stress while influencing carbon and water fluxes at the ecosystem scale (Feng & Dietze, 2013). For instance, Crassulacean Acid Metabolism (CAM)[1] represents a convergent drought-adaptive functional strategy that maximises WUE by temporally separating CO_2 uptake and fixation, allowing assimilation at night when evapotranspiration is lowest (Cushman & Bohnert, 1999; Hultine et al., 2019). This strategy confers a major advantage in arid environments, enabling species to maintain productivity under extreme water limitation. Consequently, identifying CAM species is essential for dryland restoration because they expand the pool of native taxa with proven physiological drought tolerance. Despite Namibia's rich succulent flora, systematic CAM surveys remain limited, and the distribution of CAM across taxa has not been comprehensively documented.

This study purposively focused on succulent species that perform CAM because they represent an important, yet comparatively under-documented, drought-adaptive functional group within Namibia's most water-limited landscapes. In hyper-arid to arid zones, long-term rainfall and soil-moisture regimes often preclude the persistent establishment of C_4 grasses, resulting in recurrent failure of grass-based interventions (Mganga et al., 2010; Báez et al., 2013). While this does not imply that succulents dominate all drylands, or that CAM species universally outperform grasses, these extreme moisture limitations highlight why CAM taxa warrant targeted study in parts of Namibia. In such settings, CAM succulents can persist under moisture deficits and contribute stabilising functions such as maintaining cover and buffering microsites (Ackerly et al., 2000; Luttge, 2004; Borland et al., 2009). This focus does not discount the ecological and restoration importance of C_4 grasses in grazing-oriented or less arid landscapes where precipitation and soils support them. Rather, the emphasis on CAM species complements grass-based approaches by generating much-needed physiological and functional information for a plant group whose distribution and adaptive strategies remain less well characterised, thereby aligning species choice to site aridity and restoration objectives.

An important functional trait axis relevant to dryland restoration is the Leaf Economics Spectrum (LES), which describes a continuum of plant resource-use strategies ranging from acquisitive to conservative (Reich, 2014). At the acquisitive end of the spectrum, species typically exhibit traits such as high specific leaf area (SLA) and rapid tissue turnover, allowing for fast resource capture and growth (Faitanin et al., 2026). In contrast, conservative strategies are characterised by traits such as low SLA, high leaf dry matter content (LDMC), and longer leaf lifespans, which enhance resource conservation and tolerance to environmental stress (Maracahipes et al., 2018; Pierce et al., 2017). Along aridity gradients, conservative trait strategies are generally associated with improved persistence under water-limited conditions, whereas acquisitive strategies may facilitate rapid establishment during short periods of favourable moisture availability (Maracahipes et al., 2018). The LES, therefore, provides a useful framework for comparing plant strategies and guiding species selection in restoration planning. Within this context, this thesis examined key leaf-level traits, including SLA, LDMC, stomatal characteristics, and relative water content (RWC), to evaluate how plant functional strategies vary along an aridity gradient in Namibian drylands.

[1] CAM is a whole-plant photosynthetic pathway rather than a single trait. It is included here because it functions as an integrated drought-adaptive functional strategy with ecological relevance

The leaf-level traits investigated in this study illustrate the interplay between response and effect functions. The SLA and LDMC define a plant's position on the Leaf Economic Spectrum (LES), which reflects trade-offs between acquisitive strategies that favour rapid resource capture and conservative strategies that enhance survival under stress (Wright et al., 2004; Reich, 2014). These traits directly influence WUE by controlling photosynthetic capacity, transpiration, and carbon assimilation efficiency. The RWC and SD together determine a plant's ability to manage water stress and maintain photosynthetic efficiency (Rosales et al., 2013). These LES traits are closely linked to WUE, which is fundamental for plant persistence and productivity in drylands, where water availability governs ecological function and restoration success.

1.1.5 Global trait databases and knowledge gaps

Evidence from drylands confirms that matching trait values to climate and microsite improves outcomes. For instance, a 15-year synthesis of seeding trials in the Colorado Plateau showed higher success when seed size and plant height were matched to temperature seasonality (Balazs et al., 2020). Similarly, extreme-drought field tests in Mediterranean drylands highlighted xylem resistance to cavitation, stomatal control, and rooting depth as key predictors of survival in record-dry years, directly informing species choice for harsh sites (Padilla & Pugnaire, 2007). Rule of thumb: pair conservative water-use and stress-tolerant hydraulics with the driest, most exposed micro-sites; reserve more acquisitive species for run-on pockets, shade patches, or protected microsites (Cheng et al., 2025; Li et al., 2023).

For planning and data access, the TRY global plant trait database is the main, open infrastructure for standardised trait data (Fraser, 2020). While coverage is strongest for some categorical traits, it remains uneven for continuous traits in under-sampled floras. Nevertheless, the TRY database is widely used to source trait values and identify regional data gaps. This study contributed to addressing such gaps by providing new data on CAM occurrence and leaf traits from Namibian drylands.

1.1.6 Trait-based restoration gaps in Africa

In natural-resource management and ecological restoration, plant functional traits are used to predict species establishment, productivity, and resilience under varying climatic and edaphic conditions. While earlier reviews highlighted that much trait knowledge originated in temperate systems (Hortal et al., 2015), South Africa's arid zones, especially the Karoo, are notable exceptions with a substantial and growing body of work across ecology, land-use change, and restoration practice. Recent syntheses and long-term assessments from the Succulent and Nama-Karoo document extensive research activity and also identify remaining gaps and coordination needs (Hoffman et al., 2021; Milton & Dean, 2021). Applied restoration trials and practitioner guides from the Karoo further show progress on techniques (e.g., gypsum/mulch to improve infiltration; species selection; micro-site approaches) and cost/efficiency considerations in degraded rangelands (Beukes & Cowling, 2003; Bourne et al., 2017). Across much of arid Africa beyond these hotspots, however, systematic trait datasets and restoration-focused trials remain sparse, which can hamper evidence-based species selection and lead practitioners to fall back on availability or socioeconomic value alone rather than combining these with ecological fit. Clarifying this distinction helps explain why some restoration efforts still fail under present-day aridity and why regionally grounded trait data remain a priority for scaling success across the continent.

Ecological restoration increasingly relies on functional ecology to guide species selection and improve establishment success under environmental stress. Trait-based restoration (TBR) provides a conceptual framework linking plant functional traits to ecosystem processes and restoration outcomes (Laughlin et al., 2014). Within this framework, species are selected not only for their availability or economic value but for traits that influence survival, resource acquisition, and resilience under site-specific conditions. In drylands, traits related to water-use efficiency, drought tolerance, and resource conservation are particularly important because water limitation is the dominant ecological constraint. By identifying species possessing physiological strategies such as CAM photosynthesis and functional traits associated with conservative resource use, restoration practitioners can improve species–site matching and increase the probability of long-term restoration success.

It became clear that Africa is behind in the study and application of plant functional-trait knowledge for natural-resource management in general, and for dryland restoration in particular. To address this gap, I first contextualised the study within the broader scientific and policy landscape of functional trait-based restoration (TBR) in Africa. I critically analysed existing research, identified barriers and opportunities for applying functional-trait approaches on the continent, and highlighted the urgent need to integrate ecological-trait data into restoration policy and practice. Building on this conceptual foundation, the empirical component of the study employed two complementary approaches to generate trait data relevant to Namibian drylands. I examined the occurrence of CAM among indigenous species, expanding knowledge of water-use-efficient plants suited to arid restoration contexts. I then quantified selected functional traits to explore how species balance resource acquisition and conservation along aridity gradient. Although these trait–environment relationships cannot be interpreted as deterministic predictors of survival, they offer probabilistic guidance for species–site matching in restoration planning and lay the basis for more work in this field. Overall, this study represented the first systematic survey of CAM in Namibia and the first systematic measurement of drought-tolerant plant traits along a strong rainfall gradient in Namibia, contributing regionally novel data to the global trait database.

1.2 Problem statement

Dryland restoration has become a growing priority in Namibia and across sub-Saharan Africa; however, the success of many initiatives remains limited. A central challenge lies in species selection, which is often guided by economic value, availability, or rapid growth rather than ecological suitability. This mismatch is especially problematic in drylands, where water scarcity and nutrient-poor soils are defining constraints and where species without adaptive strategies struggle to establish. Functional traits that underpin survival, including WUE, drought tolerance, and resource-conservation mechanisms, are frequently overlooked in current practice. Compounding this problem is the scarcity of trait-based data for native African species and the broader underinvestment in functional ecology across the region. In addition to classical morphological and physiological traits, drought-adaptive functional strategies such as Crassulacean Acid Metabolism (CAM) also play a critical role in determining which species can persist and remain productive in highly water-limited environments. Yet these strategies are similarly under-documented, leaving practitioners uncertain about which taxa possess the metabolic characteristics needed for success in arid-zone restoration. As a result, a persistent knowledge gap constrains evidence-based decision-making. Without a clear understanding of which native species possess adaptive traits and strategies suited to arid conditions, restoration

efforts remain vulnerable to high failure rates, undermining both ecological recovery and long-term sustainability.

1.3 Research objectives

To identify and evaluate drought-adaptive functional strategies and traits in selected Namibian species, to provide knowledge that supports smarter species selection for dryland restoration. The specific objectives are as follows:

1. To assess the use of functional trait-based restoration in African drylands,
2. To characterise CAM photosynthesis in selected succulent plant species, and
3. To investigate relationships between selected leaf functional traits and an aridity gradient across northwestern Namibia.

1.5 Significance of the study

Dryland restoration in Namibia faces persistent challenges from water scarcity, nutrient-poor soils, and the selection of unsuitable plant species, leading to low survival rates and poor recovery (Inman et al., 2020a). Most existing trait-based ecological knowledge originates from temperate regions (Hortal et al., 2015), limiting its applicability to African drylands, while underinvestment in functional ecology has left major gaps in understanding the adaptive strategies of native species. Addressing this gap is critical for improving restoration outcomes under current and future climate pressures. This study contributed by combining two complementary approaches. First, a systematic survey of crassulacean acid metabolism (CAM) expanded the pool of candidate species with intrinsic water-saving physiology. Second, analysis of functional traits such as specific leaf area, leaf dry matter content, stomatal density, and relative water content across aridity gradients in key forage species revealed how native taxa balance carbon gain and water conservation under aridity. Together, these findings provided both new ecological insights and practical guidance for species-site matching in restoration planning. This work, therefore, strengthened the scientific basis for climate-resilient restoration in Namibia and offers a model applicable to other African drylands.

This research is also relevant to emerging restoration policy frameworks at both global and regional levels. The findings directly support evidence-based species–site matching for dryland restoration, aligning with Sustainable Development Goal (SDG) 15 (Life on Land) and SDG 13 (Climate Action), and with Namibia's commitments under the United Nations Convention to Combat Desertification (UNCCD). By providing regionally grounded information on CAM distribution and leaf functional traits along an aridity gradient, the study contributes evidence that can inform national restoration planning led by the Ministry of Environment, Forestry and Tourism, and enhances the knowledge base required for donor-supported landscape programmes. In practice, these results help practitioners select drought-adaptive native species capable of establishing under present and projected aridity, thereby improving the durability and cost-effectiveness of restoration outcomes.The findings of this research directly benefit restoration practitioners, land managers, policymakers, and dryland communities who rely on ecologically appropriate species for the rehabilitation of degraded ecosystems. The study provided practical evidence for species–site matching, supports national restoration planning, and enhances implementation of Namibia's dryland conservation initiatives. These insights further benefit the scientific community through expanded knowledge of drought-adaptive pathways in under-studied African flora.

1.6 Limitations of the study

The study provided important insights into drought-adaptive traits and their relevance for restoration in Namibia; however, several methodological and contextual limitations should be acknowledged.

In Chapter 3, the identification of Crassulacean Acid Metabolism (CAM) species was constrained by the availability of fresh leaf material. Titratable acidity measurements could therefore only be performed on a limited number of species. This restricted the ability to detect weak or facultative CAM and likely led to the underestimation of the true diversity of CAM expression in the flora.

In Chapter 4, the focus was placed exclusively on aboveground leaf traits, which are widely used in functional ecology due to their accessibility and cost-effectiveness. However, root traits and whole-plant physiological responses that are critical for understanding water uptake, drought tolerance, and carbon allocation were not assessed. This limited the ability to fully interpret plant responses to water stress, particularly in systems where root architecture strongly influences survival.

The environmental context of the trait analyses also carries limitations. Climate data were based on 30-year averages, which provide robust baselines but do not capture local microclimatic variation. Fine-scale conditions such as soil moisture pockets, shading, or wind exposure could influence trait expression in heterogeneous dryland environments. Furthermore, soil and topographic variables (e.g., texture, depth, organic matter, slope, elevation) were not measured directly, even though these abiotic factors are known to shape trait variability and species performance. Their omission may explain additional variation not captured by aridity gradient alone.

Future research should address these gaps by:

1. Conducting longitudinal trait monitoring across seasons and years to capture temporal plasticity under variable conditions;
2. Expanding analyses to a broader set of species and regions to test the generality of trait–environment relationships; and
3. Directly linking trait data to restoration outcomes such as establishment success, biomass accumulation, and long-term survival in field trials.

1.7 Thesis structure

This thesis is presented as a compilation of two research papers and one review paper, each of which has been submitted or prepared for submission to peer-reviewed journals. The work is organised into five chapters.

1. **Chapter 1** provided the general introduction, outlined the research context, problem statement, aims, and objectives.
2. **Chapter 2** presented an opinion paper entitled *"Trait-based restoration to improve outcomes in African dryland restoration projects: Overcoming systemic and scientific barriers for a viable future"*, which examined conceptual and systemic challenges to applying functional trait-based approaches in African restoration.
3. **Chapter 3** reported on the identification of new crassulacean acid metabolism (CAM) genera within southern African succulents, contributing novel insights into the distribution of this water-saving photosynthetic pathway.

4. **Chapter 4** investigated selected leaf functional traits in dominant woody forage species across aridity gradient in northwest Namibia, highlighting trait–environment relationships relevant for restoration planning.

Chapter 5 synthesised and critically analysed the findings from the preceding chapters, drawing together broader implications for trait-based restoration and identifying future research directions.

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A. Editorial note on publication status

Chapter 2 is reproduced verbatim from a peer-reviewed opinion article published in Restoration Ecology (Naupu et al., 2026). As an opinion piece, the journal format does not include a formal methods section. To provide the transparency requirements of the thesis examination, a brief Narrative Synthesis Methods addendum follows below. This addendum was not part of the published article." (Citation: Naupu P. N., Wassenaar T. D., Becker R. W., & Kwembeya E. (2026). Trait-based restoration in African dryland restoration projects: overcoming systemic and scientific barriers for a viable future. Restoration Ecology, Opinion Article.)

As an opinion piece, the journal's format emphasises argumentation built on curated evidence, rather than an exhaustive systematic review; consequently, strict word- and structure-limits necessitated concise treatment of subsections and citations within the published article. The chapter's role is conceptual and agenda-setting, providing the foundation that motivated the empirical components on photosynthetic pathways (CAM) and functional traits that follow in Chapters 3–4, and the synthesis in Chapter 5.

B. Narrative Synthesis Methods (Thesis Addendum).

To support the arguments developed in this opinion article, a structured narrative synthesis was used to identify relevant scholarly and practitioner reports. Searches were conducted in Web of Science, Scopus, Google Scholar, and the UNCCD Knowledge Hub using combinations of the terms: "functional traits," "trait-based restoration," "dryland restoration," "African drylands," "plant traits," "water-use efficiency," and "drought adaptation." Searches focused on the period 2000–2024 to capture the emergence of trait-based ecology and recent African restoration initiatives.

Inclusion criteria were: (i) studies conducted in African drylands; (ii) work linking plant functional traits to restoration outcomes, ecosystem processes, or drought adaptation; (iii) policy or practitioner reports relevant to restoration implementation; and (iv) global trait-based restoration studies with concepts transferable to African contexts. Exclusion criteria included studies unrelated to restoration, lacking empirical or conceptual relevance, or limited to temperate systems without clear transferability.

Approximately 80 sources were initially screened; 41 sources were retained and cited in the chapter and organised thematically around: (a) status and gaps in trait data in Africa; (b) systemic and institutional barriers to trait-based restoration; and (c) opportunities to integrate functional traits and Indigenous Ecological Knowledge into African restoration practice.

C. Objective-linking note

Within the thesis, this chapter directly addresses Objective 1 ("assess the use of functional trait-based restoration in African drylands") by evaluating the extent to which functional traits are being applied in project planning and policy across African drylands, identifying gaps, and outlining enabling conditions for uptake. The article synthesised practice-oriented evidence and barriers to TBR in Africa and thereby fulfils Objective 1 at the level of assessment of use, rather than a conventional systematic review.

Note: This Opinion article was produced after a comprehensive literature synthesis. A conventional literature review document exists and can be provided to the examiners upon request for additional depth. on African trait evidence and restoration applications.

Chapter 2: Trait-based restoration in African dryland restoration projects: overcoming systemic and scientific barriers for a viable future

Running head

Trait-based approaches in African drylands restoration

Authors and affiliations

Paulina N. Naupu[1, *], Rolf W. Becker[2], Ezekeil Kwembeya[3] Theo D. Wassenaar[1,2]

[1] Biodiversity Research Centre, School of Agriculture and Natural Resources Sciences, Namibia University of Science and Technology, Private Bag 13388, Windhoek, Namibia.

[2] Ongava Research Centre, Private Bag 12041, Windhoek, Namibia.

[3] Department of Environmental Science, University of Namibia, Private Bag 13301, Windhoek, Namibia.

Corresponding Author:

Paulina N. Naupu
Email: pnaupu@nust.na

Authors' Contributions:

PN designed, conceptualized, and led the writing; TW, RB, EK contributed to conceptualization, critical revisions, and writing.

2.1 Abstract

Despite major restoration pledges, African dryland restoration continues to show low success rates. Persistent water scarcity, ecological complexity, and the limited use of trait-based restoration (TBR) weaken ecosystem resilience. Functional trait-based approaches, which match species selection to adaptive traits, could strengthen ecosystem recovery under arid conditions, yet their application in Africa remains rare. This opinion article examined why TBR remains underutilised in African drylands and argued for its systematic integration into restoration planning and policy. A narrative synthesis of recent research and practitioner reports was used to assess the scope of functional TBR and identify institutional, scientific, and socio-economic barriers limiting its adoption. Restoration projects across Africa often emphasize socio-economic outcomes over ecological functionality. Only a few African studies explicitly link plant functional traits to dryland restoration. Barriers include scarce trait data for native species, limited long-term trials, weak integration of Indigenous Ecological Knowledge (IEK), and short donor-driven project cycles. Functional TBR offers a practical framework for improving ecosystem resilience in African drylands but requires region-specific research, inclusive co-design, and policy alignment. Embedding TBR into African dryland projects can transform restoration outcomes. Practitioners should focus on measurable functional traits to guide species selection under water-limited conditions. Integrating IEK with scientific trait data will enhance species suitability and community ownership. Long-term funding and national policy frameworks that prioritize functional performance over symbolic metrics are essential for achieving durable ecological and livelihood benefits.

Keywords: African drylands; functional traits; trait-based restoration; dryland restoration; water-use efficiency

2.2 Introduction

The United Nations (UN) Decade on Ecosystem Restoration (2021- 2030) underscored the urgent need to reverse the ecological degradation and build resilience in ecosystems that sustain biodiversity and livelihoods (Aronson et al. 2020; Waltham et al. 2020). Among the most vulnerable ecosystems are drylands (aridity index 0.03 – 0.65) (Zomer et al. 2022), which cover over 40% of the Earth's land surface and are home to over two billion people (Martinez-Valderrama et al. 2023). In Africa, drylands face escalating pressures from desertification, land degradation, and climate change (Burrell et al. 2020).

Despite major restoration commitments such as the Bonn Challenge, the Great Green Wall, and the African Forest Landscape Restoration Initiative (AFR100), success rates across African drylands remain low (James et al. 2013). Restoration outcomes often emphasise the number of trees planted or hectares pledged rather than actual ecological recovery. Low plant survival, limited ecosystem resilience, and slow soil recovery reflect approaches that overlook the ecological realities of water-limited environments (Svejcar & Kildisheva 2017; Shriver et al. 2018). Effective restoration in such conditions demands a framework that prioritizes species' drought tolerance, water-use efficiency (WUE), and survival under climatic extremes. Trait-based restoration (TBR) offers such a framework by aligning species selection with measurable traits that predict performance and survival (Laughlin et al. 2014; Balazs et al. 2020; Funk et al. 2024). However, its application across Africa remains limited. Barriers include scarce trait data, minimal integration of Indigenous Ecological Knowledge (IEK), and weak links between research, policy, and implementation (Djenontin et al. 2018; Wells et al. 2021; Sacande & Muir 2022).

This article argues that improving restoration outcomes in African drylands requires moving beyond symbolic planting targets toward trait-informed approaches that integrate ecological science, policy support, and community knowledge.

2.3 Functional Trait-Based Restoration: The Missing Link

Studies from Mediterranean drylands, Costa Rica, and Brazil demonstrated that traits such as rooting depth, wood density, and stomatal dynamics can predict survival and guide species choice (Giannini et al. 2017; Werden et al. 2018; del Campo et al. 2020). Tools such as the Restoring Ecosystem Services Tool (REST) help translate these traits into practice (Rayome et al. 2019).

In African drylands, however, evidence for functional TBR remains limited. A recent review by Ben-Enukora and Ejem (2024) found that most restoration projects rely on participatory approaches and Indigenous knowledge rather than trait-based methods. We found two East African studies that demonstrated clear applications of functional traits. Lohbeck et al. (2018) showed that functional diversity and weighted-mean traits improved soil carbon and reduced erosion, while Mens et al. (2023) linked woody plant traits such as leaf thickness to better soil hydrology and fertility. These isolated examples underscore the potential of functional TBR but also reveal the continent's lag compared to other regions. Beyond these cases, few peer-reviewed studies apply trait-based frameworks in African drylands. Although global precedents offer valuable lessons, African

approaches must be adapted to local ecological contexts, species pools, and IEK to ensure both ecological and social relevance.

2.4 Barriers to implementing TBR in Africa

A major constraint to adopting TBR in Africa is the lack of trait data for native dryland species (Merchant et al. 2023). Most existing plant trait knowledge comes from temperate or humid regions (Hortal et al. 2015), leaving the functional ecology of African species poorly documented (Karlsson et al. 2007; Hortal et al. 2015; Wilson et al. 2016). Limited research investment further restricts practitioners' ability to select species based on functional performance.

Large-scale trait databases like TRY exist, but they are heavily biased toward non-African flora (Kattge et al. 2020). High environmental variability across Africa's drylands also challenges the transfer of generic trait–environment frameworks (Eviner & Hawkes 2008). Few long-term trials test trait–performance relationships, and short project cycles rarely support the monitoring needed to validate trait relevance in field conditions (Carlucci et al. 2020).

The IEK into TBR remains limited. Initiatives such as the Great Green Wall have engaged local communities in species selection, yet choices often prioritize socio-economic benefits over ecological suitability (Sacande et al. 2015; Sacande & Berrahmouni 2016). The IEK holds valuable observations of plant resilience, drought behavior, and regrowth under stress (Fremout et al. 2021), but this knowledge is seldom translated into measurable trait frameworks.

2.5 Overcoming the Barriers

2.5.1 Strengthen locally relevant research

Advancing TBR in Africa requires expanding empirical studies on native dryland species. Despite global progress, trait-based work across Africa's semi-arid zones remains scarce. Despite global progress, trait-based work across Africa's semi-arid zones remains scarce (Wassenaar et al. 2013; Chomba et al. 2020; Mills et al. 2023). More regionally grounded field trials and long-term monitoring are needed to test how traits influence species survival and ecosystem recovery. Without locally derived data, restoration continues to rely on assumptions that often fail under African conditions.

2.5.2 Integrate indigenous ecological knowledge (IEK)

The IEK offers rich observations on plant drought tolerance, regrowth, and landscape suitability (Fremout et al. 2021). Translating this knowledge into trait-based language could enhance restoration design and adoption (Schultz et al. 2022). Yet few studies make this link, leaving a major opportunity for co-designed projects that merge local experience with ecological science. Restoration initiatives that systematically combine both knowledge systems are more likely to succeed ecologically and socially (Constant & Taylor 2020; Obiero et al. 2023).

2.5.3 Focus on practical, measurable traits

Given limited resources, restoration in African drylands should emphasise traits that are easy to measure and directly relevant to water-limited conditions (Loureiro et al. 2023). Specific leaf area (SLA) is one such trait. Defined as the ratio of leaf area to dry mass, SLA provides insight into a plant's resource-use strategy (Wilson et al. 1999; Costa-Saura et al. 2016; Wellstein et al. 2017). Low SLA values suggest a conservative water-use strategy well suited to arid environments (Hodgson et al.

1999; Dwyer et al. 2014). Leaf Dry Matter Content (LDMC) is another key trait. Higher LDMC typically signals better tolerance to water stress, herbivore resistance, and a "slower" economic strategy (Wilson et al. 1999; Blumenthal et al. 2020). On the other hand, stomatal density serves as a simple proxy for drought response and gas-exchange regulation (Hepworth et al. 2015; Lawson et al. 2014). These traits can be assessed with minimal equipment, making them feasible for student-led or community-based restoration.

Crassulacean Acid Metabolism (CAM) is not a trait in the strictest sense, but it defines a group of species that are well adapted to dry conditions due to their nocturnal carbon fixation strategy (Winter et al. 2015). Confirming CAM at a biochemical level requires gas exchange or isotopic measurements. However, it can often be inferred based on plant growth form or literature records, making it a practical and informative proxy in the African context.

Prioritizing such response traits (those that determine how plants tolerate stress) offers immediate, scalable benefits. Focusing on a small suite of ecologically meaningful and low-cost traits might help practitioners to apply functional TBR approaches even in resource-constrained settings. This entry point can help bridge science, policy, and local practice, paving the way for more resilient restoration outcomes across Africa's drylands.

2.6 Conclusion

Africa's drylands stand at the heart of the global restoration agenda, yet current approaches remain fragile, with low survival rates and uncertain ecological outcomes. Large-scale initiatives continue to prioritize planting numbers and socio-economic utility, while neglecting the functional traits that determine resilience in water-limited ecosystems. Although isolated studies in East Africa demonstrate the value of TBR, their narrow scope contrasts sharply with more developed frameworks in Latin America, the Mediterranean, and other dryland ecoregions.

I argued that integrating functional TBR into African restoration is both urgent and feasible. A step forward involves focusing on a small set of measurable traits, systematically incorporating IEK, and aligning policy and donor frameworks with ecological resilience rather than symbolic targets. Embedding trait-based thinking at the core of African restoration offers the best chance to improve resilience and long-term success.

D. Conclusions Crosswalk

This crosswalk is provided to support thesis examination. The notes below indicate where each conclusion is grounded in the article's main sections.

1. TBR can improve restoration outcomes under aridity.

   Supported in: Functional Trait-Based Restoration: The Missing Link (global evidence on matching traits to environment).

2. TBR adoption in Africa remains limited.

   Supported in: Barriers to Implementing TBR in Africa (data gaps, limited long-term trials, weak research-policy links).

3. Focusing on a small set of measurable drought-related traits is practical for implementation.

   Supported in: Focus on Practical, Measurable Traits (SLA, LDMC, stomatal traits as feasible entry points).

4. Integrating Indigenous Ecological Knowledge enhances species-site matching.

   Supported in: Integrate Indigenous Ecological Knowledge (alignment of IEK indicators with drought-adaptive traits).

5. Locally grounded trait research and monitoring are needed to scale TBR.

   Supported in: Strengthen Locally Relevant Research (importance of region-specific trials and monitoring in African drylands).

E. Contextual integration note

As an opinion piece, the published article emphasises high-level synthesis and implementation barriers. Beyond the studies cited in the published article, we acknowledge additional African work, particularly on C4 grass traits relevant to arid and semi-arid restoration to situate TBR across multiple life-forms (grasses, shrubs, and trees). While these studies strengthen the continental backdrop, the central knowledge gap motivating this thesis concerned drought-tolerant woody/succulent taxa and CAM physiology in Namibia's dryland flora, which are comparatively under-documented and are therefore treated in depth in Chapters 3–4. On subsection structure (2.5.1 & 2.5.2). The brevity and separation of these subsections reflect the journal's Opinion format and word limits; they address distinct levers (locally relevant research and Indigenous Ecological Knowledge) and cannot be merged in the reproduced text.

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Chapter 3: Identification of New CAM Species in Southern African Succulent Plants

Paulina N. Naupu[1, *], Theo Wassenaar[1], Vera De Cauwer[1], Aune Angobe[1], Rolf W. Becker[2], Ezekeil Kwembeya[3], Andrew Smith[4]

[1] Biodiversity Research Centre, School of Agriculture and Natural Resources Sciences, Namibia University of Science and Technology, Private Bag 13388, Windhoek, Namibia.

[2] Ongava Research Centre, Private Bag 12041, Windhoek, Namibia.

[3] Department of Environmental Science, University of Namibia, Private Bag 13301, Windhoek, Namibia.

[4] Department of Biology, University of Oxford, South Parks Road, United Kingdom.

***Correspondence**

Paulina N. Naupu
pnaupu@nust.na

3.1 Abstract

Crassulacean Acid Metabolism (CAM) represents one of the most important drought-adaptation strategies among succulent plants, yet the taxonomic and ecological distribution of CAM in southern Africa remains incompletely documented. Namibia, one of the driest countries in sub-Saharan Africa, harbours succulent diversity but has never been comprehensively surveyed for CAM prevalence. This study provided the most extensive assessment to date of CAM photosynthesis in the succulent flora of Namibia and adjacent regions, focusing particularly on taxa that have historically been understudied. Carbon-isotope analysis ($\delta^{13}C$) was conducted on 273 species representing 113 genera and 34 families, using specimens sourced from natural field populations, herbaria, and cultivated collections. Values less negative than −20‰ were interpreted as evidence of substantial nocturnal CO_2 fixation, while day–night titratable acidity measurements were performed in selected 15 taxa to detect weak or facultative CAM activity. The results expanded the known distribution of CAM substantially, documenting CAM in numerous genera of Aizoaceae, Apocynaceae, Asphodelaceae, Didiereaceae, and several asterid lineages. CAM was newly confirmed in 26 genera, many for the first time in Namibia, and facultative CAM was detected in several C_3-type taxa exhibiting environmentally inducible acid accumulation. The estimated proportion of CAM species (~12%) suggested that CAM constitutes a significant component of Namibia's flora, exceeding the global average of nearly 7% of vascular plants capable of CAM. This enriched representation is consistent with Namibia's long evolutionary history of aridity, its position within the Succulent Karoo–Gariep–Kaokoveld corridor, and the presence of fog-dependent microhabitats along the Namib Desert. Beyond refining the regional and global understanding of CAM evolution, these findings have practical implications for dryland management. CAM species exhibit high water-use efficiency (WUE) and persistence on nutrient-poor or degraded substrates, making them valuable candidates for ecological restoration in drought-affected landscapes. By improving Namibia's CAM inventory and identifying previously unrecognised CAM genera, this study provided a foundation for selecting climate-resilient native species for restoration, conservation planning, and future trait-based ecological research in African drylands.

3.2 Introduction

Interest in plant adaptations to arid climates has intensified with the growing recognition that many regions of the world will face rising temperatures and increasingly unpredictable precipitation patterns in the coming decades (Cushman et al., 2022). Recent data indicate that 2023 and 2024 were the two warmest years in recorded Earth history, with the accompanying decline in precipitation causing widespread water shortages, reduced food supplies, and power rationing across several parts of the world (UNCCD, 2025). Understanding how drought-tolerant plants have evolved and the mechanisms underlying these adaptations offers valuable insights for crop improvement, water-use efficiency, the restoration of degraded drylands, and sustainable agronomic practices. A more comprehensive appreciation of the biodiversity and ecology of the world's arid regions is therefore essential to elucidate the relationships between climatic extremes and plant survival in marginal habitats.

One of the life forms characteristically associated with warm arid and semi-arid environments worldwide is succulent plants, which are particularly abundant in regions with strongly seasonal or episodic rainfall. Their high water-storage capacity enables them to accumulate water during periods of availability and to utilise it sparingly during subsequent intervals of water shortage and drought (Walter, 1931; Eggli and Nyffeler, 2009; Ogburn and Edwards, 2010). Many succulents also exhibit the distinctive metabolic adaptation known as Crassulacean Acid Metabolism (CAM), which enhances water-use efficiency by allowing carbon dioxide (CO_2) uptake at night rather than during the day (Kluge & Ting, 1978; Osmond et al., 1982; Winter, 1985). This adaptation minimises transpirational water loss by enabling stomatal closure during the hottest daylight hours, while the CO_2 fixed nocturnally is reassimilated photosynthetically via the conventional Calvin–Benson–Bassham (CBB) cycle day (Kluge & Ting, 1978; Osmond et al., 1982; Winter, 1985).

Beyond its physiological and evolutionary significance, identifying whether a species performs CAM has considerable applied value. Knowledge of photosynthetic pathways enhances understanding of plant ecological strategies, productivity, and resilience under water-limited conditions (Borland et al., 2011; Ehleringer & Monson, 1993; Perron et al., 2024). CAM plants, in particular, exhibit water-use efficiency (WUE), tolerance to elevated temperatures, and the ability to persist on marginal or degraded land, attributes that have made them effective candidates for restoration and sustainable land-use practices in arid and semi-arid ecosystems (Borland et al., 2009; Buckland et al., 2023). For example, the CAM species *Portulacaria afra* has been used extensively in South Africa's subtropical thicket restoration programs, where its reintroduction has been shown to accelerate soil organic carbon accumulation, improve soil moisture retention, and re-establish woody recruitment processes (Mills and Cowling, 2006; Van Der Vyver et al., 2013; Wilman et al., 2014). More broadly, CAM plants have been recognised for their potential to reduce land degradation when used as cover crops, support agricultural diversification through fodder and bioenergy production, and enhance carbon sequestration in arid regions (Borland et al., 2009; Yang et al., 2015; Honorato-Salazar et al., 2021).

CAM photosynthesis is a highly convergent trait, estimated to have evolved independently at least 66 times across the plant kingdom (Gilman et al., 2023). It represents one of the most striking examples of the metabolic basis of ecological adaptation (Gilman et al., 2023). Despite substantial progress in elucidating the origins and functional significance of CAM, the ecological diversity and distribution of CAM plants remain incompletely understood. To date, field investigations have focused predominantly on the cacti and agaves of the Americas (Nobel, 1988; Hultine et al., 2016; Heyduk et al., 2023). However, the African continent harbours an exceptional diversity of succulents across families such as

Aizoaceae (ice plants), Apocynaceae (stapeliads), Asphodelaceae (aloes), Asteraceae, Crassulaceae (leaf-succulent Crassula, Kalanchoë, and relatives), and Euphorbiaceae (stem-succulent Euphorbia species) (Nyffeler and Eggli, 2010a; Gilman et al., 2023; Holtum, 2023). Southern Africa alone is estimated to contain over 40% of the world's terrestrial succulent flora (Frandsen, 2017; Smith et al., 2017), yet the full extent of CAM expression within this assemblage remains inadequately documented. Increasing concern over habitat loss has further highlighted the urgency of prioritising conservation measures for succulent plants, many of which comprise rare or endemic species threatened by land-use change and illegal collection (Grace, 2019; Margulies et al., 2023).

Although CAM has long been recognised as a key innovation for plant survival in arid zones, surprisingly few dryland floras worldwide have been quantified regarding the proportion of species capable of CAM. This information is ecologically valuable because the distribution and prevalence of CAM can indicate how plant communities allocate water-use strategies as aridity increases, and it can directly support restoration efforts by identifying taxa likely to survive future drought conditions. In Namibia, where restoration success is limited by chronic water shortages, creating a comprehensive inventory of CAM species provides an essential basis for selecting drought-tolerant native taxa that can restore vegetation cover, stabilise soils, and enhance climate resilience.

The primary focus of this study was the succulent flora of Namibia, which, unlike that of neighbouring South Africa, has not yet been systematically surveyed for its representation of CAM plants, despite several notable earlier studies. Southern Africa is recognised as a global climate-change hotspot (Fan et al., 2021) and has recently experienced the impacts of a strong El Niño–Southern Oscillation (ENSO) event that began in late 2023 and triggered severe drought conditions across the region between 2022 and 2024 (Toreti et al., 2024; UNCCD, 2025). As the driest country in sub-Saharan Africa, Namibia is especially vulnerable to the consequences of crop failure and the cascading effects of drought on rangelands, wildlife, and livestock. Except for the semi-arid north and north-east, most of the country is classified as arid, with an aridity index (ratio of rainfall to potential evapotranspiration) below 0.20, while the entire coastal belt of the Namib Desert is hyper-arid, with an index below 0.05 (UNEP, 1997; Atlas of Namibia Team, 2022; Strohbach et al., 2025).

In total, the flora of Namibia contains over 4300 indigenous vascular plant species, including an estimated 500 succulent and more than 300 geophyte species (Burke, 2017; Atlas of Namibia Team, 2022). Notable centres of endemism occur in the Gariep region of the south, representing the northern extension of South Africa's Succulent Karoo, and in the Kaokoveld of the north-west, which continues into southern Angola (Craven and Vorster, 2006; Marshall et al., 2016; Burke and Loots, 2020; Craven and Kolberg, 2023). Although CAM species do not generally attain their highest abundance under conditions of extreme aridity (Ellenberg, 1981; Walter and Breckle, 1984; von Willert et al., 1992; Ringelberg et al., 2020), suitable microhabitats for succulent plants can be created by local topography and climatic conditions. These plants form a dominant component of the winter-rainfall region of the Succulent Karoo in south-western Namibia (Werger and Ellis, 1981; Burke and Mannheimer, 2004; Mucina et al., 2006), and are also common as cremnophytes inhabiting rock crevices and fissures on highland escarpments and granitic inselbergs (Walter and Breckle, 1984; Burke, 2013; Bruyns et al., 2023; Fradera-Soler et al., 2024). In addition, succulent halophytes occur frequently along the 2,000 km coastal belt of the Namib Desert, where the climate is moderated by the upwelling of the cold Benguela Current and persistent advective fogs. The extreme hyperaridification of this region is believed to have intensified over the past 10 million years during the

Late Miocene (Siesser, 1980), yet the Namib is often regarded as the world's oldest desert, with a continuous history of aridity dating back to the Late Cretaceous (Ward et al., 1983; Gilchrist et al.,1994). This would have provided an extended period for the evolution and diversification of drought-adapted plants.

Globally, CAM plants represent approximately 7% of all vascular plant species, distributed across at least 370 genera and 38 families, with a minimum of 66 independent evolutionary origins (Gilman et al., 2023). However, these figures include many tropical epiphytes, particularly orchids and bromeliads, which are largely absent from Namibia. Ringelberg et al. (2020), in their analysis of the world's succulent biomes, highlighted several regions where CAM-rich lineages are most concentrated: the Succulent Karoo of Namibia and South Africa, the south-western United States of America and Mexico, the central Andean deserts, Brazil's Caatinga, and parts of Madagascar. In contrast, extremely arid regions such as Australia and the Gobi Desert support relatively few CAM taxa. These contrasts highlight that CAM prevalence is shaped not only by drought intensity but also by evolutionary history, soil regimes, fog inputs, and the persistence of succulent biomes

To date, only 9 genera of CAM plants have been studied in the field in Namibia or identified in the native flora from herbarium specimens (Schulze et al., 1976; Mooney et al., 1977; Vogel & Seely, 1977; Ziegler, 1979; Schulze et al., 1991; Ziegler, 1996; Messerschmid et al., 2021; Schweiger et al., 2021). In contrast, surveys conducted in adjacent regions of the Succulent Karoo and the Greater Cape Floristic Region of South Africa have revealed a substantial representation of CAM plants within the local flora (Schütte et al., 1967; von Willert et al., 1980; Werger & Ellis, 1981; von Willert et al., 1985; von Willert et al., 1992; Rundel et al., 1999; Horn et al., 2014). The families Aizoaceae and Apocynaceae, both rich in succulent taxa, are the fourth and fifth-largest plant families in Namibia, exceeded only by Asteraceae, Poaceae, and Fabaceae in species richness. In addition to the ice plants (Aizoaceae) and stapeliads (Apocynaceae, subfamily Asclepiadoideae, tribe Ceropegieae), Namibia also harbours numerous succulent species belonging to the Euphorbiaceae (stem-succulent *Euphorbia spp*.), Crassulaceae (*Crassula spp*. and four other genera of leaf succulents), and Asphodelaceae (*Aloe spp*. and three other succulent genera) (EIS Namibia). Several other families likewise include species or lineages exhibiting degrees of succulence. Therefore, a broader ecological survey would be valuable for a more complete understanding of the importance of CAM plants in the flora of Namibia.

To investigate photosynthetic pathways in this study, we primarily used the technique of stable carbon isotope ($^{13}C/^{12}C$) analysis, which can be performed on preserved specimens (e.g., in herbaria) collected from the field, as well as on freshly sampled material. Plants performing CAM photosynthesis differ in their carbon-isotope ratios from C_3 plants because of a kinetic isotope effect, since the enzyme responsible for the initial dark CO_2 fixation step in CAM plants, phosphoenolpyruvate carboxylase, discriminates less against $^{13}CO_2$ than does ribulose bisphosphate carboxylase, which fixes CO_2 directly into the CBB cycle in C_3 plants (Bender et al., 1973; Osmond et al., 1973; O'Leary, 1981). Consequently, large-scale surveys often reveal a strongly bimodal distribution of carbon-isotope ratios, enabling CAM and C_3 species to be readily distinguished (Winter and Holtum, 2002; Winter et al., 2015). However, two important qualifications apply to this generalisation. First, some species perform CAM only weakly or facultatively, typically in response to environmental stress such as water deficit a trait characteristic of the Aizoaceae (Winter and von Willert, 1972; Messerschmid et al., 2021; Winter and Holtum, 2024). In such cases, their carbon-isotope ratios may overlap with those of C_3 plants. Second, C_4 plants often exhibit similar carbon-isotope ratios to CAM species. Therefore, additional diagnostic tests such as

detecting nocturnal acidification, malate accumulation, or direct measurements of dark CO_2 uptake are required to confirm CAM activity and differentiate it from C_3 and C_4 photosynthetic modes.

In this study, we conducted a broad survey of CAM photosynthesis within the flora of Namibia to determine the prevalence of this pathway in one of the world's most arid environments. While genera such as *Aloe*, *Crassula*, *Kalanchoë*, and *Euphorbia* are well known as model taxa in CAM research, the focus was on previously understudied taxa to improve understanding of the occurrence and ecological representation of CAM among Namibia's drought-tolerant flora. We analysed carbon-isotope ratios ($^{13}C/^{12}C$) in specimens collected in their natural habitats, supplemented by data from herbarium specimens. To complement the isotope analysis, we also examined day–night changes in titratable acidity in living specimens of selected species to detect weak or facultatively expressed CAM activity. Because this inducible form of CAM is particularly characteristic of the Aizoaceae, the study extended the survey to include several genera within this family from the Succulent Karoo and other regions of the Greater Cape Floristic Region of South Africa that had not been sampled in earlier studies.

3.3 Materials and methods

3.3.1 Plant material

The selection of species in this study was based primarily on checklists of the native flora of Namibia (Klaasen & Kwembeya, 2013; Craven & Kolberg, 2023). In addition, several previously unstudied members of the Aizoaceae native to the Greater Cape Floristic Region of South Africa were included (Smith et al., 1998; Hartmann, 2017). Taxonomic nomenclature generally follows Plants of the World Online (Royal Botanic Gardens, Kew, 2024), except for specific cases in the Caryophyllales (https://caryophyllales.org) and Asteraceae (http://www.compositae.org).

The samples for carbon-isotope analysis were obtained under licence from herbarium specimens housed at the National Herbarium of Namibia (WIND), the University of Oxford (OXF/FHO), and the Royal Botanic Gardens, Kew (K). Additional living material was collected from species in their natural habitats with permission from the National Commission on Research, Science and Technology (NCRST), Namibia. Further samples were obtained from cultivated plants at the Namibia University of Science and Technology (NUST), the University of Oxford (UK), and the Cambridge University Botanic Garden (UK), as described in the Results section.

3.3.2 Sampling strategy

Previous surveys of the semi-arid flora of southern Africa have documented numerous CAM species, primarily within well-studied succulent families such as Aizoaceae, Apocynaceae, Asphodelaceae, Asteraceae, Crassulaceae, and Euphorbiaceae (see Introduction). However, many genera within these groups, as well as other lineages described in the botanical literature as semi-succulent or fleshy, remain unexamined with respect to the photosynthetic pathway.

Accordingly, the sampling strategy of this study was designed to target understudied genera and species across these families to broaden the taxonomic scope of CAM investigations in the region. In terms of geographical representation, particular emphasis was placed on the succulent flora of Namibia, which has been largely undersampled in previous surveys of photosynthetic pathways. The selection of understudied genera followed a structured process. First, all known succulent and semi-succulent taxa occurring in Namibia and adjoining regions were compiled from national floras, herbarium catalogues (WIND, OXF/FHO, and Kew), and relevant taxonomic monographs. Genera were

considered understudied if they met one or more of the following criteria: (i) no carbon-isotope data were available in published CAM studies; (ii) previous work had sampled fewer than two species within the genus; or (iii) the genus contained succulent taxa of ecological significance but lacked confirmed information on photosynthetic pathways. Based on these criteria, genera were screened for gaps in existing CAM/C_3/C_4 pathway data using previous surveys (e.g., Schulze et al. 1976; Mooney et al. 1977; Ziegler 1996). Species within priority genera were then selected to maximise taxonomic coverage. Where possible, fresh material was collected during field campaigns targeting regions known for high succulent diversity, including the Gariep region, Kaokoveld, and the central escarpment. When fresh material was unavailable, herbarium specimens were included, provided that tissue quality was suitable for stable carbon isotope analysis. Using these criteria, 273 species (113 genera, 34 families) were investigated. Representative examples of the taxa included in this study are shown in Figure 3.1.

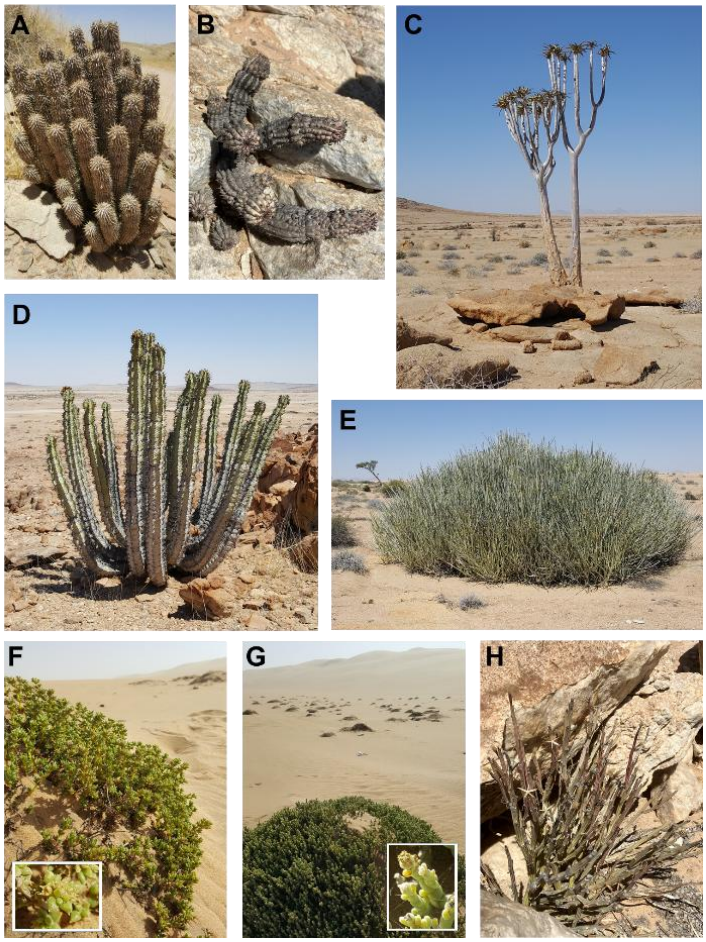


Figure 3.1. CAM plants in the succulent flora of Namibia (photographs J.A.C. Smith unless otherwise stated). **(A)** *Hoodia gordonii* (Masson) Sweet ex Decne. (Apocynaceae). **(B)** *Hoodia pedicellata* (Schinz) Plowes (Apocynaceae) (photograph V. De Cauwer). **(C)** *Aloidendron dichotomum* (Masson) Klopper & Gideon F.Sm. (Asphodelaceae). **(D)** *Euphorbia virosa* Willd. (Euphorbiaceae). **(E)** *Euphorbia damarana* L.C.Leach (Euphorbiaceae). **(F)** *Trianthema hereroensis* Schinz (Aizoaceae). **(G)** *Mesembryanthemum kuntzei* Schinz (syn. *Psilocaulon kuntzei* (Schinz) Dinter & Schwantes) (Aizoaceae). **(H)** *Kleinia longiflora* DC. (Asteraceae) (photograph V. De Cauwer).

3.3.3 Carbon isotope analysis

The natural abundance of ^{12}C and ^{13}C in dried plant material was analysed by isotope ratio mass spectrometry (IRMS) in the Stable Isotope Laboratory, School of Archaeology, University of Oxford, under the supervision of Dr Peter Ditchfield. For samples obtained directly from living plants, specimens were oven-dried at 80 °C for 48 h in a ventilated oven. Unless otherwise indicated, mature leaf tissue was used for all analyses. Approximately 1 mg of dried sample was weighed into tin capsules (Elemental Microanalysis Ltd., Okehampton, UK) and analysed using a Sercon 20-22 continuous-flow isotope ratio mass spectrometer (Sercon Ltd., Crewe, UK) coupled to a Sercon GSL elemental analyser and gas purification module for Dumas combustion under oxygen.

The reference CO_2 was calibrated against the Vienna Pee Dee Belemnite (VPDB) scale by two-point normalisation using IAEA-CH-6 (sucrose) and IAEA-CH-7 (polyethylene) standards (Coplen et al., 2006). A combustion system and instrument drift check was performed after every ten samples using a working alanine standard with a $\delta^{13}C$ value of −27.11 ± 0.08 ‰. Measured ^{12}C and ^{13}C values were corrected for oxygen-isotope contribution following Bone et al. (2015), and $\delta^{13}C$ values were calculated as:

$$\delta^{13}\mathrm{C}\ (‰) = \left[\frac{\left(^{13}\mathrm{C}_{\mathrm{sample}}/^{12}\mathrm{C}_{\mathrm{sample}}\right)}{\left(^{13}\mathrm{C}_{\mathrm{VPDB}}/^{12}\mathrm{C}_{\mathrm{VPDB}}\right)} - 1\right] \times 1000.$$

Values of $\delta^{13}C$ less negative than −20.0 ‰ were interpreted as indicative of substantial carbon assimilation via the CAM pathway, whereas values more negative than −20.0 ‰ were attributed to carbon fixation occurring predominantly or exclusively through the C_3 pathway (Winter et al., 2015; Winter & Holtum, 2002).

3.3.4 Interpretation of $\delta^{13}C$ values

Interpretation of $\delta^{13}C$ values followed established conventions for distinguishing photosynthetic pathways. Species assimilating a substantial or major proportion of their CO_2 at night through strong or constitutive CAM typically exhibit $\delta^{13}C$ values between −9 and −20 ‰, whereas C_3 species show values between −20 and −38 ‰ (Winter, 2019). In larger surveys, these ranges produce a bimodal distribution of $\delta^{13}C$ values with a minimum near −20 ‰, which justifies using this value as a diagnostic threshold for identifying constitutive CAM plants (Winter & Holtum, 2002; Crayn et al., 2015; Winter et al., 2015). However, several factors must be considered when interpreting $\delta^{13}C$ values (i) Species expressing weak or facultative CAM may exhibit values more negative than −20 ‰ and cannot be distinguished from C_3 species on isotope data alone. Therefore, the possible occurrence of low-level CAM activity was assessed in selected species, mainly in the family Aizoaceae, where facultative CAM is common, through measurements of day–night changes in titratable acidity (Winter & Smith, 2022). (ii) In C_3 species, $\delta^{13}C$ values can vary with environmental aridity; under extremely dry conditions, values can approach −20 ‰, as documented for hyperarid deserts such as the Namib and Atacama (Diefendorf et al., 2010; Kohn, 2010). Such cases were carefully differentiated from borderline CAM species. (iii) C_4 species also exhibit $\delta^{13}C$ values less negative than −20 ‰ (typically −11 to −15 ‰) but were distinguished from CAM species based on their characteristic leaf anatomy and exclusively daytime CO_2 fixation. The taxonomic distribution of C_4 photosynthesis is now well established (Sage, 2016; Berasategui et al., 2023), and references to relevant C_4 taxa are provided in the Results section.

3.3.5 Titratable acidity determination

To test for CAM activity in living material of selected species, samples consisting of 2–4 combined leaves were harvested at dawn and dusk, either from plants growing in their natural habitats or from cultivated specimens (as specified in Table 3.2). Samples were immediately frozen in sealed vials. Titratable acidity was determined from pressed sap obtained by freeze–thaw disruption of freshly harvested leaf tissue (Smith & Lüttge, 1985). Sap was extracted from thawed tissue either directly using a garlic press or by filtration through a 750 µl microcentrifugal filter of regenerated cellulose with pore size 0.45 µm (Thermo Fisher Scientific Ltd., Altrincham, UK). Titrations were performed on 50 µl subsamples of pressed sap diluted in 5.0 ml of deionised water, using either 10.0 mM or 2.5 mM NaOH to an endpoint of pH 7.00, measured with an Orion Star A121 portable pH meter equipped with a glass combination electrode (Thermo Fisher Scientific). Three independent samples were analysed for each time point, and results are expressed as arithmetic means ± standard deviations (SD). Dawn and dusk values for each species were compared using a paired-sample, one-tailed Student's t-test assuming equal variances, conducted in Microsoft Excel.

3.4 Results and discussion

3.4.1 Aizoaceae

The Aizoaceae represent the largest exclusively succulent plant family in southern Africa. Comprising predominantly perennial shrublets and, less commonly, annual species, this family forms a highly distinctive floristic element of the winter-rainfall regions of southwestern Africa. The family includes approximately 1,900 species distributed across 119 currently recognised genera (Klak et al., 2017; Royal Botanic Gardens, Kew, 2024). In Namibia, about 230 species of Aizoaceae are recorded, making it the fourth-largest family in the country's native flora (Craven & Kolberg, 2023). Members of this family are particularly characteristic of the Gariep Centre of Endemism in the southwest and the coastal fog deserts of the Namib (Walter, 1936; Burke & Mannheimer, 2004; Burke & Loots, 2020). To date, CAM activity has been demonstrated in fewer than half of all genera within the Aizoaceae (Gilman et al., 2023). However, the ability to detect CAM in this family may depend strongly on environmental conditions at the time of sampling, owing to the typically facultative expression of this photosynthetic pathway.

To assess the expression of CAM photosynthesis within previously unsampled genera of the Aizoaceae, $\delta^{13}C$ was determined for 39 genera from Namibia and adjoining parts of the Greater Cape Floristic Region in South Africa. Values less negative than −20.0 ‰ were recorded in representatives of 20 genera, indicating substantial nocturnal CO_2 assimilation (Table 3.1). For ten genera, all belonging to the subfamily Ruschioideae, this is the first documented occurrence of CAM photosynthesis. Newly confirmed CAM taxa include *Amphibolia*, *Dinteranthus*, *Gibbaeum*, *Jensenobotrya*, *Juttadinteria*, *Lapidaria*, *Namibia*, *Ruschianthus*, *Schwantesia*, and *Wooleya*. In a further seven genera of Ruschioideae, the $\delta^{13}C$ values corroborate earlier reports of CAM expression in *Dracophilus*, *Hartmanthus*, *Lithops*, *Pleiospilos*, *Stoeberia*, *Titanopsis* (Gilman et al., 2023), and *Leipoldtia* (von Willert et al., 1979, 1980).

The $\delta^{13}C$ values consistent with constitutive CAM (i.e., less negative values near the −20‰ threshold) were also found in all six species of *Mesembryanthemum* examined, the sole genus of the subfamily Mesembryanthemoideae, which is well known for its drought-inducible facultative CAM behaviour (Winter & von Willert, 1972; Winter & Holtum, 2024). Three additional genera with $\delta^{13}C$ values less

negative than −20 ‰ (*Sesuvium*, *Trianthema*, and *Zaleya*) belong to the early-diverging subfamily Sesuvioideae, a halophytic lineage that also contains many C_4 species (Bohley et al., 2015). An example in this study is the Namibian endemic *Trianthema hereroensis*,[2] a perennial forming semi-globose "dune cushions'' (Figure 3.1) on the shifting sands of the central Namib Desert. This species endures virtually rainless years moderated by coastal fogs and continues stem elongation even when buried by sand (Friedrich, 1970; Seely et al., 1977; Vogel & Seely, 1977; Henschel & Jürgens, 2024). Although its $\delta^{13}C$ values (−12 to −13‰) fall within the CAM-like range, *T. hereroensis* is a confirmed C_4 species (Seely et al., 1977; Vogel & Seely, 1977), and the observed isotope values therefore reflect C_4 photosynthesis rather than CAM. This clarification explains why the species is notable in this context, as its ecological specialisation contrasts with its C_4 physiology.

Although members of the Sesuvioideae typically exhibit $\delta^{13}C$ values between −11 ‰ and −15 ‰ and display C_4 anatomical features (Bohley et al., 2015), small CAM-like day–night acid fluctuations have been reported in both the C_4 species *Trianthema portulacastrum* (Winter et al., 2021) and two non-C_4 species of *Sesuvium* (*S. maritimum* and *S. portulacastrum*) (Winter et al., 2019). The two genera of Sesuvioideae examined here, *Anisostigma schenckii* and *Tribulocarpus dimorphanthus*, displayed $\delta^{13}C$ values characteristic of C_3 metabolism, although living material has not yet been analysed for possible nocturnal acid accumulation.

None of the species sampled from genera belonging to the two subfamilies of Aizoaceae (Acrosanthoideae (*Acrosanthes*) and Aizooideae (*Aizoanthemum*, *Aizoon*, and *Tetragonia*)) exhibited $\delta^{13}C$ values less negative than −20 ‰. However, several species of Aizooideae, particularly within the genus *Aizoanthemum*, showed values close to this threshold (−20 to −23 ‰) (Mooney et al., 1977). Such intermediate $\delta^{13}C$ values may indicate a small but physiologically meaningful contribution of CAM activity to overall carbon assimilation (Winter et al., 2015) and warrant further investigation using living material to test for day–night changes in tissue acidity. Evidence from previous work supports this interpretation: *Tetragonia fruticosa* has been shown to exhibit day–night fluctuations in titratable acidity despite possessing a C_3-type $\delta^{13}C$ signature (Schütte et al., 1967; Messerschmid et al., 2021), while a CAM-type $\delta^{13}C$ value was reported for *T. reduplicata* (Mooney et al., 1977). These observations suggest that facultative or weak CAM expression may occur sporadically within Aizooideae, possibly as an adaptive response to episodic drought stress. In contrast, all four species of Acrosanthes (subfamily Acrosanthoideae) examined in the present study, as well as those analysed by Messerschmid et al. (2021), displayed C_3-like $\delta^{13}C$ values, consistent with their ecological distribution in mesic fynbos habitats of the Western Cape, South Africa. The genus Acrosanthes comprises six species restricted to nutrient-poor soils of the fynbos biome (Klak et al., 2017), a habitat that likely imposes selection for resource conservation rather than WUE via CAM.

A notable feature of these results is the co-occurrence of CAM-like and C_3-like $\delta^{13}C$ values (less negative and more negative than −20 ‰, respectively) within individual genera—and in some cases, even within species—of the Aizoaceae. This pattern is evident in species of *Amphibolia*, *Dracophilus*,

[2] Spelling of the specific epithet follows the published basionym of Schinz (1897), as the genus name *Trianthema* is interpreted as feminine singular rather than neuter plural (Hartmann et al., 2011; Hartmann, 2017).

Gibbaeum, *Leipoldtia*, and *Ruschianthus*. Such intra-generic and intra-specific variability in $\delta^{13}C$ values is well documented for the family, reflecting the facultative nature of CAM expression and its sensitivity to prevailing environmental conditions at the time of sampling (Winter & von Willert, 1972; Winter, 2019; Messerschmid et al., 2021).

To evaluate whether taxa exhibiting C_3-like $\delta^{13}C$ values could nonetheless perform CAM under certain conditions, and to expand the survey to additional unstudied genera available in cultivation, day–night changes in titratable acidity were measured in freshly harvested leaf material (Table 3.2). All species tested showed statistically significant dawn–dusk differences in titratable acidity, confirming the presence of CAM activity.

This is the first documented evidence of CAM in the following genera of the subfamily Ruschioideae: *Aloinopsis*, *Ebracteola*, *Machairophyllum*, and *Nananthus*. These measurements also confirmed CAM expression in *Dinteranthus*, *Gibbaeum*, and *Wooleya*, taxa that had already shown $\delta^{13}C$ values less negative than −20 ‰. Collectively, these findings reinforce the view that CAM is widespread within the Aizoaceae, particularly in Ruschioideae, and that environmental plasticity in CAM expression may contribute significantly to the ecological success of this family in arid and semi-arid landscapes.

3.4.2 Other Caryophyllid families

The order Caryophyllales encompasses numerous lineages adapted to drought and salinity, making it a major centre of evolutionary convergence in stress tolerance (White et al., 2017; Vásquez-Cruz et al., 2025). Of the 39 currently recognised families within this order (APG IV, 2016; Thulin et al., 2016), nine families are known to include species capable of CAM photosynthesis (Gilman et al., 2023), while eight families contain C_4 taxa—with Chenopodiaceae now subsumed within Amaranthaceae *sensu lato* (Sage et al., 2011). Given the close phylogenetic relationship between Molluginaceae and Aizoaceae, and recent taxonomic revisions that have split the former into several segregate genera, representatives of these lineages were included in this study to screen for possible evidence of CAM photosynthesis. Four of the monogeneric families recently segregated from Molluginaceae include taxa described as fleshy or slightly succulent, yet none showed isotope evidence consistent with CAM photosynthesis. The Corbichoniaceae (Thulin et al., 2016) comprise three species in the genus *Corbichonia*, all of which occur in Namibia and exhibit C_3-like $\delta^{13}C$ values (Table 3.1). Similarly, the Lophiocarpaceae, the sister group to Corbichoniaceae, include four species in the genus *Lophiocarpus*. This family is analysed here for the first time; three of its species occur in Namibia, and all displayed C_3-type isotope values.

Analysis of Gisekiaceae confirmed the occurrence of C_4 photosynthesis in Namibian accessions of *Gisekia africana*, consistent with previous findings by Schulze et al. (1976) and Bissinger et al. (2014), as well as the C_4 pathway reported for *G. pharnaceoides* (Vogel & Seely, 1977). In contrast, the Kewaceae, established following the transfer of eight species from Hypertelis to the new genus Kewa (Christenhusz et al., 2014), exhibited C_3-type $\delta^{13}C$ values, as shown by the present analysis of *K. salsoloides* and by three additional Namibian species sampled by Christin et al. (2011). Collectively, these results indicate that while several lineages derived from the former Molluginaceae show mild succulence, no CAM activity has yet been detected, suggesting that their drought tolerance relies primarily on morphological water-storage adaptations rather than metabolic specialisation. In their recircumscribed form, the Molluginaceae *sensu stricto* now comprise 11 genera (Thulin et al., 2016), of which eight are native to Namibia**.** Within this family, a single C_4 taxon has been documented,

Hypertelis umbellata (formerly *Mollugo cerviana* var. *umbellata*), while all other species examined exhibited C_3-type $\delta^{13}C$ values. In the present analysis, the Namibian genera *Paramollugo*, *Pharnaceum*, and *Suessenguthiella* also showed C_3-like isotope signatures, consistent with earlier reports by Christin et al. (2011) and Thulin et al. (2016).

In Nyctaginaceae, the genus *Boerhavia* is well established as C_4, as confirmed here by the $\delta^{13}C$ value of *B. coccinea* (Table 3.1). Seven of the eight *Boerhavia* species native to Namibia have now been sampled, further substantiating the predominance of C_4 photosynthesis in this lineage (Khoshravesh et al., 2020). In contrast, *Phaeoptilum spinosum*, a xerophytic shrub with somewhat fleshy leaves (Struwig et al., 2015), exhibited C_3-like isotope values, indicating that succulence in this species is likely a morphological rather than metabolic adaptation to aridity. The related Limeaceae, represented here by *Limeum argute-carinatum*, also showed C_3-type $\delta^{13}C$ values, consistent with previous findings for all eight Namibian *Limeum* species examined to date (Vogel & Seely, 1977; Christin et al., 2011).

By far the largest family of C_4 eudicots is the Amaranthaceae *sensu lato* (including Chenopodiaceae), in which C_4 photosynthesis has evolved across approximately 50 genera (Kadereit et al., 2003; Sage et al., 2007; Kapralov et al., 2012; Sage, 2016). Many Namibian members of this family are succulent or semi-succulent C_4 halophytes, as exemplified in this study by species of *Caroxylon*, *Gomphrena*, and *Suaeda* (Table 3.1). However, the thick-stemmed "pencil bush" *Arthraerua leubnitzii*, a Namib Desert endemic confined to sandy substrates within the coastal fog belt (Loris et al., 2004; Dinter & Haas, 2008), displayed a C_3-type $\delta^{13}C$ value. This indicated that it maintains C_3 metabolism despite its extreme xeromorphic morphology. Collectively, these findings demonstrated that while C_4 metabolism dominates the Nyctaginaceae and Amaranthaceae of Namibia, isolated occurrences of C_3 taxa with morphological succulence highlighted the diversity of physiological strategies underpinning adaptation to arid environments.

The occurrence of CAM photosynthesis in many of the sampled taxa often coincides with xeromorphic structural adaptations such as succulence, reduced leaf surface area, and thickened cuticles. Within this functional context, CAM enhances water-use efficiency (WUE) through nocturnal CO_2 uptake and reduced daytime stomatal opening, while xeromorphic traits contribute to drought tolerance by limiting transpirational loss, buffering plant water status, and promoting structural water storage. In taxa where CAM and pronounced xeromorphy co-occur (e.g., several Ruschioideae genera and stapeliads), these features appear to function as complementary drought-adaptation strategies, combining metabolic timing with morphological conservation mechanisms. At the same time, the dataset also includes xeromorphic species without constitutive CAM, as well as CAM species showing varying degrees of succulence, indicating that these strategies are not mutually dependent. Their co-occurrence, however, likely enhances persistence under extreme water limitation and may help explain the frequent association of CAM physiology and xeromorphic traits among species inhabiting the most arid environments surveyed. Among the core Caryophyllales**,** CAM photosynthesis is particularly common within the suborder Portulacineae**,** which comprises several smaller families derived from the former, highly paraphyletic Portulacaceae (Nyffeler and Eggli, 2010b). In the Anacampserotaceae, all *Anacampseros* species analysed to date exhibit CAM-type $\delta^{13}C$ values, including seven natives to Namibia (Mooney et al., 1977; Guralnick et al., 2008). The *Portulacaceae sensu stricto* now contain only the genus *Portulaca*, which is dominated by C_4 species, including *P. foliosa*, *P. kermesina*, *P. oleracea*, and *P. quadrifida* in the Namibian flora (Table 3.1; Ziegler, 1979; Ocampo et al., 2013). This genus is also notable as the first in which low-level CAM activity was

demonstrated in plants otherwise performing C_4 photosynthesis. The Talinaceae represent another segregate lineage in which facultative CAM has been reported. Although *Talinum* species typically display C_3-type $\delta^{13}C$ values, they can exhibit significant diel fluctuations in titratable acidity, as confirmed here for *T. afrum* (Tables 3.1 and 3.2). Within the recircumscribed Didiereaceae, two field-collected Namibian species of *Portulacaria* showed $\delta^{13}C$ values less negative than −20 ‰, consistent with constitutive CAM metabolism, as observed in numerous studies on *P. afra* (Gilman et al., 2023). In contrast, three other species of *Portulacaria* (formerly Ceraria; Bruyns et al., 2014) displayed C_3-type $\delta^{13}C$ values, although low-level CAM has previously been reported in *P. fruticulosa* (von Willert et al., 1992; Veste et al., 2001).

Finally, within the Caryophyllales, the Cactaceae, one of the most iconic CAM families globally, is represented in Namibia by nine genera, all considered invasive, with the possible exception of *Rhipsalis baccifera* (Craven & Kolberg, 2023), a widely distributed epiphyte extending from tropical America across sub-Saharan Africa and Madagascar to Sri Lanka.

3.4.3 Other Asterid families

The Caryophyllales are sister to the large asterid clade of eudicots, which also includes several families with prominent succulent representatives. Within this group, the Apocynaceae form one of the most ecologically and morphologically diverse families, and southern Africa constitutes a major centre of diversification for the stapeliad clade (subtribe Stapeliinae, tribe Ceropegieae, subfamily Asclepiadoideae; Endress et al., 2018). Members of this lineage are stem-succulent, highly drought- and heat-tolerant, and frequently occur as chasmophytes in rock crevices or on slopes where they benefit from surface runoff and fog precipitation (Walter, 1936; Bruyns, 2014; Pilbeam, 2014). More than half of all stapeliad species occur in southern Africa (Bruyns, 2005; Court, 2010).

The Stapeliinae constitute a monophyletic group comprising 36 traditionally recognised genera (Endress et al., 2018), though it has been suggested that these might be consolidated into a single expanded genus *Ceropegia* (Bruyns et al., 2017), analogous to the reduction of the Mesembryanthemoideae of Aizoaceae to *Mesembryanthemum* (Klak et al., 2007). Previously, 12 stapeliad genera had been confirmed as performing CAM photosynthesis (Gilman et al., 2023). The present study expands this list with evidence for CAM-type $\delta^{13}C$ values (less negative than −20 ‰) in eight additional genera, *Australluma*, *Larryleachia*, *Lavrania*, *Piaranthus*, *Stapeliopsis*, *Tavaresia*, *Tridentea*, and *Tromotriche*, based on field-collected specimens (Table 3.1).

Within *Ceropegia* (*sensu stricto*), *C. brachyceras* was the only taxon identified with CAM-type isotope values. Two species of *Orthanthera* (subtribe Leptadeniinae) exhibited C_3-like $\delta^{13}C$ values, although these were relatively high (less negative) and near the −20 ‰ threshold (Table 3.1). In tribe Asclepiadeae, CAM photosynthesis was verified in *Cynanchum viminale*, a widely distributed succulent-stemmed vine (Schulze et al., 1976; Rundel et al., 1999), whereas its sister genus *Schizostephanus* appears to be C_3, as does the massive-stemmed liana *Fockea multiflora* in tribe Fockeeae.

Beyond the Asclepiadoideae, the tuberous geophyte *Raphionacme haeneliae* (subfamily Periplocoideae) and the two pachycaul Namibian species of *Pachypodium* (subfamily Apocynoideae) also exhibited C_3-type $\delta^{13}C$ values. However, previous reports have detected small diel changes in titratable acidity in *P. namaquanum*, suggesting facultative or drought-inducible CAM activity in the cortical chlorenchyma of its succulent stems (von Willert et al., 1980, 1992). These results reaffirm that

CAM metabolism is widespread but heterogeneously expressed within the Apocynaceae, particularly among the stapeliads, where it underpins extreme adaptations to arid, rock-dominated landscapes in southern Africa.

CAM activity has been reported in several species of *Coleus* (Lamiaceae) with moderately succulent leaves that were previously classified under *Plectranthus* (Winter et al., 2021). In this study, all eight *Coleus* species from Namibia exhibited C_3-type $\delta^{13}C$ values (Table 3.1). However, significant day–night fluctuations in titratable acidity were detected in *C. neochilus* (Table 3.2), despite its $\delta^{13}C$ values being more negative than −27 ‰. The species that showed the least-negative $\delta^{13}C$ value, near the −20 ‰ threshold, was *C. cylindraceus*, suggesting a notable contribution of nocturnal CO_2 fixation to its total carbon gain. This interpretation aligns with previous studies of the heterotypic synonym *Plectranthus marrubioides* (von Willert et al., 1992; Herppich & Herppich, 1996). Nevertheless, $\delta^{13}C$ values in this intermediate range can also occur in C_3 species inhabiting extremely arid or hyperarid environments (Diefendorf et al., 2010; Kohn et al., 2010). These suggested that facultative or weak CAM expression may occur sporadically within *Coleus*, representing an example of incipient metabolic flexibility in a family not typically associated with CAM photosynthesis.

Carbon-isotope values less negative than −20 ‰ were also recorded in several asterid families from Namibia, representing some of the most drought-tolerant C_4 lineages known (Berasategui et al., 2023). C_4 photosynthesis has been confirmed in three of the nine species of *Anticharis* (Scrophulariaceae) native to Namibia, while the remaining six species exhibit C_3–C_4 intermediate characteristics based on their leaf anatomy and ultrastructure. This pattern suggests that Namibia may represent a plausible centre of origin for C_4 photosynthesis within this clade (Khoshravesh et al., 2012). A similar pattern is observed in the genus *Blepharis* (Acanthaceae), which comprises 15 species in Namibia. Eight of these species, all belonging to the derived section *Acanthodium*, display either full C_4 photosynthesis or intermediate phenotypes, indicating an evolutionary continuum of carbon-fixation strategies within the group (Vogel & Seely, 1977; Fisher et al., 2015; Stata et al., 2025). In the Boraginaceae, two of the four Namibian species of *Euploca* have likewise been shown to perform C_4 photosynthesis (Frohlich et al., 2022). These findings reinforce the view that Namibia serves as a hotspot for photosynthetic innovation, where strong environmental gradients and chronic aridity have likely favoured multiple evolutionary transitions between C_3, C_4, and intermediate pathways among asterid lineages.

The Asteraceae, together with the Poaceae, constitute the largest family of flowering plants in Namibia, encompassing approximately 100 species of succulents and xeromorphic taxa distributed across southern Africa and Madagascar (Cicuzza et al., 2017). CAM photosynthesis has been reported in several genera within the tribe Senecioneae, where phylogenetic evidence suggested at least four independent origins of the pathway (Gilman et al., 2023). Most succulent species of Asteraceae historically classified under *Senecio* have now been transferred to more narrowly defined genera that better reflect their morphological and molecular distinctiveness.

In the Namibian flora, CAM activity has been documented in two species of *Kleinia* (*K. cephalophora* and *K. longiflora*; Schütte et al., 1967; von Willert et al., 1980) and in three species of *Curio* (*C. corymbifer*, *C. herreanus*, and *C. radicans*; Mooney et al., 1977; Fioretto & Alfani, 1988; von Willert et al., 1992). In contrast, all six of the seven Namibian species of *Crassothonna* tested in this study exhibited C_3-type $\delta^{13}C$ values (Table 3.1). However, drought-induced nocturnal acid accumulation has previously been observed in *C. opima* (von Willert et al., 1992), indicating that the genus may possess facultative or environmentally induced CAM, warranting further field investigation.

Other xerophytic genera of Asteraceae represented in the Namibian flora, *Didelta*, *Eremothamnus*, *Galgera*, *Osteospermum*, *Pechuel-Loeschea*, *Tarconanthus*, and *Tripteris*, all displayed C_3-type $\delta^{13}C$ signatures (Table 3.1). The absence of strong CAM signals among these taxa suggested that succulence and drought tolerance in Asteraceae are not always linked to CAM metabolism, underscoring the diverse physiological strategies employed by this family to persist in arid environments.

3.4.4 Rosids

3.4.4.1 Geraniaceae:

Within the Geraniaceae, all four species analysed in this study exhibited C_3-type $\delta^{13}C$ values (Table 3.1), consistent with previous field measurements for *Sarcocaulon mossamedense* (Mooney et al., 1977; Ziegler, 1996). Nonetheless, small diel fluctuations in titratable acidity, indicative of weak or facultative CAM activity, have been reported in the Namibian species *Sarcocaulon patersonii* (Schütte et al., 1967) and in three species of *Pelargonium* (Schütte et al., 1967; Kluge & Ting, 1978; Jones et al., 2003). In contrast, no evidence of CAM metabolism has been documented in *Monsonia sensu stricto* or in any other genus of the family. While CAM expression in Geraniaceae is rare and typically facultative, it may occur opportunistically in certain stem- or leaf-succulent lineages under extreme drought stress.

3.4.5 Monocots

3.4.5.1 Asphodelaceae:

The $\delta^{13}C$ values obtained for *Aloe asperifolia* and *A. zebrina* (Table 3.1) confirmed the widespread occurrence of CAM photosynthesis within this genus, consistent with previous findings (Gilman et al., 2023). Several Namibian taxa formerly classified in *Aloe* and known to perform CAM have been reassigned to newly established genera, including the arborescent species *Aloidendron dichotomum* (Schulze et al., 1991; Ziegler, 1996) and *A. ramosissimum* (Rundel et al., 1999), as well as *Gonialoe variegata* (Troughton et al., 1974).

Three additional genera of Asphodelaceae, *Gasteria*, *Haworthiopsis*, and *Tulista*, are each represented by a single species in the Namibian flora and are known or strongly suspected to exhibit CAM metabolism: *Gasteria pillansii* (Mooney et al., 1977), *Haworthiopsis tessellata*, and *Tulista dinteri*, the latter two supported by CAM evidence in closely related taxa (Bender et al., 1973; Mooney et al., 1977).

The genus *Bulbine* is of particular interest, as it is phylogenetically resolved as sister to the succulent subfamily Alooideae. While its $\delta^{13}C$ values are generally C_3-like, small diel changes in titratable acidity have been recorded (Gilman et al., 2023), suggesting that *Bulbine* may represent an evolutionary intermediate in the early stages of CAM evolution. This makes it a promising lineage for further physiological and molecular investigation into transitional states of CAM expression within Asphodelaceae.

TABLE 3.1. Carbon-isotope ratios ($\delta^{13}C$ values) for leaf samples from herbarium material or freshly collected specimens for 273 species from 113 genera belonging to 34 families native to Namibia and South Africa. Bold font indicates genera newly identified in this study as capable of performing CAM photosynthesis.

Taxon	Source*	Locality (coordinates are given as E, S)	Collector/ Accession	Date	$\delta^{13}C$ (‰)
AIZOACEAE					
Acrosanthes angustifolia Eckl. & Zeyh.	OXF 00220516	Western Cape, South Africa	Ecklon 2147[a]	1829–1832	−25.96
Acrosanthes humifusa (Thunb.) Sond. (syn. *Didaste pentandra* E.Mey. ex Harv. & Sond.)	OXF 00220515	Western Cape, South Africa	Drège, J.F. s.n.[a]	December 1830	−24.74
Acrosanthes teretifolia Eckl. & Zeyh. (syn. *Didaste icosandra* E.Mey. ex Harv. & Sond.)	OXF 00220517	Western Cape, South Africa	Drège, J.F. s.n.[a]	1826–1827	−27.00
Aizoanthemum dinteri (Schinz) Friedrich	WIND 78566	Namibia −19.62444444, 13.83222222	Hennig, G. 6	01/06/2000	−22.73
Aizoanthemum galenioides (Fenzl ex Sond.) Friedrich	WIND 7710	Namibia −22.12500000, 14.37500000	Giess, W. 7840	10/04/1964	−20.35
Aizoanthemum rehmannii (Schinz) H.E.K.Hartmann	WIND 7728	Namibia −23.12500000, 15.62500000	Giess, W. 13551	16/05/1973	−23.43
Aizoon africanum (L.) Klak	NP	Namibia −22.92055556, 15.20469444	De Cauwer, V., Naupu, P.N. and Smith. J.A.C.	13/09/2023	−22.05
Aizoon asbestinum Schltr.	WIND 7593	Namibia −23.37500000, 16.37500000	Giess, W. 7829	08/04/1964	−25.17
Aizoon giessii Friedrich	WIND 85441	Namibia −23.13888889, 16.90361111	WittneStro, M. 4-268	03/07/2004	−27.24
Aizoon papulosum Eckl. & Zeyh.	NP	Namibia −22.65138889, 14.52866667	De Cauwer, V., Naupu, P.N. and Smith, J.A.C.	13/09/2023	−26.01
Aizoon papulosum Eckl. & Zeyh.	NP	ERO, Namibia	De Cauwer, V.		−28.81
Aizoon schellenbergii Adamson	WIND101767	Namibia −26.23416667, 19.50611111	Crawford, F. 971	12/02/2016	−27.85
Aizoon virgatum Welw. ex Oliv.	WIND 82065	Namibia −19.80916667, 14.44722222	Kolberg, H. 1389	08/04/2004	−24.56

Taxon	Source*	Locality (coordinates are given as E, S)	Collector/ Accession	Date	$\delta^{13}C$ (‰)
Aloinopsis luckhoffii (L.Bolus) L.Bolus	Cult.[C]	(South Africa)	20140131	11/08/2001	−21.39
Amphibolia rupis-arcuatae (Dinter) H.E.K.Hartmann	WIND 77411	Namibia −27.66777778, 16.34833333	Mannheimer, C.A. 1595		−23.21
***Amphibolia rupis-arcuatae* (Dinter) H.E.K.Hartmann**	Cult.[W]	(Namibia, South Africa)		17/04/2019	−16.22
Anisostigma schenckii (Schinz) Schinz (syn. *Tetragonia schenckii* Schinz)	NP	Namibia	Strohbach, B. 8268	01/04/2022	−23.17
Carpanthea pomeridiana (L.) N.E.Br. (syn. *Mesembryanthemum pomeridianum* L.)	OXF 00220467	Western Cape, South Africa	Burke & Zeyher 708[a]	1840–1842	−23.10
Carpobrotus edulis (L.) N.E.Br.	NP	Namibia −22.68147222, 14.52216667	Naupu, P.N. and Angobe, A.T. 9992	29/09/2023	−27.49
Cleretum bellidiforme (Burm.f.) G.D.Rowley (syn. *Dorotheanthus bellidiformis* (Burm.f.) N.E.Br.)	FHO	Skilpad, Northern Cape, South Africa	White, F. 5480	22/08/1959	−25.64
Cleretum bellidiforme (Burm.f.) G.D.Rowley (syn. *Mesembryanthemum criniflorum* L.f.)	OXF 00220472	Cape Provinces, South Africa	Ecklon & Zeyher 2094[a]	1829–1832	−25.11
Cleretum papulosum (L.f.) N.E.Br.	WIND 4534	Namibia −27.05083333, 16.48472222	Kolberg, H.	04/09/2023	−27.25
Conicosia pugioniformis (L.) N.E.Br. (syn. *Mesembryanthemum pugioniforme* L.)	OXF 00220469	Western Cape, South Africa	Ecklon & Zeyher 1991[a]	1829–1832	−27.49
Conicosia pugioniformis (L.) N.E.Br. (syn. *Mesembryanthemum pugioniforme* L.)	Cult.[W]	(South Africa)	Angobe, A.T. 8888	15/01/2024	−27.49
***Dinteranthus microspermus* (Dinter & Derenberg) Schwantes**	Cult.[W]	(Namibia)	Naupu, P.N. 108		−19.38

Taxon	Source*	Locality (coordinates are given as E, S)	Collector/ Accession	Date	$\delta^{13}C$ (‰)
***Dinteranthus vanzylii* (L.Bolus) Schwantes**	Cult.^{O}	(South Africa)	MSG 2571		−15.75 (*n* = 3)
Dracophilus dealbatus (N.E.Br.) Walgate	WIND 77730	Namibia −27.61694444, 16.31277778	Mannheimer, C.A. 1572	10/08/2001	−21.92
Dracophilus delaetianus (Dinter) Dinter & Schwantes	WIND 81956	Namibia −27.56250000, 16.19722222	Mannheimer, C.A. 1619	13/08/2001	−16.38
Ebracteola derenbergiana (Dinter) Dinter & Schwantes	WIND 77538	Namibia −26.75138889, 16.20861111	Mannheimer, C.A.2276	15/10/2002	−23.14
Fenestraria rhopalophylla N.E.Br. subsp. *aurantiaca* (N.E.Br.) H.E.K.Hartmann	Cult.^{C}	(Namibia)	20150559		−24.96
Frithia humilis Burgoyne	Cult.^{O}	(South Africa)	MSG s.n.		−26.04
Frithia pulchra N.E.Br.	Cult.^{O}	(South Africa)	MSG 2574		−27.69
Gibbaeum hortenseae (N.E.Br.) Thiede & Klak (syn. *Muiria hortenseae* N.E.Br.)	Cult.^{O}	(South Africa)	MSG 2711		−21.34
Gibbaeum pachypodium (Kensit) L.Bolus	Cult.^{C}	(South Africa)	20191955		−22.43
***Gibbaeum petrense* (N.E.Br.) Tischler**	Cult.^{O}	(South Africa)	MSG 2777		−16.75
***Gibbaeum pubescens* (Haw.) N.E.Br.**	Cult.^{O}	(South Africa)	MSG 2778		−19.03
Gibbaeum shandii (N.E.Br.) N.E.Br.	Cult.^{O}	(South Africa)	MSG 2463		−24.69
Hartmanthus pergamentaceus (L.Bolus) S.A.Hammer	WIND 61386	Namibia −28.62500000, 16.37500000	Williamson, G. 5045	16/07/1993	−15.00
***Juttadinteria albata* (L.Bolus) L.Bolus**	WIND 99201	Namibia −28.23500000, 16.78444444	Noli, D.17	28/05/2004	−14.88
***Juttadinteria albata* (L.Bolus) L.Bolus**	Cult.^{W}	(Namibia, South Africa)	Naupu, P.N. 104		−16.96
***Juttadinteria albata* (L.Bolus) L.Bolus**	Cult.^{W}	(Namibia, South Africa)	Naupu, P.N.	17/04/2019	−19.15

Taxon	Source*	Locality (coordinates are given as E, S)	Collector/ Accession	Date	$\delta^{13}C$ (‰)
***Jensenobotrya lossowiana* A.G.J.Herre**	WIND 8013	Namibia −25.62500000, 14.87500000	Giess, W. 13207	14/03/1974	−14.39
***Lapidaria margaretae* (Schwantes) Dinter & Schwantes**	WIND 72619	Namibia −28.75027778, 19.08361111	Mannheimer, C.A. 824	01/11/2000	−14.47
***Lapidaria margaretae* (Schwantes) Dinter & Schwantes**	Cult.^{O}	(Namibia, South Africa)	MSG 2578		−14.10
Leipoldtia alborosea (L.Bolus) H.E.K.Hartmann & Stüber	WIND 98483	Namibia −28.32916667, 16.75916667	Kolberg, H. 2470	28/02/2008	−22.05
Leipoldtia uniflora L.Bolus	Cult.^{C}	(South Africa)	20191382		−31.27
Leipoldtia weigangiana (Dinter) Dinter & Schwantes ex H.Jacobsen	WIND 62184		Merxmüller, H. 2613		−16.15
Lithops otzeniana Nel	Cult.^{O}	(South Africa)	MSG C128a		−14.17
Mesembryanthemum coriarium Burch. ex N.E.Br.	NP	Namibia −22.92016667, 15.20502778	De Cauwer, V. 8265	13/09/2023	−15.32
Mesembryanthemum guerichianum Pax	NP	ERO, Namibia	Strohbach,B. 8292	01/05/2022	−17.61
Mesembryanthemum kuntzei Schinz	NP	Namibia −22.77277778, 14.54111111	De Cauwer, V., Naupu, P.N. and Smith. J.A.C. 9991		−18.17
Mesembryanthemum marlothii Pax (syn. *Brownanthus marlothii* (Pax) Schwantes)	WIND 8186	Namibia −26.62500000, 15.12500000	Giess, W. 702	07/08/1959	−14.85
Mesembryanthemum salicornioides Pax (syn. *Psilocaulon salicornioides* (Pax) Schwantes)	WIND 8123	Namibia −18.12500000, 12.62500000	Giess, W. 7504	10/06/1963	−10.29
Mesembryanthemum schlichtianum Sond.	WIND 93762	Namibia −26.71972222, 15.73000000	Mannheimer, C.A. 2772	13/09/2005	−13.83

Taxon	Source*	Locality (coordinates are given as E, S)	Collector/ Accession	Date	$\delta^{13}C$ (‰)
(syn. *Brownanthus arenosus* (Schinz) Ihlenf. & Bittrich)					
***Namibia cinerea* (Marloth) Dinter & Schwantes**	WIND 78790	Namibia −26.99333333, 15.35972222	Mannheimer, C.A. 1395	02/08/2001	−17.04
Nananthus margaritifer L.Bolus	Cult.[W]	(Botswana, Namibia, South Africa)	Naupu, P.N. 107	07/09/2023	−20.83
Nelia schlechteri Schwantes	Cult.[C]	(South Africa)	20191399		−22.20
Pleiospilos nelii Schwantes	Cult.[O]	(South Africa)	MSG 3032		−17.22
Pleiospilos simulans (Marloth) N.E.Br.	Cult.[O]	(South Africa)	MSG 2713		−14.47
***Ruschianthus falcatus* L.Bolus**	WIND 85222	Namibia −27.85722222, 16.88972222	Bartsch, S. 1520	20/09/2003	−19.83
Ruschianthus falcatus L.Bolus	Cult.[W]	(Namibia)		17/04/2019	−24.94
***Schwantesia loeschiana* Tischer**	Cult.[W]	(Namibia)	Naupu, P.N. 102		−14.20
Sesuvium hydaspicum (Edgew.) Gonç. (syn. *Sesuvium nyasicum* (Baker) Gonç.)	WIND 7315	Namibia −22.12500000, 16.62500000	Merxmüller, H. 21	03/01/1958	−11.32
Sesuvium portulacastrum (L.) L. subsp. *portulacastrum* (syn. *Aizoon canariense* Andrews)	WIND 94773	Namibia −26.55083333, 16.13444444	Mannheimer, C.A. 2959	15/06/2006	−23.68
Sesuvium sesuvioides (Fenzl) Verdc.	WIND 70209	Namibia −26.62500000, 16.37500000	Kolberg, H. 209	23/10/1987	−11.75
Stoeberia gigas (Dinter) Dinter & Schwantes	WIND 89956	Namibia −27.61583333, 16.31194444	Burgoyne, P.M. 8421	10/08/2001	−18.11
Stomatium duthieae L.Bolus	Cult.[O]	(South Africa)	MSG 2825		−22.68
Tanquana hilmarii (L.Bolus) H.Hartmann & Liede	Cult.[O]	(South Africa)	MSG 2619		−20.33
Tetragonia arbuscula Fenzl	WIND 81731	Namibia −26.67583333, 16.22833333	Mannheimer, C.A. 2464	23/09/2003	−23.13

Taxon	Source*	Locality (coordinates are given as E, S)	Collector/ Accession	Date	$\delta^{13}C$ (‰)
Tetragonia calycina Fenzl	WIND 101423	Namibia −26.37944444, 18.48277778	Crawford, F. 913	10/02/2016	−26.57
Tetragonia microptera Fenzl	WIND 90450	Namibia −26.99305556, 15.35833333	Burgoyne, P.M. 8243	03/08/2001	−26.30
Tetragonia reduplicata Welw. ex Oliv.	NP	Namibia −22.65155556, 14.52866667	De Cauwer, V., Naupu, P.N. and Smith, J.A.C.	13/09/2023	−21.95
Tetragonia reduplicata Welw. ex Oliv.	WIND 83207	Namibia −27.00694444, 15.65500000	Bartsch, S. 1029	05/09/2002	−25.95
Tetragonia reduplicata Welw. ex Oliv.	NP	ERO, Namibia	Strohbach, B. 8294		−22.56
Tetragonia reduplicata Welw. ex Oliv.	NP	ERO, Namibia	Strohbach, B. 22345		−25.12
Titanopsis hugo-schlechteri (Tischer) Dinter & Schwantes	WIND 87563	Namibia −28.62055556, 18.95694444	Bartsch, S.1918	16/06/2005	−19.82
Titanopsis schwantesii (Dinter ex Schwantes) Schwantes	WIND 57472	Namibia −26.62500000, 15.37500000	Hartmann, H.	30/03/1988	−16.20
Trianthema hereroensis Schinz	WIND 7344	Namibia −24.62500000, 15.37500000	Müller, M.A.N. 962	27/03/1978	−12.80
Trianthema hereroensis Schinz	NP	Namibia −22.77125000, 14.54166667	De Cauwer, V., Naupu, P.N. and Smith, J.A.C.	12/09/2023	−13.56
Trianthema parvifolia E.Mey. ex Sond. (syn. *Trianthema triquetra* Willd. ex Spreng. subsp. *parvifolia* (E.Mey. ex Sond.) C.Jeffrey)	NP	ERO, Namibia	Strohbach, B. 8283		−15.92
Tribulocarpus dimorphanthus (Pax) S.Moore	NP	ERO, Namibia	Strohbach, B. 8277		−26.50
Tribulocarpus dimorphanthus (Pax) S.Moore	WIND 95371	Namibia −21.37500000, 15.87500000	Craven, P. 6805	18/03/2014	−27.33
***Wooleya farinosa* (L.Bolus) L.Bolus**	Cult.^{O}	(South Africa)	MSG 2827		−19.32
Zaleya pentandra (L.) C.Jeffrey	WIND 83469	Namibia −22.62500000, 17.12500000	Friederich, W.J. 2/119	30/11/2002	−11.24
AMARANTHACEAE					

Taxon	Source*	Locality (coordinates are given as E, S)	Collector/ Accession	Date	$\delta^{13}C$ (‰)
Arthraerua leubnitziae (Kuntze) Schinz	WIND 95287	Namibia −22.42611111, 15.05083333	Rügheimer, S. 2337	21/04/2006	−22.85
Arthraerua leubnitziae (Kuntze) Schinz	NP	ERO, Namibia	Strohbach, B. 8270		−24.00
Arthraerua leubnitziae (Kuntze) Schinz	NP	Namibia −22.53130556, 14.83202778	De Cauwer, V. 22225	11/09/2023	−26.62
Calicorema capitata (Moq.) Hook.f.	NP	Namibia −24.65586111, 17.93494444	De Cauwer, V. 8279	23/01/2022	−25.11
Calicorema squarrosa (Schinz) Schinz	WIND 96554	Namibia −27.67666667, 16.71694444	Kolberg, H. 2437	24/10/2007	−26.65
Caroxylon aphyllum (L.f.) Tzvelev	WIND 100832	Namibia −28.37972222, 19.73250000	Hochobes, M.M. 1607	08/03/2008	−13.83
Caroxylon nollothense (Aellen) Mucina (syn. *Salsola nollothensis* Aellen)	NP	ERO, Namibia	Strohbach, B. 8290		−12.47
Caroxylon zeyheri Moq.	WIND 62926	Namibia −27.87500000, 15.62500000	Williamson, G. 5115	23/07/1993	−13.61
Gomphrena celosioides Mart.	NP	ERO, Namibia	Strohbach, B. 8291		−14.68
Leucosphaera bainesii (Hook.f.) Gilg	WIND 6153	Namibia −19.62500000, 14.87500000	Goldblatt, P. 1883	22/05/1974	−24.06
Suaeda fruticosa Forssk. ex J.F.Gmel.	NP	ERO, Namibia	Strohbach, B. 8267		−18.16
APOCYNACEAE					
***Australluma peschii* (Nel) Plowes** (syn. *Caralluma peschii* Nel)	WIND 91145	Namibia −17.71388889, 15.27000000	Strohbach, B.J. 6532	11/03/2006	−14.75
Ceropegia brachyceras Schltr. (syn. *Ceropegia crassifolia* Schltr.)	WIND 24832	Namibia −21.62500000, 18.87500000	Tölken, H.R. 175	07/01/1963	−18.68
Ceropegia carnosa E.Mey.	WIND 73292	Namibia −17.62500000, 12.87500000	Bruyns, P.V. 8039	22/12/1999	−29.13
Ceropegia lugardiae N.E.Br.	WIND 24840	Namibia −19.62500000, 17.37500000	Merxmüller, H. 30127	07/03/1974	−27.85
Ceropegia nilotica Kotschy	WIND 87050	Namibia −19.08083333, 18.90638889	Strohbach, B.J. 5406	15/02/2002	−25.61
Cynanchum meyeri (Decne.) Schltr.	WIND 89396	Namibia −27.15972222, 15.63777778	Bartsch, S. 2079	12/09/2005	−27.05

Taxon	Source*	Locality (coordinates are given as E, S)	Collector/ Accession	Date	$\delta^{13}C$ (‰)
Cynanchum viminale (L.) L. (syn. *Sarcostemma viminale* (L.) R.Br.)	NP	ERO, Namibia	Strohbach, B. 8282		−12.97
Duvalia caespitosa (Masson) Haw.	WIND 82772	Namibia −27.62500000, 16.87500000	Bruyns, P.V. 7204	05/07/1997	−13.15
Duvalia caespitosa (Masson) Haw.	Cult.[C]	(South Africa)	20191405		−14.55
Fockea multiflora K.Schum.	WIND 91058	Namibia −17.81416667, 15.72000000	Strohbach, B.J. 6435	13/02/2006	−27.51
Hoodia gordonii (Masson) Sweet ex Decne.	Cult.[O]	(Namibia, South Africa)		05/12/2024	−15.16
Huernia oculata Hook.f.	WIND 89812	Namibia −18.87500000, 18.62500000	Bruyns, P.V. 10340	01/06/2006	−12.87
Huernia plowesii L.C.Leach	WIND 95265	Namibia −25.95444444, 16.44111111	Rügheimer, S. 2826	11/03/2009	−11.74
***Larryleachia marlothii* (N.E.Br.) Plowes**	WIND 59692	Namibia −25.12500000, 16.62500000	Bruyns, P.V. 5669	07/03/1993	−15.85
***Larryleachia marlothii* (N.E.Br.) Plowes**	Cult.[W]	(Namibia, South Africa)		17/04/2019	−17.80
Larryleachia perlata (Dinter) Plowes	Cult.[C]	(Namibia, South Africa)	20191332		−20.99
***Lavrania haagnerae* Plowes**	Cult.[N]	(Namibia)	Naupu, P. 103		−15.52
Orbea caudata (N.E.Br.) Bruyns	WIND 25078	Namibia −17.87500000, 24.37500000	Bruyns, P.V. 2338	27/03/1981	−15.64
Orbea lugardii (N.E.Br.) Bruyns	WIND 87275	Namibia −18.78694444, 14.34694444	Bartsch, S. 1160	04/03/2003	−12.05
Orbea lutea (N.E.Br.) Bruyns	WIND 25080	Namibia −26.12500000, 16.62500000	Giess, W. 10281	03/04/1968	−12.63
Orbea maculata (N.E.Br.) L.C.Leach	WIND 73287	Namibia −27.12500000, 18.12500000	Bruyns, P.V. 8135	07/01/2000	−13.19
Orthanthera albida Schinz	WIND 73117	Namibia −19.12500000, 13.62500000	Sullivan, S. 55392	02/01/1966	−21.51
Orthanthera jasminiflora (Decne.) N.E.Br. ex Schinz	WIND 53229	Namibia −17.87500000, 23.37500000	Potgieter, J.A. 60	14/02/1985	−23.71
Pachypodium lealii Welw.	WIND 89446	Namibia −19.56361111, 17.95861111	Bartsch, S. 2172	01/03/2006	−25.13
Pachypodium lealii Welw.	Cult.[W]	(Angola, Namibia)	Naupu, P. 105		−25.85

Taxon	Source*	Locality (coordinates are given as E, S)	Collector/ Accession	Date	$\delta^{13}C$ (‰)
Pachypodium namaquanum (Wyley ex Harv.) Welw.	WIND 24405	Namibia −27.87500000, 16.87500000	Jankowitz, W.J. 269	17/08/1973	−21.60
***Piaranthus cornutus* N.E.Br.**	WIND 77804	Namibia −27.37500000, 18.62500000	Bruyns, P.V. 5816	17/03/1993	−15.69
***Piaranthus decipiens* (N.E.Br.) Bruyns**	WIND 59825	Namibia −21.87500000, 18.37500000	Bruyns, P.V. 5476	31/01/1993	−15.12
***Piaranthus punctatus* (Masson) Schult.**	Cult.[C]	(South Africa)	20210178		−14.22
Quaqua incarnata (L.f.) Bruyns	WIND 72438	Namibia −27.65333333, 16.32444444	Burke, A. 99202	29/09/1999	−13.16
Quaqua mammillaris (L.) Bruyns	WIND 101040	Namibia −28.01861111, 16.89305556	Rügheimer, S. 3733	03/08/2016	−13.23
Raphionacme haeneliae Venter & R.L.Verh.	WIND 52626	Namibia	Seely, M.K. 10	03/04/1972	−25.70
Schizostephanus gossweileri (S.Moore) Liede	Cult.[W]	(Angola, Namibia)	Swanepoel, W. 336		−25.51
Stapelia kwebensis N.E.Br.	Cult.[W]	(Botswana, Mozambique, Namibia, South Africa, Zimbabwe)	Naupu, P.N. 112		−13.83
Stapelia schinzii A.Berger & Schltr.	WIND 25150	Namibia −19.12500000, 17.62500000	Giess, W. 8645	05/04/1965	−13.84
***Stapeliopsis neronis* Pillans**	WIND 71157	Namibia −27.87500000, 16.62500000	Giess, W.	18/09/1973	−12.57
***Stapeliopsis urniflora* Lavranos**	WIND 77797	Namibia −27.62500000, 16.87500000	Bruyns, P.V. 7190	04/07/1997	−15.32
***Tavaresia angolensis* Welw.**	WIND 25054	Angola	Leach, L.C. 13914	02/03/1968	−13.88
***Tavaresia barklyi* (Dyer) N.E.Br.**	WIND 95239	Namibia −25.77027778, 17.14583333	Rügheimer, S. 2799	01/04/2009	−14.18
***Tridentea jucunda* (N.E.Br.) L.C.Leach**	WIND 95255	Namibia −25.92000000, 16.44027778	Rügheimer, S. 2815	11/03/2009	−13.82
***Tridentea marientalensis* (Nel) L.C.Leach**	WIND 25191	Namibia −25.62500000, 16.87500000	Giess, W. 5560	28/02/1963	−10.68
***Tridentea pachyrrhiza* (Dinter) L.C.Leach**	WIND 71158	South Africa −33.37500000, 24.37500000	Plowes, D.C.H. 3055	01/01/2002	−16.55
***Tromotriche aperta* (Masson) Bruyns**	WIND 25183	Namibia −28.12500000, 16.62500000	Müller, M.A.N. 845	27/01/1978	−12.76

Taxon	Source*	Locality (coordinates are given as E, S)	Collector/ Accession	Date	$\delta^{13}C$ (‰)
***Tromotriche herrei* (Nel) Bruyns**	Cult.[C]	(South Africa)	20191981		−13.24
***Tromotriche pedunculata* (Masson) Bruyns**	WIND 99956	Namibia −27.63194444, 16.61472222	Rügheimer, S. 3521	11/09/2014	−13.15
***Tromotriche pedunculata* (Masson) Bruyns**	Cult.[C]	(South Africa)	20191338		−17.04
***Tromotriche ruschiana* (Dinter) Bruyns**	WIND 25194	Namibia −27.37500000, 15.62500000	Oosthuizen. 61321	01/04/1977	−19.06
***Tromotriche umdausensis* (Nel) Bruyns**	Cult.[C]	(Namibia, South Africa)	20191397		−16.76
ASPHODELACEAE					
Aloe asperifolia A.Berger	NP	ERO, Namibia	Strohbach, B. 8286		−15.18
Aloe zebrina Baker	NP	ERO, Namibia	Strohbach, B. 8281		−13.92
Bulbine caput-medusae G.Will.	WIND 63551	Namibia −27.61416667, 16.31555556	Mannheimer, C.A. 332	26/09/1996	−28.28
Asparagaceae					
Dracaena pearsonii (N.E.Br.) Byng & Christenh. (syn. *Sansevieria pearsonii* N.E.Br.)	WIND 94847	Namibia −19.62361111, 13.87361111	Rügheimer, S. 2697	05/02/2009	−12.27
Asteraceae					
Crassothonna clavifolia (Marloth) B.Nord.	WIND 37850	Namibia −27.12500000, 15.37500000	Müller, M.A.N. 670	26/07/1977	−26.39
Crassothonna cylindrica (Lam.) B.Nord.	WIND 81116	Namibia −28.26500000, 16.31916667	Klaassen, E.S. 1111	04/09/2003	−25.49
Crassothonna opima (Merxm.) B.Nord.	WIND 63560	Namibia −27.64861111, 16.31527778	Mannheimer, C.A. 341	27/09/1996	−24.92
Crassothonna protecta (Dinter) B.Nord.	WIND 53591	Namibia −27.87500000, 16.87500000	Müller, M.A.N. 1515	22/09/1981	−27.17

Taxon	Source*	Locality (coordinates are given as E, S)	Collector/ Accession	Date	$\delta^{13}C$ (‰)
Crassothonna sedifolia (DC.) B.Nord.	WIND 81112	Namibia −28.01694444, 15.73972222	Klaassen, E.S. 1106	03/09/2003	−24.81
Crassothonna sparsiflora (S.Moore) B.Nord.	WIND 99930	Namibia −27.76055556, 16.59388889	Rügheimer, S. 3495	10/09/2014	−24.67
Galgera decurrens (Vahl) Anderb. & Bengtson (syn. *Laggera decurrens* (Vahl) Hepper & J.R.I.Wood)	WIND 34890	Namibia −22.62500000, 17.12500000	Hanekom, W.J. 22	25/06/1962	−26.11
Kleinia longiflora DC.	Cult.[W]	(Southern and Eastern Africa)	De Cauwer, V. 8884		−19.36
Osteospermum karrooicum (Bolus) Norl.	WIND 96252	Namibia −26.84138889, 16.08694444	Kolberg, H. 2822	07/08/2009	−26.43
Osteospermum microcarpum (Harv.) Norl.	WIND 67445	Namibia	Ward, C.J. 13753	31/03/1996	−30.33
Osteospermum spinescens Thunb.	WIND 38397	Namibia −25.12500000, 16.87500000	Giess, W. 10685	05/03/1969	−28.64
Osteospermum crassifolium (O.Hoffm.) Norl.	WIND 58980	Namibia −28.12500000, 17.12500000	Ward, C.J. 10327	14/09/1988	−29.08
Osteospermum namibense Swanepoel	NP	ERO, Namibia	Strohbach, B. 102806		−29.39
Pechuel-loeschea leubnitziae (Kuntze) O.Hoffm.	NP	KHO, Namibia	Strohbach, B. 8284		−23.30
BURSERACEAE					
Commiphora africana (A.Rich.) Engl.	WIND 16665	Namibia −17.87500000, 13.12500000	Winter, B. de. 5452	08/04/1957	−28.20
Commiphora glandulosa Schinz	WIND 96896	Namibia −18.62500000, 17.87500000	Hoffmann, L. 1265	30/01/2006	−28.62
Capparaceae					
Boscia foetida Schinz	WIND 9785	Namibia −28.87500000, 19.12500000	Giess, W. 12168	25/05/1972	−22.98
Boscia tomentosa Toelken	WIND 95805	Namibia −17.80694444, 12.41555556	Kolberg, H. 2603	15/06/2008	−23.70
Cadaba aphylla (Thunb.) Wild	WIND 9844	Namibia −24.62500000, 15.37500000	Müller, M.A.N. 954	27/03/1978	−24.21

Taxon	Source*	Locality (coordinates are given as E, S)	Collector/ Accession	Date	$\delta^{13}C$ (‰)
Cadaba aphylla (Thunb.) Wild	WIND 101759	Namibia −26.23555556, 19.50361111	Crawford, F. 963	12/02/2016	−25.34
Cadaba schroeppelii Suess.	WIND 9871	Namibia −21.12500000, 14.37500000	Giess, W. 3651	17/06/1961	−22.68
Capparis hereroensis Schinz	WIND 81617	Namibia −26.30166667, 15.03388889	Powrie, L.W. 1160	30/08/1999	−27.61
Capparis tomentosa Lam.	WIND 9686	Namibia −18.12500000, 21.37500000	Winter, B. de. 4296	17/01/1956	−25.87
Maerua juncea Pax	WIND 49996	Namibia −20.62500000, 14.87500000	Van Greuning, J.V. 455	21/12/1978	−25.99
COMBRETACEAE					
Terminalia sericea Burch. ex DC.	NP	OMU, Namibia	Mathew, I. 8296	31/12/2023	−28.27
Corbichoniaceae					
Corbichonia decumbens (Forssk.) Exell (syn. *Orygia decumbens* Forssk.)	OXF 00220534	Socotra	Balfour, I.B. 297	February–March 1880	−23.20
Corbichonia exellii Sukhor.	WIND 7266	Namibia	Giess, W. 8466	23/03/1965	−25.71
Corbichonia exellii Sukhor.	NP	Namibia −25.26186111, 15.98197222	De Cauwer, V. 8883	31/03/2024	−25.61
Corbichonia rubriviolacea (Friedrich) C.Jeffrey	WIND7288	Namibia −28.12500000, 19.37500000	Giess, W. 7093	19/05/1963	−26.11
CRASSULACEAE					
Cotyledon orbiculata L.	WIND 89367	Namibia −27.08861111, 15.42500000	Bartsch, S. 2047	01/11/2005	−12.69
Crassula ausensis Hutchison	WIND 89416	Namibia −26.73055556, 15.66138889	Bartsch, S. 2099	14/09/2005	−15.51
Crassula brevifolia Harv.	WIND 10345	Namibia −27.87500000, 16.87500000	Herre, H. s.n.	25/05/1971	−13.30
Crassula capitella Thunb.	WIND 10352	Namibia −22.62500000, 17.12500000	Giess, W. 13695	19/03/1975	−17.29
Crassula muscosa L.	NP	ERO, Namibia	Strohbach, B. 8276		−22.35
Kalanchoë brachyloba Welw. ex Britten	WIND 10399	Namibia −22.12500000, 18.62500000	Giess, W. 10178	27/05/1968	−19.00
Kalanchoë rotundifolia (Haw.) Haw.	WIND 96851	Namibia −23.40002778, 17.29500000	Strohbach, B.J. 7782	16/04/2014	−16.62

Taxon	Source*	Locality (coordinates are given as E, S)	Collector/ Accession	Date	$\delta^{13}C$ (‰)
CUCURBITACEAE					
Acanthosicyos horridus Welw. ex Benth. & Hook.f.	NP	Namibia	Smith, J.A.C., Austen, N., Becker, R.W. and Möller, A.	27/11/2022	−23.41
DIDIEREACEAE					
Portulacaria armiana van Jaarsv.	WIND 60461	Namibia −28.37500000, 17.37500000	Clark, D.H.M.	06/01/1988	−13.36
Portulacaria carrissoana (Exell & Mendonça) Bruyns & Klak (syn. *Ceraria kuneneana* Swanepoel)	WIND 95623	Namibia −17.30361111, 12.58055556	Kolberg, H. 1979	02/06/2006	−26.52
Portulacaria carrissoana (Exell & Mendonça) Bruyns & Klak (syn. *Ceraria kuneneana* Swanepoel)	WIND 89149	Namibia −19.12500000, 13.62500000	Jaarsveld, E. van.	01/07/2000	−26.44
Portulacaria fruticulosa (H.Pearson & Stephens) Bruyns & Klak (syn. *Ceraria fruticulosa* H.Pearson & Stephens)	WIND 77386	Namibia −27.43388889, 16.07111111	Mannheimer, C.A. 1465	06/08/2001	−20.93
Portulacaria longipedunculata (Merxm. & Podlech) Bruyns & Klak	WIND 72931	Namibia −17.12500000, 12.87500000	Bruyns, P.V. 8010	17/12/1999	−26.67
Portulacaria pygmaea Pillans	WIND 76575	Namibia −28.33444444, 16.76138889	Burke, A. 98201	06/11/1998	−15.28
Portulacaria pygmaea Pillans	Cult.[W]	(Namibia, South Africa)	Naupu, P.N. 111		−20.48
EUPHORBIACEAE					
Euphorbia damarana L.C.Leach	NP	ERO, Namibia	Strohbach, B. 8289		−12.24
Euphorbia giessii L.C.Leach	NP	ERO, Namibia	Strohbach, B. 8278		−18.80
Euphorbia giessii L.C.Leach	NP	Namibia	Smith, J.A.C., Austen, N., Becker, R.W. and Möller, A.	28/11/2022	−23.06
Euphorbia mauritanica L.	NP	Namibia −24.26086111, 16.22769444	De Cauwer, V. 8273	17/04/2022	−14.28
Euphorbia monteiroi Hook.f.	NP	ERO, Namibia	Strohbach, B. 8287		−28.28

Taxon	Source*	Locality (coordinates are given as E, S)	Collector/ Accession	Date	$\delta^{13}C$ (‰)
Euphorbia namibensis Marloth	Cult.[W]	(Namibia)	Naupu, P.N. 106		−21.42
Euphorbia negromontana N.E.Br. subsp. *rimireptans* (Swanepoel, R.W.Becker & Alma Möller) Bruyns	WIND102152	Namibia −18.00833333, 12.00833333	Swanepoel, W. 359	21/02/2019	−16.64
Euphorbia otjingandu Swanepoel	WIND 94446	Namibia −17.37500000, 14.12500000	Swanepoel, W. 269	28/07/2007	−13.34
Euphorbia phylloclada Boiss.	NP	ERO, Namibia	Strohbach, B. 8295		−26.19
Euphorbia racemosa E.Mey. ex Boiss. (syn. *E. spartaria* N.E.Br.)	NP	Namibia	Smith, J.A.C., Austen, N., Becker, R.W. and Möller, A.	26/11/2022	−19.31
Euphorbia racemosa E.Mey. ex Boiss. (syn. *E. spartaria* N.E.Br.)	Cult.[W]	(Botswana, Namibia, South Africa)	De Cauwer, V. 8274		−29.11
FABACEAE					
Adenolobus garipensis (E.Mey.) Torre & Hillc.	WIND 92985	Namibia −28.83444444, 18.48444444	Hochobes, M.M. 1693	11/03/2008	−24.95
Adenolobus garipensis (E.Mey.) Torre & Hillc.	NP	ERO, Namibia	Strohbach, B. 8266		−27.53
Adenolobus pechuelii (Kuntze) Korcz. & Hillc.	NP	ERO, Namibia	Strohbach, B. 8285		−27.73
Oberholzeria etendekaensis Swanepoel, M.M.le Roux, M.F.Wojc. & A.E.van Wyk	K	Namibia	Swanepoel 316		−23.05
Geraniaceae					
Sarcocaulom inerme S.E.A.Rehm	NP	ERO, Namibia	Strohbach, B. 15611		−24.85
Sarcocaulon marlothii Engl.	NP	ERO, Namibia	Strohbach, B. 95291		−23.63
Sarcocaulon mossamedense (Welw. ex Oliv.) Hiern	WIND 15659	Namibia −22.12500000, 14.87500000	Moffett, R.O. 1327	09/03/1977	−24.72
Sarcocaulon patersonii (DC.) G.Don	WIND 98061	Namibia −27.74194444, 16.86166667	Nanyeni, L. 680	03/10/2013	−24.02

Taxon	Source*	Locality (coordinates are given as E, S)	Collector/ Accession	Date	$\delta^{13}C$ (‰)
GISEKIACEAE					
Gisekia africana (Lour.) Kuntze	WIND 6969	Namibia −18.62500000, 20.37500000	Giess, W. 10043	26/04/1967	−12.15
KEWACEAE					
Kewa salsoloides (Burch.) Christenh. (syn. *Hypertelis salsoloides* (Burch.) Adamson)	NP	ERO, Namibia	Strohbach, B. 8288		−26.23
LAMIACEAE					
Coleus caninus (B.Heyne ex Roth) Vatke	WIND 27495	Namibia −19.37500000, 17.12500000	Giess, W. 6418	24/04/1964	−28.60
Coleus caninus (B.Heyne ex Roth) Vatke	WIND 27496	Namibia −20.37500000, 16.62500000	Kers, L.E. 793	22/04/1963	−27.90
Coleus cylindraceus (Hochst. ex Benth.) A.J.Paton (syn. *Plectranthus cylindraceus* Hochst. ex Benth.)	WIND 27500	Namibia	Winter, B. de. 2882	22/03/1955	−20.78
Coleus dinteri (Briq.) A.J.Paton	WIND 27512	Namibia −19.62500000, 17.62500000	Merxmüller, H. 30211	10/03/1974	−31.10
Coleus hereroensis (Engl.) A.J.Paton (syn. *Plectranthus hereroensis* Engl.)	WIND 97027	Namibia −18.71527778, 13.84472222	Klaassen, E.S. 2538	16/05/2014	−31.89
Coleus hereroensis (Engl.) A.J.Paton (syn. *Plectranthus hereroensis* Engl.)	WIND 102464	Namibia −20.48694444, 17.02027778	Kruger, S. 878	15/04/2008	−32.65
Coleus lasianthus Gürke (syn. *C. tetensis* Baker)	WIND 56718	Namibia −17.87500000, 24.12500000	Hardy, D.S. 7106	03/03/1990	−23.44
Coleus mirabilis Briq.	WIND 70419	Namibia −18.10916667, 21.66361111	Burke, A. 96317	14/11/1996	−29.09
Coleus neochilus (Schltr.) Codd (syn. *Plectranthus neochilus* Schltr.)	WIND78906	Namibia −21.01388889, 19.29000000	Mannheimer, C.A. 1346	15/05/2001	−27.39
Coleus neochilus (Schltr.) Codd (syn. *Plectranthus neochilus* Schltr.)	WIND 27557	Namibia −19.62500000, 17.12500000	Merxmüller, H. 30168	09/03/1974	−30.03

Taxon	Source*	Locality (coordinates are given as E, S)	Collector/ Accession	Date	$\delta^{13}C$ (‰)
Coleus unguentarius (Codd) A.J.Paton (syn. *Plectranthus unguentarius* Codd)	WIND 90708	Namibia −17.51527778, 12.92916667	Kolberg, H. 1981	03/06/2006	−25.28
LIMEACEAE					
Limeum argute-carinatum Wawra	WIND 52951	Namibia −19.87500000, 20.37500000	Hines, C.J.H.308	25/02/1985	−25.28
LOPHIOCARPACEAE					
Lophiocarpus dinteri Engl.	WIND 49893	Namibia −21.12500000, 15.62500000	Craven, P. 2015	03/03/1985	−27.15
Lophiocarpus polystachyus Turcz. (syn. *L. burchellii* Hook.f.)	WIND 82235	Namibia −26.56722222, 16.40583333	Burgoyne, P.M. 5026	01/02/1997	−28.41
Lophiocarpus tenuissimus Hook.f.	WIND 86387	Namibia −18.28527778, 17.05500000	Strohbach, B.J. 4001	23/01/1999	−26.98
NYCTAGINACEAE					
Boerhavia coccinea L.	NP	Namibia −22.57833333, 17.13947222	De Cauwer, V. 9997	10/02/2014	−13.66
Phaeoptilum spinosum Radlk.	WIND 6639	Namibia −21.87500000, 15.62500000	Schmidt, E. 134	09/04/1972	−25.24
ORCHIDACEAE					
Ansellia africana Lindl.	WIND 4105	Namibia −22.62500000, 17.12500000	Giess, W. 11528	01/11/1971	−18.85
Habenaria kilimanjari Rchb.f.	WIND 97583	Namibia −17.95472222, 24.52888889	Mannheimer, C.4850	29/02/2015	−25.94
OXALIDACEAE					
Oxalis ausensis R.Knuth	WIND 15731	Namibia −27.87500000, 16.87500000	Giess, W. 14352	13/06/1976	−25.11
Oxalis laxicaulis R.Knuth	WIND 15764	Namibia −27.87500000, 16.87500000	Giess, W. 12937	13/09/1973	−27.39
Oxalis luederitzii Schinz	WIND 15799	Namibia −26.62500000, 16.12500000	Wendt, W.E.	01/07/1977	−27.92
Oxalis pes-caprae L. var. *pes-caprae*	WIND 57066	Namibia −28.12500000, 17.37500000	Strohbach, B.J. 137	05/08/1989	−29.39
PASSIFLORACEAE					
Adenia pechuelii (Engl.) Harms	WIND 97187	Namibia −25.29694444, 15.80055556	Rügheimer, S. 3150	09/03/2011	−25.39
Adenia pechuelii (Engl.) Harms	NP	Namibia −22.60863889, 15.18713889	Naupu, P. 109	19/06/2023	−25.71

Taxon	Source*	Locality (coordinates are given as E, S)	Collector/ Accession	Date	$\delta^{13}C$ (‰)
Adenia pechuelii (Engl.) Harms	Cult.[W]	(Namibia)	Naupu, P. 109	07/09/2023	−28.79
Adenia repanda (Burch.) Engl.	WIND 92269	Namibia −24.04611111, 18.55002778	Kwembeya, E.G. 96	10/02/2006	−28.46
PORTULACACEAE					
Portulaca kermesina N.E.Br.	NP	Namibia −22.62927778, 17.11772222	De Cauwer, V. 67608	05/02/2023	−12.80
Portulaca quadrifida L.	WIND 8502	Namibia −19.87500000, 17.37500000	Giess, W. 3375	07/06/1961	−14.16
SALVADORACEAE					
Salvadora persica L.	Cult.[W]	(Africa, Arabian Peninsula)	De Cauwer, V. 8272		−27.24
SANTALACEAE					
Thesium equisetoides Welw. ex Hiern	WIND 92512	Namibia −17.12500000, 13.12500000	van Jaarsveld, E.J. 18824	05/11/2004	−26.06
Thesium xerophyticum A.W.Hill	WIND 76456	Namibia −22.78111111, 17.00055556	Mannheimer, C.A. 1162	05/03/2001	−21.01
Thesium zeyheri A.DC.	WIND 85295	Namibia	Burke, A. 4047	06/03/2003	−28.27
SOLANACEAE					
Lycium amoenum Dammer	WIND 87165	Namibia −28.11138889, 17.19388889	Kolberg, H. 1719	16/10/2005	−25.63
Lycium cinereum Thunb.	WIND 27816	Namibia	Jankowitz, W.J. 160	19/03/1971	−26.08
Lycium decumbens Welw. ex Hiern	WIND 70465	Namibia −26.87500000, 15.62500000	Kolberg, H. 178	22/10/1987	−27.90
Lycium tetrandrum Thunb.	WIND 47234	Namibia −26.62500000, 16.37500000	Leippert, H. 4820	18/02/1963	−26.55
TALINACEAE					
Talinum afrum (Thunb.) Eckl. & Zeyh.	WIND 67723	Namibia −18.96583333, 18.70861111	Strohbach, B.J. 3138	12/03/1997	−26.09
Talinum afrum (Thunb.) Eckl. & Zeyh.	NP	Namibia −22.63016667, 17.10475000	Naupu, P.N. and Angobe, A.T. 9998	13/01/2024	−25.98
Talinum tenuissimum Dinter	WIND 8367	Namibia −19.62500000, 20.62500000	Giess, W. 11025	13/01/1971	−26.68
TIGANOPHYTACEAE					

Taxon	Source*	Locality (coordinates are given as E, S)	Collector/ Accession	Date	$\delta^{13}C$ (‰)
Tiganophyton karasense Swanepoel, F.Forest & A.E.van Wyk	WIND 102437	Namibia −25.00000278, 18.00000278	Swanepoel, W. 365	19/12/2010	−25.73
Tiganophyton karasense Swanepoel, F.Forest & A.E.van Wyk	Cult.[W]	(Namibia)	Swanepoel, W.	02/12/2022	−27.13
Tiganophyton karasense Swanepoel, F.Forest & A.E.van Wyk	Cult.[W]	(Namibia)	Swanepoel, W.	02/12/2022	−27.57
VITACEAE					
Cissus nymphaeifolia (Welw. ex Baker) Planch.	WIND 19705	Namibia −17.37500000, 13.12500000	Viljoen, P.J. 428	23/06/1977	−25.84
Cyphostemma bainesii (Hook.) Desc.	WIND 82371	Namibia −24.37500000, 16.37500000	Dreyer, L.L. 429	06/01/1995	−14.49
Cyphostemma juttae (Dinter & Gilg) Desc.	WIND 19816	Namibia −18.12500000, 12.62500000	Giess, W. 10547	02/01/1969	−11.93
Cyphostemma uter (Exell & Mendonça) Desc.	WIND 19838	Namibia −18.12500000, 13.87500000	Winter, B. de. 5286	01/04/1957	−12.00
Cyphostemma uter (Exell & Mendonça) Desc.	Cult.[W]	(Namibia)	Naupu, P.N. 101		−13.77
Welwitschiaceae					
Welwitschia mirabilis Hook.f.	NP	Namibia	Smith, J.A.C., Austen, N., Becker, R.W. and Möller, A.	27/11/2022	−23.25
ZYGOPHYLLACEAE					
Roepera pubescens (Schinz) Beier & Thulin (syn. *Zygophyllum pubescens* Schinz)	WIND 16101	Namibia −26.62500000, 16.37500000	Winter, B. de. 7933	08/03/1963	−27.79
Sisyndite spartea E.Mey. ex Sond.	NP	Namibia −28.17897222, 18.04005556	De Cauwer, V. 8271	05/01/2022	−29.08
Zygophyllum clavatum Schltr. & Diels	Cult.[W]	(Namibia)	Naupu, P.N. 8293		−24.20
Zygophyllum cylindrifolium Schinz	WIND 15938	Namibia −18.62500000, 12.62500000	Giess, W. 7503	10/06/1963	−24.26

Taxon	Source*	Locality (coordinates are given as E, S)	Collector/ Accession	Date	$\delta^{13}C$ (‰)
(syn. *Tetraena cylindrifolia* (Schinz) Beier & Thulin)					
Zygophyllum decumbens Delile (syn. *Tetraena decumbens* (Delile) Beier & Thulin)	WIND 2668	Namibia −28.12500000, 19.37500000	van Wyk, A.E. 718	14/12/1974	−25.85
Zygophyllum rigidum Schinz (syn. *Tetraena rigida* (Schinz) Beier & Thulin)	WIND 16244	Namibia −25.62500000, 18.12500000	Giess, W. 6833	13/05/1963	−24.39
Zygophyllum simplex L.	NP	ERO, Namibia	Strohbach, B. 8280		−15.18
Zygophyllum simplex L.	NP	ERO, Namibia	Smith, J.A.C., Austen, N., Becker, R.W. and Möller, A.	28/11/2022	−16.19
Zygophyllum stapffii Schinz	NP	ERO, Namibia	Strohbach, B. 8269		−24.58
Zygophyllum stapffii Schinz	NP	ERO, Namibia	Smith, J.A.C., Austen, N., Becker, R.W. and Möller, A.	28/11/2022	−25.32
Zygophyllum stapffii Schinz	Cult.[W]	(Namibia)	Naupu, P.N. 110		−28.74
***Zygophyllum tenue* R.Glover (syn. *Tetraena tenuis* (R.Glover) Beier & Thulin)**	**WIND 67005**	**Namibia −27.66638889, 18.34722222**	**Strohbach, B.J. 3796**	**30/03/1998**	**−26.08**

*For samples deposited in herbaria under a species name different from the currently accepted name, the original name is indicated as a synonym (syn.) in parentheses. Herbarium designations are as follows: K, Royal Botanic Gardens Kew; OXF/FHO, Oxford University Herbaria; WIND, National Herbarium of Namibia, Windhoek. Cultivated material was from the following sources as indicated by superscripts: [C], University of Cambridge Botanic Gardens, UK; [O], University of Oxford, UK; [W], National Botanical Research Institute, Windhoek, Namibia; for cultivated material, the native range of the species is indicated in parentheses. Locality information was converted from degrees/minutes/seconds, where available, to decimal degrees. s.n., *sine numero*.

[a] For specimens collected by Ecklon, Zeyher, J. Burke and Drège, the herbarium sheets did not record information on the exact locality or date of collection, which have been inferred from the relevant descriptions in Ecklon and Zeyher (1837), Drège (1843), Harvey and Sonder (1864), Clokie (1964), and Glen and Germishuizen (2010).

Table 3.2. Titratable acidity values (mmol H^+ kg^{-1} fresh mass) for selected succulent species grown in cultivation. All species tested exhibited statistically significant dawn–dusk differences in titratable acidity. Genera newly identified in this study as capable of CAM photosynthesis are shown in bold.

Species	Source*	Location	Dusk titratable acidity	Dawn titratable acidity	*P*-value
AIZOACEAE					
***Aloinopsis malherbei* (L.Bolus) L.Bolus**	NT	NUST	6.03 ± 0.94	48.0 ± 2.47	<0.001
***Dinteranthus vanzylii* (L.Bolus) Schwantes**	MSG 2773	OXF	16.4 ± 3.93	61.2 ± 2.55	<0.001
***Ebracteola derenbergiana* (Dinter) Dinter & Schwantes**	NBRI	NBRI	16.9 ± 2.15	55.1 ± 0.45	<0.001
***Gibbaeum petrense* (N.E.Br.) Tischler**	MSG 2777	OXF	14.7 ± 3.93	40.7 ± 4.29	<0.001
***Gibbaeum pubescens* (Haw.) N.E.Br.**	MSG 2778	OXF	20.4 ± 6.13	84.2 ± 2.55	<0.001
***Machairophyllum albidum* (L.) Schwantes**	NT	NUST	5.69 ± 0.37	27.1 ± 6.28	0.0127
***Nananthus margaritifer* L.Bolus**	NT	NUST	4.48 ± 1.58	46.4 ± 6.81	0.00290
***Rhombophyllum dolabriforme* (L.) Schwantes**	NT	NUST	6.21 ± 4.86	43.1 ± 3.45	0.00174
Ruschia axthelmiana (Dinter) Schwantes	NBRI	NUST	3.46 ± 0.26	53.0 ± 4.08	0.0127
***Stomatium duthieae* L.Bolus**	MSG 2825	OXF	25.5 ± 10.2	59.5 ± 2.94	0.00258
***Tanquana prismatica* (Schwantes) H.E.K.Hartmann & Liede**	MSG	OXF			
Titanopsis calcarea (Marloth) Schwantes	NT	NUST	5.16 ± 1.28	29.4 ± 1.11	0.00161
***Wooleya farinosa* (L.Bolus) L.Bolus**	MSG 2827	OXF	20.4 ± 1.70	57.8 ± 8.96	0.00104
LAMIACEAE					
Coleus neochilus (Schltr.) Codd	NBRI	NUST	14.8 ± 14.7	68.9 ± 57.1	0.0139
TALINACEAE					
Talinum afrum (Thunb.) Eckl. & Zeyh.	Farm Windhoek	NUST	21.7 ± 7.49	97.9 ± 15.9	0.00355

**Plant material was originally obtained from the following sources: MSG, Mesemb Study Group (https://www.mesemb.org); NBRI, National Botanical Research Institute, Windhoek, Namibia; NT, Namib Trees, Klein Windhoek, Namibia. Plants were cultivated at either the Biodiversity Research Centre, Namibia University of Science and Technology (NUST) or at the Department of Biology, University of Oxford, UK (OXF). Samples of fresh leaf material were harvested within 1 h of dusk or dawn. Measurements of titratable acidity were performed on extracted leaf-cell sap as described in Materials and Methods; results are expressed as arithmetic means ± standard deviations for 3 independent samples.* P*-values indicate statistical significance of the difference between dawn and dusk values of titratable acidity determined using a paired-sample, one-tailed Student's* t*-test with equal variance.*

3.5 Conclusion

This study presented the first comprehensive evaluation of CAM photosynthesis within the succulent flora of Namibia and revealed a far richer representation of CAM than previously recognised. I analyzed 273 species across 34 families and documented new occurrences of CAM in many genera, especially within the Aizoaceae, Apocynaceae, Asphodelaceae, and Didiereaceae, and demonstrated that CAM species comprise a significant part of Namibia's vascular flora, making up approximately 12% of all species. This proportion is notably higher than the global estimate of nearly 7% (Gilman et al., 2023), reflecting Namibia's position within the Succulent Karoo–Gariep–Kaokoveld arid corridor, a region that supports nearly 40% of the world's terrestrial succulents (Craven & Vorster, 2006; Marshall et al., 2016; Frandsen, 2017; Smith et al., 2017; Burke & Loots, 2020; Craven & Kolberg, 2023). The combination of ancient aridity, prolonged landscape stability, and fog-dependent microhabitats has promoted the persistence and diversification of CAM taxa in Namibia's flora, even if comparable quantitative assessments are lacking for many other global drylands.

Beyond expanding the taxonomic inventory, these findings carry applied significance. CAM species possess high WUE, strong drought tolerance, and the capacity to establish on nutrient-poor or disturbed substrates. These traits make CAM plants strategically valuable for ecological restoration in arid and semi-arid landscapes. Because conventional C_3 species often fail under severe moisture stress, the confirmation of additional CAM genera expands the restoration toolkit available for Namibia, particularly for interventions in fog-influenced coastal zones, escarpment habitats, degraded rangelands, and other marginal environments where planting success is typically low. The consolidated $\delta^{13}C$ dataset identified CAM-positive taxa with potential for use in hyper-arid to arid restoration settings in Namibia and beyond. As Namibia continues to face intensifying drought under climate change, the expanded knowledge generated here supports long-term conservation prioritisation, targeted ecological monitoring, and the development of restoration strategies that leverage the metabolic resilience of CAM plants.

CAM plants generally exhibit higher water-use efficiency (WUE) than typical C_3 species because a larger fraction of carbon gain occurs at night when evaporative demand is lower. This may translate into lower transpirational water loss per unit carbon fixed and could improve establishment in very water-limited restoration contexts. Nevertheless, outcomes may still depend on micro-site conditions, soil properties, grazing pressure, and event-scale drought. With these caveats, our consolidated $\delta^{13}C$ dataset suggested candidate genera for site-matched use in Namibia's drylands. In very dry flats such as the Namib margin and Namaqualand, one may consider low, compact Aizoaceae to hold the surface and cut dust. Candidates from our dataset include *Juttadinteria, Lapidaria, Dinteranthus, Schwantesia, Pleiospilos, Gibbaeum, Wooleya, Aloinopsis, Ebracteola, Tanquana, Ruschianthus,* and selected *Mesembryanthemum* species (all showed CAM signals and strong drought form). On rocky slopes and escarpment mosaics, there may be a potential in combining a mix of rock-crevice (chasmophytic) Aizoaceae (e.g., *Lapidaria, Dinteranthus, Pleiospilos, Gibbaeum*) with *stapeliads* to lock into cracks and provide small patches of shade and litter. Suitable stapeliads from our list are *Larryleachia, Lavrania, Piaranthus, Stapeliopsis, Tridentea, Tavaresia, Orbea, Huernia, Quaqua, plus Cynanchum viminale*. Where one needs light framework shade or longer-lasting litter, one may add a few Asphodelaceae/Euphorbiaceae individuals (e.g., *Aloe sensu lato*) at low density so they don't monopolise scarce water. These are evidence-informed recommendations based on $\delta^{13}C$ signatures,

succulence, and habitat association observed in this study. Species–site matching should be verified in field trials under local conditions.

3.6 Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

3.7 Author contribution

EZK, RB, TW, and AS were responsible for design, conceptualisation, funding acquisition, and supervision, with AS also serving as the subject-matter expert. NN and AS conducted the data analysis and investigation. VDC and AA participated in manuscript review and editing. All authors contributed to the writing and approved the final version of the manuscript.

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Chapter 4: Functional trait responses to aridity gradient in three Namibian woody forage species

Paulina N. Naupu[1, *], Rolf W. Becker[2], Ezekeil Kwembeya[3], Theo Wassenaar[1,2]

[1] Biodiversity Research Centre, School of Agriculture and Natural Resources Sciences, Namibia University of Science and Technology, Private Bag 13388, Windhoek, Namibia.

[2] Ongava Research Centre, Private Bag 12041, Windhoek, Namibia.

[3] Department of Environmental Science, University of Namibia, Private Bag 13301, Windhoek, Namibia.

***Corresponding author**: pnaupu@nust.na

4.1 Abstract

Dryland ecosystems are highly vulnerable to intensifying aridity, yet the functional mechanisms enabling woody species to persist under drought remain poorly quantified in Namibia. To date, no systematic field-based evaluation of drought-related plant functional traits has been conducted across Namibia's aridity gradient. This study, therefore, provided the first comprehensive, transect-based assessment of how four selected leaf functional traits (specific leaf area (SLA), leaf dry matter content (LDMC), stomatal density (SD), and relative water content (RWC)) respond to long-term climatic variations in three dominant forage species (*Terminalia prunioides*, *Colophospermum mopane*, and *Catophractes alexandri*) across two west–east transects in northwestern Namibia. Climatic predictors were derived from 30-year CHIRPS and TerraClimate datasets, and trait–environment relationships were assessed through Spearman correlations and multiple linear regressions. Hydroclimatic gradients were expressed in both transects, with west–east increases observed in rainfall, evapotranspiration, temperature, vapor pressure deficit, and aridity. Across these gradients, species displayed contrasting drought-response strategies. *Terminalia prunioides* showed high phenotypic plasticity, with SLA, SD, and RWC responding sensitively to moisture and temperature variability. *Colophospermum mopane* exhibited conservative and context-dependent responses: traits were largely unresponsive in the northern transect but strongly coupled to climate variables in the south, suggesting hydraulic regulation. In contrast, *C. alexandri* relied primarily on structural adjustments, reduced SLA and increased LDMC, while showing weaker physiological buffering (RWC). These results revealed that woody species in Namibia's drylands achieve drought resistance through markedly different combinations of functional strategies, plasticity, conservative hydraulic control, and structural reinforcement. The findings provided foundational insight into trait–environment relationships in arid-zone vegetation and offer a functional basis for selecting climate-resilient species for dryland restoration. While traits alone do not guarantee establishment success, they are critical indicators of drought tolerance and provide valuable guidance for restoration planning under increasing climatic variability in Namibia and comparable arid regions.

Keywords: dryland restoration, functional traits, leaf dry matter content, specific leaf area, stomatal density, trait–environment relationships, relative water content

4.2 Introduction

In southern Africa, increasing aridity and recurrent droughts are intensifying land degradation and threatening the sustainability of rangelands (Slayi et al., 2024b). Namibia, one of the driest countries in sub-Saharan Africa, exemplifies these challenges, as recurrent droughts reduce vegetation productivity, livestock forage, and local livelihoods (Nakanyete et al., 2020; Shikangalah, 2020). It is therefore crucial to understand how plants function and persist in these environments for predicting and managing ecosystem responses to climate change (James et al., 2013b; Wang et al., 2022).

Plant functional traits are measurable characteristics that directly influence plant performance through complex evolutionary trade-offs between growth strategies and environmental adaptation (Violle et al., 2007; Pérez-Harguindeguy et al., 2013). Functional traits can be broadly classified as response traits, which mediate plant reactions to stress, and effect traits, which influence ecosystem processes (Lavorel & Garnier, 2002; Suding et al., 2008). Trait-based ecology has therefore become central to understanding plant responses to climate extremes, offering predictive frameworks for vegetation dynamics under changing climates (Anderegg et al., 2019; Guo, 2019; Kühn et al., 2021). Traits governing carbon gain, water transport, and tissue integrity are particularly critical in drylands, as they determine a species' ability to maintain hydraulic function and a positive carbon balance during water deficits (Martin-StPaul et al., 2017; Deans et al., 2020). In dryland ecosystems, such traits not only determine individual plant survival but also shape community composition and ecosystem functioning (Reich, 2014; Maestre et al., 2016; Gross et al., 2017). Consequently, functional trait analyses have become a cornerstone of modern ecology, facilitating cross-species comparisons to identify adaptive strategies and predict vegetation shifts under future climatic scenarios (Funk et al., 2017).

The Leaf Economics Spectrum (LES) provides a key framework for interpreting trait–environment relationships, describing a continuum from fast resource acquisition to conservative resource use (Wright et al., 2004). Traits linked to carbon gain, water conservation, and tissue structure are particularly informative for assessing drought adaptation (Sreeman et al., 2018). Accordingly, this study focused on SLA, LDMC, SD, and RWC, which together reveal trade-offs between resource-use efficiency and water retention (Bongers et al., 2017; Da Sois et al., 2024). High specific leaf area (SLA) and stomatal density (SD) typically characterise acquisitive species that maximise growth under favourable moisture, whereas high leaf dry matter content (LDMC) and stable relative water content (RWC) reflect conservative strategies enhancing tissue toughness and drought resistance (Reich, 2014; Gorné et al., 2022). Despite their ecological importance, trait-based data remain scarce in Namibia due to limited research capacity and laboratory infrastructure. The selected traits were therefore chosen for their ecological relevance and practicality for field-based studies in remote arid landscapes.

Woody species dominate Namibia's drylands, providing essential forage and stabilising ecosystems during drought (Inman et al., 2020b; Nikodemus et al., 2025). This study examined three widespread species (*Colophospermum mopane*, *Catophractes alexandri*, and *Terminalia prunioides*), which represent the dominant functional strategies of woody vegetation along northwestern Namibia's aridity gradient. They were selected because they are widespread, drought-tolerant, and critical to rangeland productivity. Furthermore, they play pivotal roles in dryland restoration, stabilising soils, enhancing microclimates and infiltration, and acting as nurse or facilitation species that help other plants establish under water-limited conditions. Yet little is known about the traits underlying their survival strategies.

This study examined the relationships between four leaf functional traits and drought-related environmental factors for three dominant woody species in northwestern Namibia. The research aimed to identify how specific traits (SLA, LDMC, SD, and RWC) respond to environmental factors. The study provided insights into plant adaptive strategies under increasing water stress in Namibia.

4.3 Materials and methods

4.3.1 Study area

The research was carried out in northwestern Namibia, an area marked by environmental gradients and diverse ecosystems typical of arid and semi-arid landscapes (Strohbach et al., 2025). The two transects, which extend across portions of northwestern Namibia that differ in long-term water availability, were established in the study area. The northern transect is approximately 280 km long, and the southern transect is approximately 240 km long (Figure 4.1). Although the aridity index forms a continuous environmental variable, its spatial representation in Figure 4.1 appeared as discrete aridity classes (hyper-arid, arid, and semi-arid). This map, therefore, illustrates categorical zones rather than a continuous gradient surface, but the underlying climatic data used in the analyses capture continuous variation across the transects.

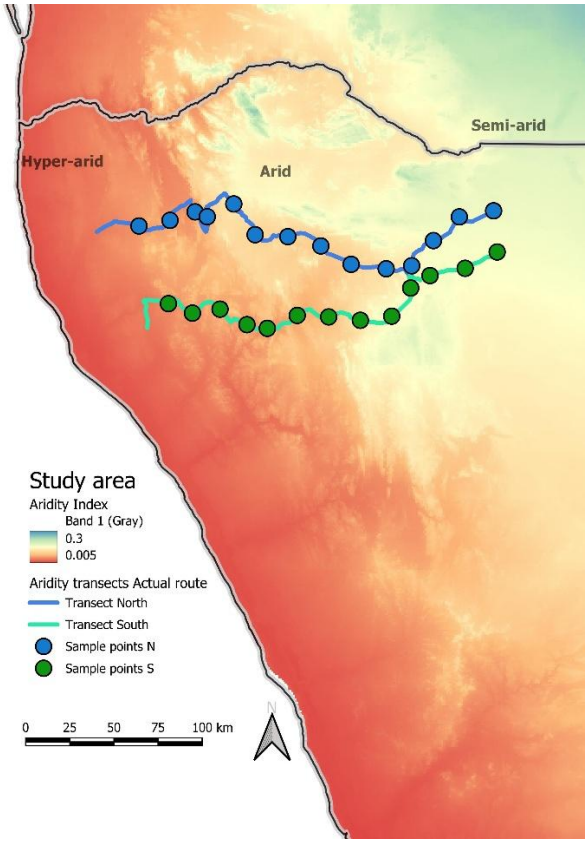


Figure 4.1: Locations of the northern and southern transects (northern transect, blue dots; southern transect, green dots) overlaid on categorised aridity index zones (hyper-arid, arid, and semi-arid). The transects traverse areas differing in long-term water availability, forming a functional aridity gradient based on underlying climatic variables, although the map representation shows discrete aridity classes for visual clarity. Aridity indices were derived from TerraClimate datasets (Abatzoglou et al., 2018).

4.3.2 Study species and sampling strategies

Three woody species (*C. mopane*, *T. prunioides*, and *C.alexandri)* were selected for this study. These species are dominant components of northwestern Namibia's dryland vegetation and are critical to rangeland productivity due to their role as key forage resources for livestock and wildlife, particularly during drought periods. Species occurrence records were obtained from the National Botanical Research Institute (NBRI), Namibia, and used to map their national distributions. These records were overlaid on the aridity index derived from TerraClimate datasets (Abatzoglou et al., 2018) to illustrate each species' natural range in relation to aridity gradients (Figure 4.2). All three species occur within semi-arid to arid regions, but with notable differences in distribution extent and climatic niche, making them ideal models for examining functional trait variation along environmental gradients.

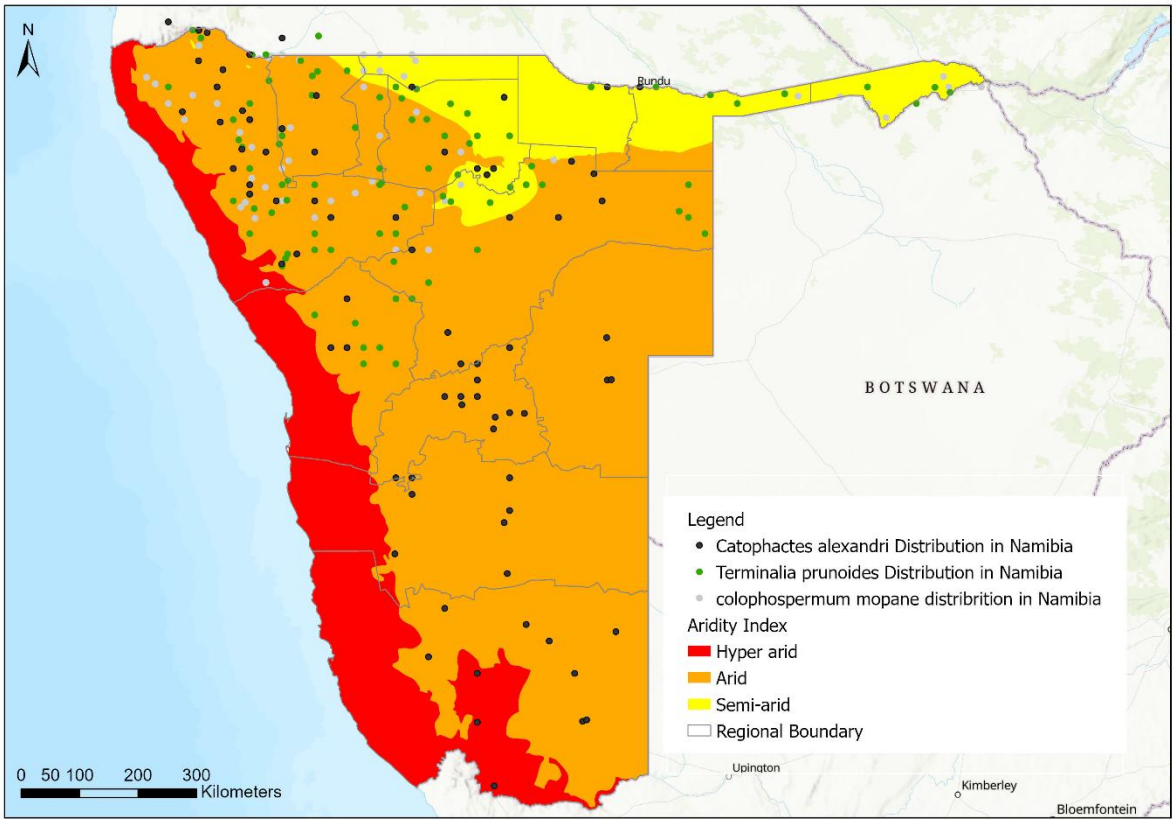


Figure 4.2: Distribution records of *Colophospermum mopane*, *Terminalia prunioides*, and *Catophactes alexandri* in Namibia shown in relation to classified aridity zones based on the aridity index (hyper-arid, arid, and semi-arid). The map illustrates the spatial context of the study area and the broad aridity classes within which the study species occur. Data sources: National Botanical Research Institute (NBRI), Namibia, and TerraClimate datasets (Abatzoglou et al., 2018).

Four functional traits were measured for each of the three study species along two west-to-east transects (Figure 4.1). Sampling was conducted during May 2024, corresponding to the onset of the dry season when vapour pressure deficit (VPD) begins to increase. It is acknowledged that some trait expressions, particularly those associated with resource acquisition, may partially reflect conditions from the preceding wetter season.

To minimise the influence of short-term temporal variability, sampling was conducted in two rounds within the same seasonal window, approximately two weeks apart. This repeated sampling approach ensured that observed trait patterns were consistent and not driven by transient environmental fluctuations. The traits measured in this study are relatively stable structural traits and are therefore less sensitive to short-term seasonal variation. Furthermore, environmental variables were derived from long-term climatic datasets, representing broader hydroclimatic conditions rather than short-term temporal changes. As such, the study design prioritised capturing spatial variation along the aridity gradient while minimising the influence of seasonal effects on the interpretation of results. Table 4.1 summarises the main functional roles of the four traits. Species were randomly sampled at approximately 20 km intervals along each transect, with the westernmost point designated as 0 km.

Table 4.1: Leaf functional traits and their related function based on literature [a]

Functional trait	Unit	Related function [a]
Leaf dry matter content (LDMC)	%	Leaf tissue density, leaf physical resistance, and stress tolerance
Specific leaf area (SLA)	$cm^{-2}.g^{-1}$	Leaf longevity, photosynthetic rate, and relative growth rate
Stomatal density (SD)	$stomata/mm^2$	Controls gas exchange, water loss, and energy regulation
Relative water content (RWC)	%	Measures water retention, growth rates, and drought resilience

[a] (Grime et al., 1997; Weiher et al., 1999; McIntyre et al., 1999; Cornelissen et al., 2003; Bernard-Verdier et al., 2012; Garnier & Navas, 2012)

For each measurement, five matured leaves taken from a randomly selected branch on each sampled tree were collected to form a composite leaf sample (Clausen & Kozlowski, 1965). Each leaf sample was treated as a single experimental unit and weighed collectively. The fresh weight of the leaf samples was measured immediately or within two hours of collecting using an analytical balance with a precision of 0.001 grams.

To determine the leaf area, the same five leaves from each sample were arranged on a sheet of white paper next to a ruler and photographed. ImageJ, an open-source image-processing software, was used to calculate leaf area. The same leaf samples were then submerged in distilled water for 72 hours, and the turgid weight (the maximum weight a piece of plant tissue can attain after full rehydration) was measured. After weighing the turgid weight, the leaf samples were oven-dried at 70°C for eight days (8) to achieve a constant dry weight. Dry weight measurements were repeated on the 11th day to confirm consistency.

Stomatal density (SD) was determined from separate leaves collected from the same branch and of similar condition as those used for the other measurements. The lower (abaxial) surface of each leaf was coated with clear nail varnish while lying flat. After approximately five minutes, once the varnish had dried, a thin film was peeled off using adhesive tape to create a leaf impression. Each impression

was mounted on a microscope slide and examined at 10× magnification for general assessment, followed by stomatal counting at 400× magnification. Stomatal density was expressed as the number of stomata per field of view (0.45 mm in diameter).

The following formulae were used to calculate the functional traits:

- Relative water content: $\frac{Fresh\ weight - Dry\ weight}{Turgid\ weight - Dry\ weight}\ x\ 100$ (Beadle et al., 1985; González & González-Vilar, 2003)
- Leaf dry matter content: $\frac{Dry\ weight}{Turgid\ weight}\ x\ 100$ (Wilson et al., 1999b)
- Specific leaf area: $\frac{Leaf\ area}{Dry\ weight}$ (Wilson et al., 1999b)
- Stomatal density: $\frac{Average\ number\ of\ \ stomata}{Area\ of\ field\ of\ view\ (mm^2)}$ (Royer, 2001)

4.3.3 Hydroclimatic data

The Climate Hazards Group InfraRed Precipitation with Stations (CHIRPS) dataset is a land-only, quasi-global rainfall dataset (50°S–50°N) that provides varying temporal and spatial resolutions depending on the region and period (Funk et al., 2015). CHIRPS data are generated through a multi-step process that merges satellite infrared cold-cloud duration data with in-situ rain-gauge measurements. CHIRPS has been extensively used in various studies (Muthoni et al., 2019; Toté et al., 2015; Obahoundje et al., 2020). On the other hand, TerraClimate is a high-resolution global climate dataset (1/24°, ~4 km) that provides monthly climate data and climatic water balance for terrestrial surfaces (Abatzoglou et al., 2018). Multiple studies have used it for climate and environmental variables assessments (Lemenkova, 2022; Araghi et al., 2023; Hanchane et al., 2023; Solaimani & Bararkhanpour; Ahmadi, 2024). For this study, annual precipitation data were extracted from CHIRPS 2.0, while other environmental variables (Vapor pressure deficit (VPD), Evapotranspiration (ET), Potential water deficit (PWD), Minimum temperature (Tmax), Maximum temperature (Tmin), and Aridity index) were obtained from TerraClimate. These variables were selected as they directly influence drought conditions and plant water availability. To capture long-term climate trends, the datasets covered 30 years (January 1994 to December 2023). A raster layer encompassing all environmental variables was generated for all the Kunene and Omusati regions. These raster layers were uploaded into QGIS 3.34, where long-term averages were calculated. Point-specific climate data for each sampling location (coordinate) were then extracted using spatial analysis tools in QGIS 3.34. The term aridity gradient is used to describe the environmental variation experienced along the north and south transects. This gradient reflects progressive differences in water availability across space, even though the mapped categories (Figures 4.1 and 4.2) simplify this variation for visual presentation. The transects intersect a range of vegetation types and geomorphological settings whose distribution is strongly shaped by these aridity differences, making the gradient a suitable basis for examining functional trait responses in the study species.

Multiple drought indices were also computed using different climate datasets and geospatial tools.

Priestley-Taylor Alpha Index (PTAI) (Nikolaou et al., 2023)

PTAI $\alpha = \frac{(\Delta + \gamma)\lambda}{\Delta} \times 0.0135\ (T_{mean} + 17.8)$ (1)

where α (alpha) is the Priestley-Taylor coefficient, Δ (delta) is the slope of the saturation vapor pressure curve, γ (gamma) is the psychrometric constant, and λ (lambda) is the latent heat of vaporization.

Temperature inputs were obtained from Terraclimate (Abatzoglou et al., 2018), and PTAI values were computed in Google Earth Engine (GEE).

The Keetch-Byram Drought Index (KBDI) (Keetch & Byram, 1968)

$$KBDI = \frac{[800 - KBDIt-1] \times [0.968 \times \mathrm{Exp}(0.875\mathrm{Tmax} + 1.5552) - 8.30}{1 + 10.88 \times \mathrm{Exp}(-0.001736\mathrm{R})} \times 10^3 \quad (2)$$

This equation was applied using ERA5-Land datasets for maximum temperature and precipitation. Data processing and index computation were conducted in GEE.

Drought Severity Index (DSI)

$$DSI = \frac{P_{obs} - P_{avg}}{PET} \quad (3)$$

where P_{obs} is observed precipitation, P_{avg} is the long-term mean precipitation, and potential Evapotranspiration (PET) was derived from TerraClimate (Abatzoglou et al., 2018). DSI was computed in QGIS 3.34 after spatially processing the dataset.

The Standard Precipitation Index (SPI) (Naresh Kumar et al., 2009)

$$SPI = \frac{P_{sum} - P_{mean}}{P_{std}} \quad (4)$$

where P_{sum} is the total precipitation for the study area, P_{mean} is the mean precipitation, and P_{std} is the standard deviation. Precipitation values were extracted, preprocessed, and averaged using GEE, with zonal statistics applied in QGIS for spatial summarization.

Evaporation Stress Index (ESI) (Anderson et al., 2011)

$$ESI = \frac{ET}{PET} \quad (5)$$

where Actual Evapotranspiration (ET) and Potential Evapotranspiration (PET) were sourced from the MODIS MOD16A2 dataset. The index was computed in GEE.

4.3.4 Data analyses

All statistical analyses were conducted separately for each species. Data processing and statistical tests were performed using IBM SPSS Statistics version 30.0.0.0 (172) (IBM Corp., 2023). Data were tested for normality using the Shapiro–Wilk test. Homogeneity of variance was checked by examining

standardized residuals plotted against standardized predicted values, which indicated constant variance. Spearman's rank correlations were used to examine associations between plant functional traits and climatic predictors. Simple and multiple linear regressions were then fitted for climatic variables that showed significant relationships in the correlation matrices. Spearman's rank correlations and variance inflation factors were used to characterise the degree of covariation among predictors.

A key analytical issue in this dataset was the expected multicollinearity among drought-related climatic variables, a well-documented feature of dryland systems. Hydroclimatic drivers such as precipitation, vapour pressure deficit, evapotranspiration, drought indices, and temperature typically co-vary along a shared moisture–energy gradient. Thus, these variables represent interconnected components of an integrated drought–heat syndrome rather than independent causal factors.

For this reason, predictors were retained in the regression models even when VIF values were high. This decision is supported by ecological modelling literature showing that in systems where predictors jointly describe a single environmental gradient, multicollinearity does not necessarily compromise inference—provided that interpretation focuses on the overall environmental complex rather than isolated effects (Dormann et al., 2013; Vanhove, 2020; Zheng et al., 2022). Removing correlated predictors can obscure meaningful ecological structure and oversimplify multi-driver drought processes (Murray et al., 2012).

Accordingly, regression outputs in this study were interpreted as trait responses to composite drought–heat conditions rather than as estimates of fully independent predictor effects (De Marco & Nóbrega, 2018; Berdugo et al., 2020). Statistical significance was evaluated at $p < 0.05$.

4.4 Results

4.4.1 Hydroclimatic gradients across the northern and southern transects

The environmental data revealed clear and coherent west–east hydroclimatic gradients in both transects (Table 4.2). In the northern transect, moisture-related variables such as precipitation, evapotranspiration, and drought indices all increased steadily eastward, indicating a gradual shift from drier to wetter conditions. Atmospheric and heat-related variables (maximum temperature, vapor pressure deficit) showed similar eastward increases, reinforcing the presence of a strong aridity gradient across the transect.

The southern transect exhibited the same directional pattern but with stronger and more consistent gradients. Moisture availability increased sharply from west to east (precipitation, evapotranspiration aridity index, and potential water deficit), while heat and atmospheric stress indicators (maximum temperature, vapour pressure deficit) also rose significantly. Minimum temperature showed only a weak positive trend. The Priestley-Taylor Alpha Index values could not be computed because one of its component variables remained constant across all sampling locations.

Table 4.2: Hydroclimatic gradients across the northern and southern transects. The table presents the coefficients of determination (R^2), slope, and *p*-value for each environmental factor. The longitudinal gradient column indicates whether a significant trend ($p < 0.05$) is present in each transect. The "consistent gradient" column highlights environmental factors that showed a significant trend in both transects.

Environmental Factor	Northern R^2	Northern Slope	Northern *p*-value	Northern long. gradient?	Southern R^2	Southern Slope	Southern *p*-value	Southern long. gradient?	Consistent Gradient?
Precipitation	0.77	16.595	< 0.001	Yes	0.88	24.399	< 0.001	Yes	Yes
Evapotranspiration (ET)	0.63	13.445	0.005	Yes	0.84	23.163	< 0.001	Yes	Yes
Vapour Pressure Deficit (VPD)	0.74	0.039	< 0.001	Yes	0.80	0.034	< 0.001	Yes	Yes
Potential Water Deficit (PWD)	0.00	1.071	0.811	No	0.57	17.946	0.008	Yes	No
Minimum Temperature (Tmin)	0.08	0.072	0.421	No	0.40	0.241	0.039	No	No
Maximum Temperature (Tmax)	0.71	0.338	0.001	Yes	0.75	0.310	< 0.001	Yes	Yes
Aridity Index	0.57	0.006	0.010	Yes	0.84	0.010	< 0.001	Yes	Yes
Palmer Drought Severity Index (PDSI)	0.80	0.280	< 0.001	Yes	0.87	0.251	< 0.001	Yes	Yes
Standardised Precipitation Index (SPI)	0.73	0.150	< 0.001	Yes	0.88	0.214	< 0.001	Yes	Yes
Evaporative Stress Index (ESI)	0.51	0.002	0.014	Yes	0.69	0.004	0.001	Yes	Yes
Keetch-Byram drought Index (KBDI)	0.01	1.943	0.780	No	0.11	-7.974	0.350	No	No

4.4.2 Correlation structure among climatic predictors

A correlation matrix was used to examine covariation among the climatic predictors included in the trait analyses (Table 4.3). As expected for arid environments, the predictors showed strong interdependence, with most drought-related variables clustering along a shared moisture–energy gradient. Precipitation was positively correlated with other moisture-related variables, including evapotranspiration, Standardised Precipitation Index, Evaporative Stress Index, Palmer Drought Severity Index, and the Aridity Index. In contrast, minimum temperature showed consistently negative correlations with precipitation, evapotranspiration, potential water deficit, Standardised Precipitation Index, Palmer Drought Severity Index, and Evaporative Stress Index, indicating that warmer nights were associated with drier conditions. Maximum temperature displayed strong positive associations with vapour pressure deficit, Palmer Drought Severity Index, Standardised Precipitation Index, evapotranspiration, and the Aridity Index. All major drought indicators were highly intercorrelated. Keetch-Byram Drought Index showed a contrasting pattern, correlating negatively with evapotranspiration, Standardised Precipitation Index, Evaporative Stress Index, and Palmer Drought Severity Index, but positively with minimum temperature. This pattern of high covariation is characteristic of dryland climates, where climatic drivers of water stress rarely act independently. VIF values confirmed the presence of substantial multicollinearity among predictors (results summarised in Appendix 4.9, Table 4.10). However, because these variables represent interacting dimensions of

dryland hydroclimate, all predictors were retained in subsequent regression models. The models were interpreted as responses to integrated drought–heat conditions rather than as partitioned, independent climatic effects.

Table 4.3: Pairwise Spearman correlation coefficients among climatic predictors. Only the lower triangular portion of the matrix is displayed to remove redundancy. Positive correlations are shown in green, negative correlations in red, and near-zero correlations in white. The intensity of the colour represents the strength of the correlation, with darker shades indicating stronger relationships. Bolded values indicate statistically significant correlations at $p < 0.05$.

	Precipitation	VPD	ET	PWD	Tmin	Tmax	Aridity Index	PDSI	SPI	ESI	KBDI
Precipitation	1.000										
Vapour pressure deficit (VPD)	**0.723**	1.000									
Evapotranspiration (ET)	**0.979**	**0.639**	1.000								
Potential water deficit (PWD)	**0.684**	0.074	**0.766**	1.000							
Minimum temperature (Tmin)	**-0.720**	-0.125	**-0.806**	**-0.845**	1.000						
Maximum temperature (Tmax)	**0.695**	**0.989**	**0.610**	0.059	-0.062	1.000					
Aridity Index	**0.961**	**0.670**	**0.959**	**0.689**	**-0.744**	**0.639**	1.000				
Palmer Drought Severity Index (PDSI)	**0.901**	**0.817**	**0.848**	**0.412**	**-0.555**	**0.774**	**0.869**	1.000			
Standardised Precipitation Index (SPI)	**0.988**	**0.713**	**0.980**	**0.684**	**-0.743**	**0.676**	**0.957**	**0.886**	1.000		
Evaporative Stress Index (ESI)	**0.918**	**0.474**	**0.927**	**0.785**	**-0.849**	**0.429**	**0.901**	**0.762**	**0.919**	1.000	
Keetch-Byram Drought Index (KBDI)	**-0.480**	0.097	**-0.552**	**-0.695**	**0.818**	0.160	**-0.490**	**-0.317**	**-0.502**	**-0.684**	1.000

4.4.3 *Terminalia prunioides*

Trait–environment relationships in *T. prunioides* differed notably between transects, with the northern transect showing generally weak climatic sensitivity and the southern transect displaying clearer patterns (Table 4.4). In the northern transect, only leaf structural investment showed meaningful responses, with higher SLA occurring at wetter sites as indicated by positive associations with evapotranspiration, Palmer Drought Severity Index, and Standardised Precipitation Index. In the southern transect, however, trait responses shifted from moisture-driven to heat- and atmospheric-drought influences. Here, SLA increased at warmer and drier atmospheric sites, correlating positively with maximum temperature and vapour pressure deficit. However, the leaf water status showed contrasting behaviour, RWC declined with drought intensity (negative associations with potential water deficit and Evaporative Stress Index) but improved under warmer night-time temperatures and elevated Keetch–Byram Drought Index. The SD exhibited the strongest climatic signal, increasing with moisture stress (positive associations with potential water deficit and Evaporative Stress Index) but declining sharply with warmer minimum temperatures and higher fire-weather conditions (negative correlations with minimum temperature and Keetch-Byram Drought Index). When transect data were pooled, the dominant climate–trait patterns remained consistent. The SLA continued to rise with vapour pressure deficit and maximum temperature, while RWC and LDMC both declined with

intensified drought (negative associations with potential water deficit and Standardised Precipitation Index), and SD maintained a strong positive response to potential water deficit.

Table 4.4: Pairwise Spearman correlation coefficients among drought-related environmental parameters and plant functional traits of *Terminalia prunioides*. Positive correlations are shown in green, negative correlations in red, and near-zero correlations in white. The intensity of the colour represents the strength of the correlation, with darker shades indicating stronger relationships. Bolded values indicate statistically significant correlations at $p < 0.05$.

	Terminalia prunioides											
	Transect North				Transect South				Pooled transects			
Environmental variables	**SLA**	**RWC**	**LDMC**	**SD**	**SLA**	**RWC**	**LDMC**	**SD**	**SLA**	**RWC**	**LDMC**	**SD**
Precipitation	0.318	-0.030	0.040	-0.199	0.1	-0.035	0.065	0.149	0.105	-0.152	0.081	0.083
Evapotranspiration (ET)	**0.355**	-0.017	0.013	-0.066	0.14	-0.095	0.025	0.271	0.102	-0.156	0.081	0.145
Vapour pressure deficit (VPD)	0.316	0.068	-0.08	-0.309	**0.37**	0.307	0.042	-0.310	**0.315**	0.188	-0.020	-0.150
Potential water deficit (PWD)	0.004	-0.231	0.225	0.128	-0.14	**-0.411**	-0.112	**0.557**	-0.197	**-0.441**	**0.293**	**0.438**
Maximum temperature (Tmax)	0.316	0.068	-0.08	-0.309	**0.410**	0.322	0.043	-0.309	**0.288**	0.167	0.030	-0.094
Minimum temperature (Tmin)	-0.178	0.112	-0.11	-0.069	0.09	**0.427**	0.147	**-0.581**	-0.019	0.218	0.030	-0.121
Aridity Index	0.266	-0.054	0.053	-0.268	0.11	-0.212	-0.040	0.244	0.072	-0.186	0.090	0.118
Palmer Drought Severity Index (PDSI)	**0.372**	0.105	-0.06	-0.294	0.02	-0.095	0.053	0.107	0.207	0.002	-0.070	-0.148
Standardised Precipitation Index (SPI)	**0.347**	0.003	0.026	-0.152	0.060	-0.068	0.062	0.203	0.117	-0.109	0.050	0.041
Evaporative Stress Index (ESI)	0.191	-0.190	0.256	-0.275	-0.02	**-0.378**	-0.110	**0.537**	0.035	**-0.247**	0.104	0.077
Keetch-Byram Drought Index (KBDI)	-0.23	-0.039	0.007	-0.087	0.110	**0.517**	0.168	**-0.737**	-0.094	**0.100**	0.148	-0.017

SLA: Specific leaf area; RWC: Relative water content; LDMC: Leaf dry matter content; SD: Stomatal density.

The regression analyses showed that climate predictors explained only modest variation in the traits of *T. prunioides*, with clearer responses emerging in the southern transect (Table 4.5). In the northern transect, SLA displayed limited climatic sensitivity, with a model including Standardised Precipitation Index, Palmer Drought Severity Index, and evapotranspiration accounting for just over 20% of its variation. Among these, wetter sites reflected by a higher Palmer Drought Severity Index had the strongest positive effect on SLA. In contrast, the southern transect showed SLA responding more to atmospheric heat and dryness than to moisture, with simple models indicating that both vapour pressure deficit and maximum temperature increased SLA. This pattern remained significant when transects were pooled, where these two variables jointly provided the strongest explanation for SLA variation.

The RWC showed no significant predictors in the northern transect, but in the southern one, it responded strongly to combined drought and temperature conditions. Nearly half of its variation was explained by a model including potential water deficit, Evaporative Stress Index, minimum temperature, and Keetch–Byram Drought Index, with RWC declining with greater moisture stress (potential water deficit, Evaporative Stress Index) but increasing with warmer night-time temperatures and higher fire-weather indices (minimum temperature, Keetch–Byram Drought Index). These moisture-stress effects remained evident in the pooled dataset, where RWC consistently decreased with potential water deficit and Evaporative Stress Index.

The SD exhibited the most pronounced climatic sensitivity, with almost 80% of its variation in the southern transect explained by predictors capturing drought severity (potential water deficit, Evaporative Stress Index) and heat-related stress (minimum temperature, Keetch-Byram Drought Index). The SD increased under higher potential water deficit but declined sharply with warmer minimum temperatures and elevated Keetch–Byram Drought Index. In the pooled data, potential water deficit alone remained an important positive predictor. LDMC showed only a weak climatic response overall, with a slight increase at drier sites (potential water deficit) detected only when the transect data were combined.

Table 4.5: Results of multiple and simple linear regression analyses between the functional traits of *Terminalia prunioides* and selected environmental predictors across transects. The table presents, for each transect and trait, the number of samples (N), the unstandardised regression coefficient (B) with the corresponding p-value in parentheses from multiple linear regression (multiple B), the unstandardised B from simple linear regression (simple B), and the coefficient of determination (R^2) with its *p*-value in parentheses.

Specific leaf area ($cm^2.g^{-1}$)				
Models	N	Multiple B (*p* value)	Simple B	R^2 (*p* value)
Transect north				
SPI + PDSI +ET	36			0.214 (0.050)
ET	36	–0.110 (0.128)	0.022	0.053 (0.178)
PDSI	36	2.737 (0.870)	2.008	0.148 (0.021)
SPI	36	8.948 (0.219)	2.666	0.082 (0.090)
Transect south				
VPD + Tmax	33			0.140 (0.105)
MaxT	33	4.340 (0.728)	2.270	0.139 (0.033)
VPD	33	–19.733 (0.868)	21.363	0.136 (0.035)
Pooled transect data				
VPD + Tmax	69			0.199 (<0.001)
VPD	69	122.162 (0.005)	16.205	0.120 (0.004)
MaxT	69	–11.780 (0.013)	1.595	0.096 (0.010)
Relative water content (%)				
Models	N	Multiple B (*p* value)	Simple B	R^2 (*p* value)
Transect north				
N/A				
Transect south				
PWD + Tmin + ESI + KBDI	33			0.498 (<0.001)
PWD	33	–0.052 (0.787)	–0.080	0.148 (0.027)
Tmin	33	3.032 (0.243)	6.086	0.219 (0.006)
ESI	33	794.591 (0.078)	–323.745	0.099 (0.074)
KBDI	33	0.170 (0.012)	0.130	0.409 (<0.001)
Pooled transect data				

PWD + ESI	69			0.214 (<0.001)
PWD	69	–0.102 (<0.001)	–0.081	0.203 (<0.001)
ESI	69	162.731 (0.330)	–267.076	0.068 (0.031)
Stomatal density (stomata/mm^2)				
Models	N	Multiple B (*p* value)	Simple B	R^2 (*p* value)
Transect north				
N/A				
Transect south				
PWD + Tmin + ESI + KBDI	33			0.797 (<0.001)
PWD	33	–0.827 (<0.001)	0.114	0.133 (0.037)
Tmin	33	–90.527 (<0.001)	–9.676	0.243 (0.004)
ESI	33	–1700.236 (<0.001)	343.601	0.049 (0.216)
KBDI	33	0.187 (0.005)	–0.135	0.194 (0.010)
Pooled transect data				
PWD	69		0.626	0.180 (<0.001)
Leaf dry matter content (%)				
Models	N	Multiple B (*p* value)	Simple B	R^2 (*p* value)
Transect north				
N/A				
Transect south				
N/A				
Pooled transect				
PWD	69		0.014	0.058 (0.047)

Temperature: Tmax (Maximum temperature); Tmin (Minimum temperature). Moisture and water balance: ET (Evapotranspiration); PWD (Potential water deficit); VPD (Vapour pressure deficit). Drought and climatic indices: SPI (Standardised Precipitation Index); PDSI (Palmer Drought Severity Index); ESI (Evaporative Stress Index); KBDI (Keetch–Byram Drought Index).

4.4.4 *Colophospermum mopane*

The functional traits of *C. mopane* showed no significant climate–trait relationships in the northern transect, but clear and consistent sensitivities in the southern transect (Table 4.6). In the southern transect, SLA declined with moisture stress, showing negative correlations with multiple drought-related variables (precipitation, potential water deficit, aridity index, Standardised Precipitation Index, Palmer Drought Severity Index, Evaporative Stress Index, evapotranspiration), while increasing with warmer conditions (minimum temperature, Keetch–Byram Drought Index). The RWC responded positively to both moisture availability and atmospheric conditions, increasing with moisture-related predictors (precipitation, evapotranspiration, aridity index, Standardised Precipitation Index) as well as heat- and dryness-related drivers (vapour pressure deficit, maximum temperature). The SD also showed strong climatic responses, rising with drought severity (potential water deficit) but decreasing with warmer or more fire-prone sites (minimum temperature, maximum temperature, vapour pressure deficit, Keetch–Byram Drought Index). When transects were pooled, these patterns

persisted. The RWC increased with both moisture-related and heat-related variables, while SD increased with potential water deficit but declined under higher minimum temperature and Keetch–Byram Drought Index.

Table 4.6: Pairwise Spearman correlation coefficients among drought-related environmental parameters and plant functional traits of *Colophospermum mopane*. Positive correlations are shown in green, negative correlations in red, and near-zero correlations in white. The intensity of the colour represents the strength of the correlation, with darker shades indicating stronger relationships. Bolded values indicate statistically significant correlations at $p < 0.05$.

	Colophospermum mopane											
	Transect North				Transect South				Pooled transects			
Environmental variables	**SLA**	**RWC**	**LDMC**	**SD**	**SLA**	**RWC**	**LDMC**	**SD**	**SLA**	**RWC**	**LDMC**	**SD**
Precipitation	0.067	0.140	0.130	0.093	**-0.482**	**0.426**	0.276	0.006	-0.197	**0.293**	0.174	0.072
Evapotranspiration (ET)	0.08	0.115	0.030	0.189	**-0.350**	**0.482**	0.326	0.207	-0.160	**0.320**	0.197	0.192
Vapour pressure deficit (VPD)	0.156	0.263	0.195	-0.061	-0.292	**0.532**	0.168	**-0.428**	-0.01	**0.442**	0.203	-0.226
Potential water deficit (PWD)	-0.01	-0.076	-0.2	0.166	**-0.449**	0.195	0.238	**0.444**	-0.21	0.127	0.156	**0.290**
Maximum temperature (Tmax)	0.156	0.263	0.195	-0.061	-0.230	**0.488**	0.14	**-0.37**	-0.003	**0.428**	0.208	-0.224
Minimum temperature (Tmin)	0.009	0.019	0.125	-0.186	**0.362**	-0.173	-0.209	**-0.49**	0.166	-0.100	-0.08	**-0.364**
Aridity Index	0.019	0.368	0.187	-0.006	**-0.441**	**0.427**	0.177	0.150	-0.2	**0.378**	0.183	0.125
Palmer Drought Severity Index (PDSI)	0.132	0.305	0.089	-0.071	**-0.454**	0.307	0.171	0.076	-0.11	**0.252**	0.081	-0.018
Standardised Precipitation Index (SPI)	0.113	0.100	0.073	0.132	**-0.459**	**0.466**	0.337	0.066	-0.17	**0.315**	0.188	0.107
Evaporative Stress Index (ESI)	0.009	-0.153	-0.13	-0.126	**-0.460**	0.282	0.238	0.285	-0.21	0.176	0.125	0.089
Keetch-Byram Drought Index (KBDI)	0.058	0.150	0.146	-0.141	**0.368**	-0.069	-0.054	**-0.61**	0.190	0.034	0.080	**-0.32**

SLA: Specific leaf area; RWC: Relative water content; LDMC: Leaf dry matter content; SD: Stomatal density.

Regression models showed that the functional traits of *C. mopane* were strongly shaped by environmental predictors in the southern transect (Table 4.7). The SLA was responsive to the hydroclimatic gradient, with the full model explaining 65.6% of its variation. The SLA declined in drier sites, showing negative effects of multiple moisture-related predictors (precipitation, evapotranspiration, potential water deficit, aridity index, Palmer Drought Severity Index, Standardised Precipitation Index, Evaporative Stress Index), while increasing in warmer or more fire-prone sites (minimum temperature, Keetch–Byram Drought Index).

RWC exhibited the strongest trait–environment relationship for this species. In the southern transect, 84.9% of its variation was explained by a combination of moisture-related predictors (precipitation, evapotranspiration, Aridity Index, Standardised Precipitation Index) and heat- or atmospheric-dryness variables (vapour pressure deficit, maximum temperature), with RWC increasing consistently across all these predictors. These patterns persisted when the transect data were pooled, where the same suite of moisture-related and heat-related predictors remained significant.

Stomatal density was also strongly explained by climatic gradients in the southern transect, with 84.2% of its variation accounted for by predictors capturing drought severity (potential water deficit) and heat-related stress (minimum temperature, maximum temperature, vapour pressure deficit, Keetch–Byram Drought Index). The SD increased in drier sites (potential water deficit) but decreased in warmer or fire-weather sites (minimum temperature, maximum temperature, vapour pressure deficit, Keetch–Byram Drought Index). In the pooled dataset, SD showed a weaker but consistent pattern,

rising with drought severity (potential water deficit) and declining in warmer sites (minimum temperature, Keetch–Byram Drought Index).

Table 4.7: Results of multiple and simple linear regression analyses between the functional traits of *Colophospermum mopane* and selected environmental predictors across transects. The table presents, for each transect and trait, the number of samples (N), the unstandardised regression coefficient (B) with the corresponding p-value in parentheses from multiple linear regression (multiple B), the unstandardised B from simple linear regression (simple B), and the coefficient of determination (R^2) with its p-value in parentheses.

Specific leaf area ($cm^2.g^{-1}$)				
Models	N	Multiple B (*p* value)	Simple B	R^2 (*p* value)
Transect north				
N/A				
Transect south				
Precipitation + ET + PWD + Tmin + aridity index + PDSI + SPI + ESI + KBDI	33			0.656 (0.001)
Precipitation	33	–0.370 (0.242)	–0.019	0.007
ET	33	0.436 (0.035)	–0.017	0.020
PWD	33	–0.910 (0.004)	–0.017	0.020
Tmin	33	–44.386 (0.027)	–0.017	0.020
Aridity Index	33	–791.710 (0.047)	–39.571	0.012
PDSI	33	57.481 (0.001)	–0.798	0.008
SPI	33	15.948 (0.315)	–2.134	0.008
ESI	33	–1303.040 (0.009)	–101.147	0.008
KBDI	33	0.002 (0.984)	0.019	0.015
Pooled transect data				
N/A				
Relative water content (%)				
Models	N	Multiple B (*p* value)	Simple B	R^2 (*p* value)
Transect north				
N/A				
Transect south				
Precipitation + VPD + ET + Tmax + Aridity Index + SPI	33			0.849 (<0.001)
Precipitation	33	–2.303 (<0.001)	0.078	0.178 (0.015)
VPD	33	985.640 (<0.001)	66.758	0.274 (0.002)
ET	33	–0.267 (0.017)	0.095	0.249 (0.003)

Tmax	33	–94.517 (<0.001)	6.854	0.261 (0.002)
Aridity Index	33	–41.154 (0.827)	177.699	0.188 (0.012)
SPI	33	286.000 (<0.001)	9.942	0.222 (0.006)
Pooled transect data				
Precipitation + ET+ Tmax + VPD + Aridity index + PDSI + SPI	69			0.402 (<0.001)
Precipitation	69	–0.490 (0.004)	0.078	0.178 (0.015)
ET	69	0.213 (0.029)	0.095	0.249 (0.003)
Tmax	69	2.573 (0.773)	6.854	0.261 (0.002)
VPD	69	25.028 (0.774)	66.758	0.274 (0.002)
Aridity Index	69	254.648 (0.062)	177.699	0.188 (0.012)
PDSI	69	–3.469 (0.377)	3.410	0.083 (0.017)
SPI	69	24.538 (0.200)	9.942	0.222 (0.006)
Stomatal density (stomata/mm^2)				
Models	N	Multiple B (*p* value)	Simple B	R^2 (*p* value)
Transect north				
N/A				
Transect south				
VPD + Tmax + PWD + Tmin + KBDI	33			0.842 (<0.001)
VPD	33	–3490.597 (<0.001)	–159.189	0.081 (0.107)
Tmax	33	339.433 (<0.001)	–17.739	0.091 (0.087)
PWD	33	–1.794 (0.009)	0.372	0.178 (0.014)
Tmin	33	-212.882 (<0.001)	–29.650	0.288 (0.001)
KBDI	33	0.856 (<0.001)	–0.350	0.166 (0.019)
Pooled transect data				
PWD + Tmin + KBDI	69			0.168 (0.007)
PWD	69	0.013 (0.945)	0.305	0.129 (0.002)
Tmin	69	–27.523 (0.117)	–25.618	0.167 (<0.001)
KBDI	69	0.050 (0.766)	–0.273	0.092 (0.011)
Leaf dry matter content (%)				
Models	N	Multiple B (*p* value)	Simple B	R^2 (*p* value)
Transect north				
N/A				
Transect south				
N/A				
Pooled transect				
N/A				

Temperature: Tmax (Maximum temperature); Tmin (Minimum temperature). Moisture and water balance: ET (Evapotranspiration); PWD (Potential water deficit); VPD (Vapour pressure deficit). Drought and climatic indices: PDSI (Palmer Drought Severity Index); SPI (Standardised Precipitation Index); ESI (Evaporative Stress Index); KBDI (Keetch–Byram Drought Index).

4.4.5 *Catophractes alexandri*

The functional traits of *C. alexandri* showed contrasting climate–trait patterns between the northern and southern transects, with far stronger relationships emerging in the southern transect (Table 4.8). In the northern transect, responses were limited, although SLA increased in warmer and drier sites, showing positive associations with heat- and atmospheric-dryness variables (vapour pressure deficit, maximum temperature, Aridity Index, Palmer Drought Severity Index, Keetch–Byram Drought Index) and declining with stronger drought (potential water deficit). LDMC showed the opposite pattern, increasing with drought severity (potential water deficit) but decreasing in warmer or fire-prone sites (minimum temperature, Keetch–Byram Drought Index). The SD exhibited only a weak signal, rising slightly with drought stress (potential water deficit).

In the southern transect, climatic sensitivities were much stronger and more consistent. SLA declined across all drought- and moisture-related gradients (precipitation, evapotranspiration, potential water deficit, Aridity Index, Palmer Drought Severity Index, Standardised Precipitation Index, Evaporative Stress Index) and also decreased in warmer and drier atmospheric sites (vapour pressure deficit, maximum temperature), while increasing under warmer minimum temperatures and higher Keetch–Byram Drought Index. RWC showed limited responses in this transect, increasing only with evapotranspiration. LDMC was highly responsive, rising with a broad suite of moisture-related predictors (precipitation, evapotranspiration, potential water deficit, Aridity Index, Palmer Drought Severity Index, Standardised Precipitation Index, Evaporative Stress Index) and declining in warmer or fire-prone sites (minimum temperature, Keetch–Byram Drought Index). The SD was similarly constrained by atmospheric and drought stress, declining with heat-related variables (vapour pressure deficit, maximum temperature, Keetch–Byram Drought Index).

When transects were combined, these patterns remained evident. SLA and LDMC were consistently shaped by moisture-related gradients (evapotranspiration, potential water deficit, Aridity Index, Standardised Precipitation Index, Evaporative Stress Index), while both traits increased in warmer sites (minimum temperature, Keetch–Byram Drought Index). The SD showed a weaker but still significant pattern, declining with atmospheric dryness (vapour pressure deficit) and increasing with drought severity (potential water deficit).

Table 4.8: Pairwise Spearman correlation coefficients among drought-related environmental parameters and plant functional traits of *Catophractes alexandri*. Positive correlations are shown in green, negative correlations in red, and near-zero correlations in white. The intensity of the colour represents the strength of the correlation, with darker shades indicating stronger relationships. Bolded values indicate statistically significant correlations at $p < 0.05$.

	Catophractes alexandri											
	Transect North				Transect South				Pooled transects			
Environmental variables	**SLA**	**RWC**	**LDMC**	**SD**	**SLA**	**RWC**	**LDMC**	**SD**	**SLA**	**RWC**	**LDMC**	**SD**
Precipitation	0.249	0.029	-0.1	0.070	**-0.650**	0.220	**0.534**	-0.250	-0.24	0.003	**0.351**	0.105
Evapotranspiration (ET)	0.057	0.085	0.118	0.205	**-0.644**	**0.400**	**0.660**	-0.140	**-0.31**	0.068	**0.454**	0.185
Vapour pressure deficit (VPD)	**0.508**	-0.022	-0.29	-0.267	**-0.475**	0.085	0.214	**-0.463**	0.051	0.084	0.060	**-0.295**
Potential water deficit (PWD)	**-0.45**	0.114	**0.514**	**0.393**	**-0.487**	0.210	**0.597**	0.079	**-0.44**	-0.144	**0.541**	**0.522**
Maximum temperature (Tmax)	**0.508**	-0.022	-0.29	-0.267	**-0.475**	0.085	0.214	**-0.463**	0.040	0.014	0.026	-0.245
Minimum temperature (Tmin)	0.020	-0.105	**-0.44**	-0.243	**0.514**	-0.247	**-0.586**	-0.120	**0.327**	-0.207	**-0.560**	-0.188
Aridity Index	**0.457**	0.119	0.044	-0.064	**-0.668**	0.232	**0.453**	-0.102	**-0.27**	0.043	**0.367**	0.144
Palmer Drought Severity Index (PDSI)	**0.549**	0.210	-0.12	-0.229	**-0.600**	0.138	**0.458**	-0.331	0.080	0.093	0.173	-0.219
Standardised Precipitation Index (SPI)	0.210	0.088	-0.1	0.154	**-0.663**	0.301	**0.569**	-0.202	**-0.32**	0.105	**0.368**	0.086
Evaporative Stress Index (ESI)	0.180	-0.173	0.022	-0.130	**-0.668**	0.271	**0.533**	0.111	-0.25	0.055	**0.394**	0.111
Keetch-Byram Drought Index (KBDI)	**0.409**	0.070	**-0.44**	-0.160	**0.493**	0.231	**-0.405**	**-0.401**	**0.370**	-0.202	**0.363**	-0.116

SLA: Specific leaf area; RWC: Relative water content; LDMC: Leaf dry matter content; SD: Stomatal density.

Regression analyses revealed strong climatic controls on trait variation in *C. alexandri*, with clearer responses in the southern transect (Table 4.9). In the northern transect, SLA was strongly shaped by both drought- and heat-related predictors, with 65.4% of its variation explained by a model incorporating moisture stress (potential water deficit) and atmospheric or temperature-related variables (vapour pressure deficit, Palmer Drought Severity Index, Keetch–Byram Drought Index, Aridity Index). The SLA declined in drier sites (potential water deficit) but increased in warmer or fire-prone sites (vapour pressure deficit, Palmer Drought Severity Index, Keetch–Byram Drought Index, Aridity Index). In the southern transect, SLA responses were even stronger, with 88.6% of its variation explained by a broad suite of climatic predictors. The SLA consistently declined across drier and more drought-stressed sites (precipitation, evapotranspiration, potential water deficit, Aridity Index, Palmer Drought Severity Index, Standardised Precipitation Index, Evaporative Stress Index) and in warmer and drier atmospheric sites (vapour pressure deficit, maximum temperature), while increasing only in warmer minimum temperature sites (minimum temperature) and locations with higher Keetch–Byram Drought Index. In the pooled dataset, SLA showed a weaker but consistent pattern, decreasing with moisture- and drought-related gradients (evapotranspiration, potential water deficit, Aridity Index, Standardised Precipitation Index) and increasing in warmer sites (minimum temperature, Keetch–Byram Drought Index).

The SD was also strongly climate sensitive. In the northern transect, potential water deficit alone explained 30.9% of SD variation, with SD increasing in drier sites. In the southern transect, a model including atmospheric-dryness and heat-related variables (vapour pressure deficit, maximum temperature, Keetch–Byram Drought Index) explained 29.1% of SD variation, with SD declining in warmer and drier atmospheric sites. Across pooled sites, SD was explained by vapour pressure deficit and potential water deficit, decreasing with atmospheric dryness (vapour pressure deficit) but increasing with drought severity (potential water deficit).

The LDMC showed moderate but consistent climatic sensitivity. In the northern transect, LDMC declined in warmer and more fire-prone sites (minimum temperature, Keetch–Byram Drought Index). In the southern transect, 54.6% of LDMC variation was explained by both moisture-related predictors (precipitation, evapotranspiration, potential water deficit, Aridity Index, Palmer Drought Severity Index, Standardised Precipitation Index, Evaporative Stress Index) and warmer or fire-related gradients (Keetch–Byram Drought Index). In pooled data, LDMC maintained these relationships, increasing with moisture-related predictors and decreasing with warmer sites (minimum temperature) and fire-weather indices (Keetch–Byram Drought Index).

Table 4.9: Results of multiple and simple linear regression analyses between the functional traits of *Catophractes alexandri* and selected environmental predictors across transects. The table presents, for each transect and trait, the number of samples (N), the unstandardised regression coefficient (B) with the corresponding p-value in parentheses from multiple linear regression (multiple B), the unstandardised B from simple linear regression (simple B), and the coefficient of determination (R^2) with its p-value in parentheses.

Specific leaf area ($cm^2.g^{-1}$)				
Models	N	Multiple B (*p* value)	Simple B	R^2 (*p* value)
Transect north				
VPD + PWD + Aridity index + PDSI + KBDI	27			0.654 (<0.001)
VPD	27	–36.489 (0.045)	19.074	0.317 (0.002)
PWD	27	–0.166 (<0.001)	–0.040	0.198 (0.020)
Aridity Index	27	39.613 (0.796)	88.460	0.146 (0.050)
PDSI	27	7.046 (0.079)	2.481	0.259 (0.007)
KBDI	27	–0.071 (0.017)	0.029	0.146 (0.049)
Transect south				
Precipitation + VPD + ET + Tmax + Aridity index + PDSI + SPI + ESI + KBDI + PWD				0.886 (<0.001)
Precipitation	33	–0.351 (0.133)	–0.044	0.271 (0.002)
VPD	33	289.015 (0.091)	–26.098	0.195 (0.010)
ET		0.339 (0.258)	–0.030	0.110 (0.010)
Tmax	33	–51.884 (0.001)	–2.702	0.189 (0.012)
Aridity index	33	486.541 (0.009)	–105.950	0.313 (<0.001)
PDSI	33	65.630 (0.002)	–4.206	0.261 (0.002)
SPI	33	8.958 (0.793)	–5.163	0.293 (0.001)
ESI	33	–2972.815 (<0.001)	–262.438	0.333 (<0.001)
KBDI	33	0.079 (0.098)	0.023	0.065 (0.152)
PWD	33	–0.280 (0.171)	–0.045	0.240 (0.004)
Pooled transect data				
ET + PWD + Tmin +Aridity index + SPI + KBDI	60			0.226 (<0.001)
ET	60	0.057 (0.720)	–0.030	0.110 (0.010)
PWD	60	–0.050 (0.076)	–0.037	0.217 (<0.001)
Tmin	60	1.961 (0.657)	2.428	0.157 (0.002)
Aridity Index	60	44.615 (0.596)	–58.014	0.089 (0.021)
SPI	60	–5.524 (0.652)	–2.768	0.080 (0.028)
KBDI	60	–0.023 (0.599)	0.024	0.083 (0.026)
Relative water content (%)				
Models	N	Multiple B (*p* value)	Simple B	R^2 (*p* value)

Transect north				
N/A				
Transect south				
ET	33		0.035	0.070 (0.137)
Pooled transect data				
N/A				
Stomatal density (stomata/mm^2)				
Models	N	Multiple B (*p* value)	Simple B	R^2 (*p* value)
Transect north				
PWD	27		0.573	0.309 (0.003)
Transect south				
VPD + Tmax + KBDI	33			0.291 (0.017)
VPD	33	252.862 (0.455)	–131.127	0.267 (0.002)
Tmax	33	–69.631 (0.352)	–14.054	0.277 (0.002)
KBDI	33	0.041 (0.649)	–0.042	0.012 (0.549)
Pooled transect data				
VPD + PWD	60			0.377 (<0.001)
VPD	60	–147.535 (0.013)	–162.321	0.087 (0.022)
PWD	60	0.520 (<0.001)	0.533	0.305 (<0.001)
Leaf dry matter content (%)				
Models	N	Multiple B (*p* value)	Simple B	R^2 (*p* value)
Transect north				
PWD + Tmin + KBDI	27			0.240 (0.092)
PWD	27	–0.013 (0.685)	0.019	0.205 (0.018)
Tmin	27	–1.296 (0.421)	–1.410	0.200 (0.019)
KBDI	27	–0.015 (0.364)	–0.016	0.210 (0.016)
Transect south				
Precipitation + ET + PWD + Aridity Index + PDSI + SPI + ESI + KBDI	33			0.546 (0.007)
Precipitation	33	–0.099 (0.693)	0.023	0.173 (0.016)
ET	33	0.278 (0.141)	0.029	0.260 (0.002)
PWD	33	–0.135 (0.241)	0.034	0.313 (<0.001)
Aridity Index	33	–131.458 (0.530)	49.657	0.156 (0.023)
PDSI	33	–20.403 (0.327)	0.741	0.003 (0.744)
SPI	33	27.094 (0.364)	2.733	0.185 (0.013)
ESI	33	–299.273 (0.585)	133.294	0.195 (0.010)
KBDI	33	–0.091 (0.110)	–0.021	0.122 (0.046)
Pooled transect				
Precipitation + ET + PWD + Tmin + Aridity Index + SPI + ESI + KBDI	60			0.470 (<0.001)
Precipitation	60	–0.121 (0.171)	0.017	0.106 (0.011)
ET	60	0.313 (0.001)	0.024	0.191 (<0.001)
PWD	60	–0.024 (0.127)	0.025	0.269 (<0.001)

Tmin	60	5.136 (0.075)	–1.963	0.281 (<0.001)
Aridity Index	60	–49.453 (0.280)	41.107	0.123 (0.006)
SPI	60	–8.202 (0.339)	2.016	0.117 (0.008)
ESI	60	–73.892 (0.581)	106.025	0.140 (0.003)
KBDI	60	–0.065 (0.016)	–0.018	0.124 (0.006)

Temperature: Tmax (Maximum temperature); Tmin (Minimum temperature). Moisture and water balance: ET (Evapotranspiration); PWD (Potential water deficit); VPD (Vapour pressure deficit). Drought and climatic indices: SPI (Standardised Precipitation Index); PDSI (Palmer Drought Severity Index); ESI (Evaporative Stress Index); KBDI (Keetch–Byram Drought Index).

4.5 Discussion

The results demonstrated that drought-related environmental factors significantly influence the functional traits of the three dominant woody plants in northwestern Namibia, with all three species showing consistently stronger climate–trait relationships in the southern transect than in the northern transect. These patterns occurred against a backdrop of strong hydroclimatic gradients and high interdependence among drought variables. The southern transect's clearer moisture gradient made climate–trait relationships more detectable, whereas the northern transect's greater ecological heterogeneity and weaker gradient likely dampened trait responses. This pattern was evident across both the correlation matrices and regression models, which jointly formed the basis of our interpretations.

The differences between transects are ecologically consistent with the underlying landscape context. The northern transect spans more heterogeneous terrain and ecosystem types, ranging from rocky uplands to variable soil substrates (Strohbach et al., 2025). Such heterogeneity, together with shallow stony soils and high thermal exposure, likely increased fine-scale variability in water availability and introduced confounding factors that weakened climate–trait correlations (Zhang et al., 2020; Dao et al., 2025). In contrast, the southern transect, especially around the Hoarusib floodplain, may experience episodic moisture inputs and more uniform soil conditions, which enhance the detectability of moisture-driven trait responses. This overall pattern aligns with earlier findings that fine-scale heterogeneity weakens trait–environment relationships in drylands (Lázaro-Nogal et al., 2015; Matheny, 2021).

Across species, the functional traits followed broadly expected patterns along the drought gradients. SLA generally declined in drier sites, LDMC increased under greater aridity, RWC decreased with intensifying water stress, and SD adjusted in ways consistent with stomatal regulation under drought. Occasional deviations, such as transient increases in SLA under high atmospheric dryness, reflected short-term plastic adjustments rather than contradictions of ecological theory. These broad patterns provided the backdrop for understanding how each species responded individually to the aridity gradient.

Terminalia prunioides exhibited notable trait plasticity across aridity gradient, particularly in SLA and RWC. In the northern transect, SLA increased in wetter sites (Standardised Precipitation Index and Palmer Drought Severity Index), consistent with evidence that mesic conditions favour thinner, more acquisitive leaves to maximise carbon gain (Costa-Saura et al., 2016). In the southern transect, SLA unexpectedly increased with increasing vapour pressure deficit, suggesting transient acquisitive growth during early atmospheric drought, a pattern also observed in Mediterranean grasses (Wellstein et al., 2017). Declines in RWC with increasing potential water deficit and Evaporative Stress

Index indicated reduced tissue hydration, characteristic of water stress responses (Sapes & Sala, 2020). The rise in SD in drier sites supported the role of stomatal control in regulating transpirational loss (Blackman et al., 2019). Slight increases in LDMC with dryness aligned with the expectation that greater structural investment enhances drought tolerance (Onoda et al., 2017; Blumenthal et al., 2020). This physiological and structural flexibility resembles patterns described for *Senna candolleana* in environmentally heterogeneous drylands, where high plasticity conferred improved drought performance (Lázaro-Nogal et al., 2015). In this study, *T. prunioides* appeared capable of alternating between acquisitive and conservative strategies depending on moisture availability, supporting its resilience and suitability for restoration in variable dryland ecosystems.

Colophospermum mopane displayed a more conservative strategy, with no significant trait–climate associations in the northern transect but clear shifts in the south. The decline of SLA at drier sites supports global findings that thicker, denser leaves promote drought resistance in arid environments (Costa-Saura et al., 2016). Increases in RWC in warmer and wetter southern sites suggested efficient hydration maintenance, consistent with its deep-rooting system and stomatal control capabilities (Veenendaal et al., 2008; Krug, 2017). The LDMC remained stable across gradients, reflecting low plasticity and strong structural tolerance typical of long-lived woody savanna species (Makhado et al., 2014a; Wigley et al., 2016). Populations in stable yet chronically arid environments often rely on fixed conservative traits rather than plastic adjustments (Lázaro-Nogal et al., 2015), which aligns with *C. mopane*'s behaviour in the northern transect. Its limited plasticity, coupled with hydraulic and physiological drought tolerance, likely supports persistence in consistently dry habitats (Makhado et al., 2014b; Krug, 2017).

Catophractes alexandri displayed stronger structural than physiological responses to drought. In the southern transect, SLA declined with most dryness indicators (vapour pressure deficit, evapotranspiration, maximum temperature), signalling investment in thicker leaves to reduce water loss (Griebel et al., 2023). The LDMC increased with aridity, reinforcing leaf toughness and persistence (Onoda et al., 2017). The RWC showed only weak associations with environmental factors, suggesting limited physiological buffering capacity, while SD declined with increasing vapour pressure deficit and heat, highlighting a water-saving strategy through reduced gas exchange (Grossiord et al., 2020). These patterns aligned with evidence that many arid-adapted shrubs rely more on structural modification than physiological regulation to withstand drought (Xu et al., 2022). Accordingly, *C. alexandri* seemed to follow a structurally conservative drought-resistance strategy that enables persistence in moderately arid zones but may limit performance under prolonged or severe drought.

In the context of a progressively drier and more variable climate, these findings suggested that *T. prunioides* may be the most adaptable species due to its high phenotypic plasticity, allowing rapid trait adjustments to changing moisture regimes. *C. mopane*, while less plastic, is likely to remain dominant under sustained aridity owing to its conservative hydraulic control and proven drought tolerance. In contrast, *C. alexandri* may be more vulnerable under intensifying drought, as its reliance on structural modification without strong physiological buffering limits its capacity to cope with prolonged water stress. Collectively, these results indicate that both *T. prunioides* and *C. mopane* possess functional traits conducive to persistence under climate change, but through contrasting pathways (plastic flexibility versus conservative tolerance).

4.6 Conclusion

This study provided the first integrated assessment of how selected leaf functional traits respond to long-term aridity gradient in three dominant woody species of northwestern Namibia. Despite occupying the same arid landscape, *T. prunioides*, *C. mopane*, and *C. alexandri* displayed distinct adaptive strategies. *T. prunioides* showed high trait plasticity across both transects, indicating a strong capacity to track moisture variability and tolerate fluctuating climatic conditions. *C. mopane* demonstrated a conservative, hydraulically regulated strategy, with strong trait–climate coupling only in the south, suggesting that this species adjusts physiologically when drought becomes sufficiently acute. In contrast, C. *alexandri* relied mainly on structural modification rather than physiological flexibility, indicating a more rigid drought strategy and potential vulnerability during prolonged stress. These contrasting drought-response mechanisms highlighted the influence of fine-scale ecological heterogeneity on trait expression in Namibia's drylands. They emphasised that drought tolerance cannot be generalised even within a single dryland region, and that restoration planning must account for both species-level strategies and local environmental filters. Furthermore, the findings provided a functional foundation for selecting climate-resilient native species for dryland restoration. Species with high plasticity (*T. prunioides*) or consistent hydraulic control (*C. mopane*) may be ideal for rehabilitation efforts in degraded landscapes, whereas structurally rigid species (*C. alexandri*) may be better suited for moderately arid. As Namibia faces intensifying drought under climate change, this study contributed crucial quantitative data for conservation prioritisation, ecological forecasting, and the development of trait-based restoration frameworks tailored to arid and semi-arid environments.

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4.9 Appendix

Table 4.10. Variance Inflation Factors (VIFs) for full multiple-regression models of leaf traits versus hydroclimatic predictors.

Predictor	**VIF**
Precipitation	1490.78
Vapor pressure deficit	1367.88
Evapotranspiration	3079.31
Potential water deficit	303.22
Minimum temperature	1012.24
Aridity index	30.31
Palmer drought severity index	147.21
Standardised precipitation index	473.61
Evaporative stress index	40.67
Keetch–Byram drought index	80.24

Chapter 5: Synthesis

5.1 Background

Dryland ecosystems cover more than 40% of the Earth's terrestrial surface and support over two billion people, yet they rank among the ecosystems most vulnerable to climate change (Feng et al., 2020; Martinez-Valderrama et al., 2023). Intensifying aridity, rising temperatures, and declining soil moisture are reshaping plant community composition and undermining the ecological functioning of these landscapes. As pressures mount, dryland restoration has emerged as a critical pathway for strengthening ecosystem resilience and safeguarding the livelihoods of communities dependent on these fragile systems (Yirdaw et al., 2017). The urgency of this challenge is reflected in the declaration of 2021–2030 as the United Nations (UN) Decade on Ecosystem Restoration, which calls for effective, evidence-based strategies capable of reversing land degradation at scale (UNEP & FAO, 2021).

Despite this global momentum, restoration outcomes in African drylands remain inconsistent. Low and erratic rainfall, poor soil fertility, and climatic variability frequently undermine planting efforts and result in low survival rates (Svejcar & Kildisheva, 2017; Ben-Enukora & Ejem, 2024). Trait-based restoration (TBR) offers a promising framework for addressing this challenge by linking species selection to measurable plant traits that influence establishment, survival, and ecosystem function (Laughlin, 2014; Balazs et al., 2020). Traits associated with resource acquisition can promote rapid growth and drought avoidance, whereas resource-conserving traits facilitate persistence under long-term moisture stress (Garbowski et al., 2020). In highly variable and water-limited environments, selecting species based on such functional traits increases the likelihood of long-term establishment, ecological stability, and resilience under intensifying drought (Del Campo et al., 2020).

Despite its strong theoretical foundation, TBR remains rarely applied in African drylands (Violle et al., 2007; Merchant et al., 2023). The conceptual review undertaken in this thesis (Chapter 2) showed that several structural and scientific barriers hinder its adoption. These include the scarcity of trait data for native African species, the limited integration of Indigenous Ecological Knowledge (IEK) into trait-based frameworks, and short donor-driven project cycles that prevent the long-term monitoring required to validate trait–performance relationships (Karlsson et al., 2007; Eviner & Hawkes, 2008; Hortal et al., 2015; Kattge et al., 2020). As a result, restoration initiatives frequently rely on species chosen for socio-economic value rather than ecological suitability, with uncertain success under future climatic conditions (Sacande et al., 2015). This disconnect underscores the need for context-specific ecological data on drought-tolerant traits of indigenous species, data that are largely absent for Namibia and much of Africa. Addressing this gap formed the scientific motivation for the empirical components of this thesis, which aimed to generate the foundational trait and physiological evidence needed to advance trait-based restoration in one of the world's most arid regions.

The chapters of this thesis generated new insights into plant drought strategies in Namibia, expanded functional strategies and traits where previously little existed, and provided an empirical foundation for trait-based ecological restoration in drylands. This synthesis chapter integrates the findings, highlights the overarching contributions, and outlines a more mechanistic, ecology-driven pathway for restoration in Namibia and comparable arid regions.

5.2.3 Expanding Namibia's CAM flora

Chapter 3 produced the first comprehensive assessment of CAM in Namibia with several previously unstudied members of the Aizoaceae native to the Greater Cape Floristic Region of South Africa. By screening 273 species across 34 families, the study substantially expanded the known distribution of CAM in the country. Nearly 26 genera, particularly within Aizoaceae, Apocynaceae, Asphodelaceae, and Didiereaceae, were newly confirmed as capable of CAM. Several C_3-type taxa displayed environmentally inducible nocturnal acid accumulation, indicating facultative CAM. These findings are significant for two main reasons. First, the synthesis of newly generated $\delta^{13}C$ data together with published records suggested that approximately 12% of Namibia's vascular flora exhibit CAM, representing an enriched CAM component relative to the global estimate of nearly 7% (Gilman et al., 2023). Second, the prominence of CAM in Namibia is ecologically meaningful as its prevalence reflects the country's long evolutionary history of aridity, the influence of fog-dependent microhabitats along the Namib Desert, and the persistence of stable succulent biomes that favour the diversification and survival of CAM taxa.

5.2 Integrating the conceptual and empirical dimensions of the thesis

The three chapters (2 to 4) of this thesis, although methodologically and thematically distinct, converge on a central ecological question: *how do plant species persist and function under the chronic water limitations characteristic of Namibia's drylands, and how can this knowledge be mobilised to inform restoration?*

5.2.1 Conceptual foundation: Challenges and opportunities for TBR in Africa

Chapter 2 established the broader scientific and policy context for this study. It revealed that although functional TBR offers an evidence-based framework for matching species to site conditions (Laughlin, 2014; Balazs et al., 2020; Funk et al., 2024), its uptake in Africa remains extremely limited (Ben-Enukora & Ejem, 2024). Multiple barriers, including limited trait data for native species, weak integration of Indigenous Ecological Knowledge (IEK), short project cycles, and insufficient long-term monitoring, have constrained its application (Karlsson et al., 2007; Carlucci et al., 2020; Kattge et al., 2020; Merchant et al., 2023).

This conceptual analysis provided three key insights that underpin the empirical work:

1. Ecological suitability is rarely evaluated in restoration planning.
   Species are often chosen for socio-economic reasons (shade, fodder, fast growth) rather than their functional traits or drought-response strategies (Violle et al., 2007; Sacande et al., 2015; Sacande & Berrahmouni, 2016; Kalilou, 2021).
2. African flora are underrepresented in global trait databases.
   Without context-specific trait data, practitioners depend on generalised assumptions that often fail under extreme aridity (Eviner & Hawkes, 2008; Kattge et al., 2020).
3. There is an urgent need for mechanistic, drought-relevant data.
   This includes both physiological pathways (e.g., CAM) and measurable leaf traits (e.g., SLA, LDMC, SD).

These conceptual gaps provided the rationale for Chapters 3 and 4: to generate African-relevant physiological and functional trait data that can directly feed into restoration planning

5.3 CAM physiology as evidence of drought adaptation in Namibia

5.3.2 CAM species as restoration candidates

CAM species demonstrate high WUE, the ability to maintain cellular turgor during prolonged drought, and a remarkable capacity to establish on nutrient-poor or disturbed substrates. These advantages arise from nocturnal CO_2 uptake, tight stomatal regulation, and succulent tissues that buffer against desiccation (Winter & Holtum, 2002; Winter et al., 2015). CAM plants are therefore able to persist under extreme aridity and severe soil limitations where many C_3 species show poor survival or fail to establish (Nobel, 1996; Cushman & Bohnert, 1999; Gremer et al., 2013; Winter, 2019). These traits make CAM taxa ideal candidates for restoration in arid and semi-arid landscapes, where conventional species often struggle to establish. Empirical evidence from dryland restoration initiatives supports this potential. In south-eastern Algeria, long-term *Opuntia ficus-indica* plantations (5–20 years) substantially increased native vegetation cover, abundance, and species diversity compared to adjacent degraded rangelands (Neffar et al., 2013). Similar benefits have been documented in central Mexico, where the introduction of *O. ficus-indica* into degraded forest systems maintained soil organic carbon and microbial activity at levels comparable to intact forest, whereas maize cultivation in the same region led to losses of nearly 70% of soil organic carbon (Bautista-Cruz et al., 2018). In South Africa, large-scale restoration efforts within the Subtropical Thicket Restoration Programme have demonstrated the capacity of the CAM shrub *Portulacaria afra* to rehabilitate degraded thicket ecosystems. More than 20 million cuttings have been planted since 2016, achieving survival rates of approximately 43% in the first year and promoting long-term recovery of soil properties, vegetation structure, and carbon stocks that may exceed 245 t C ha^{-1} after several decades (van der Vyver et al., 2013; Mills & Robson, 2017).

CAM species, therefore, offer considerable practical value in restoring ecological function across diverse dryland environments. Many Aizoaceae taxa, including species in *Dinteranthus*, *Gibbaeum*, and *Amphibolia*, can act as natural pioneers on bare gravel plains, where their shallow root systems trap fine sediments and initiate early soil development on otherwise barren substrates. Along the coastal Namib, fog-dependent CAM species such as *Wooleya*, *Oophytum*, and *Mestoklema* may be particularly valuable in microhabitats where atmospheric moisture is a key driver of plant survival. In ultra-arid regions receiving less than 100 mm of annual rainfall, CAM-rich didiereoid and asphodeloid succulents may provide durable structural cover and long-term persistence in landscapes where woody C_3 species typically fail to establish. These examples illustrate how CAM taxa can form a robust foundation for designing restoration interventions matched to the extreme climatic constraints. However, each of these scenarios will require targeted field trials to evaluate their effectiveness in practice.

5.4 Functional trait strategies along environmental gradients

5.4.1 Diversity of drought strategies in Namibian woody forage species

Chapter 4 provided the first systematic measurement of leaf functional traits across a climatic gradient in northwest Namibia, focusing on *Colophospermum mopane*, *Catophractes alexandri*, and *Terminalia prunioides*. The results demonstrated that even widely distributed arid-zone species adopt contrasting drought-response strategies. *T. prunioides* displayed strong phenotypic plasticity, adjusting traits such as SLA and SD in response to environmental conditions, suggesting high suitability for restoration in areas with variable rainfall or increasing climatic uncertainty. In contrast, *C. alexandri* exhibited

structurally conservative drought tolerance, characterised by high LDMC, making it well-suited to stable arid landscapes. *C. mopane* showed notable trait stability across the gradient, reflecting physiological robustness under multiple stressors. This species may be ideal for a long-term restoration in nutrient-poor or highly degraded environments.

5.4.2 Integrating functional traits to guide species selection for dryland restoration

These findings of Chapter 4 demonstrated how functional trait measurements can be translated into actionable restoration strategies across different environmental conditions in Namibia. In areas with highly variable rainfall (200–400 mm), species with high phenotypic plasticity may be ideal, as they can adjust their resource-use traits in response to fluctuating soil moisture. *T. prunioides*, with its flexible SLA and stomatal traits, may be an ideal candidate for such zones. Severely degraded rangelands, which experience intense grazing pressure and poor soil fertility, may be better suited for species with high LDMC and conservative resource-use strategies, such as *C. alexandri*. Nutrient-poor or skeletal soils, even those that remain after bush-clearing or long-term degradation, are more likely to support species with stable traits and proven persistence under harsh conditions, exemplified by *C. mopane*. In situations requiring rapid pioneer colonisation of bare substrates, restoration can begin with CAM succulents, which can initiate soil development and microhabitat formation, after which more demanding woody species may be introduced. Although these examples provide a promising framework for trait-informed restoration, each scenario warrants targeted field investigations to validate their effectiveness and understand species performance under real-world restoration conditions. Importantly, the long-term success of TBR depends on expanding trait datasets for native dryland species in Africa. Therefore, the broader and more context-specific these databases become, the more accurately species can be matched to site conditions. This study offered an initial contribution toward that goal, but its value will grow only if followed by many more trait-focused investigations across diverse arid landscapes.

5.5 Theoretical and conceptual contributions

This research contributed to three intersecting areas of ecological theory (trait-based restoration (TBR), plant functional ecology, and resilience theory in dryland systems) by demonstrating how physiological, functional, and conceptual evidence can be integrated to strengthen both theory and application. The findings show that understanding drought adaptation in Namibia requires attention to traits operating across different temporal scales: long-term evolutionary pathways such as CAM, and shorter-term functional adjustments expressed along environmental gradients.

5.5.1 Extending functional trait-based restoration (TBR)

The TBR argues that species selection should be guided by functional traits linked to survival, performance, and ecosystem processes, rather than by taxonomic identity or general species lists (Laughlin, 2014; Aubin et al., 2024). However, most applications of TBR in drylands have focused narrowly on assumed uniform drought syndromes (Blumenthal et al., 2020; Butterfield et al., 2023).

In this study, the $\delta^{13}C$ and titratable-acidity survey revealed a far broader distribution of CAM and intermediate photosynthetic pathways in Namibia than previously recognised. This demonstrated that photosynthetic pathway diversity, particularly the presence of CAM, constitutes a critical but underutilised dimension of TBR. CAM reflects a deep evolutionary adaptation that enables persistence in semi–arid and arid conditions, and its integration into TBR may provide a mechanistic basis for

selecting species capable of maintaining productivity under water limitations. Practically, this expanded the pool of native species suitable for restoration in drylands, fog-dependent, or chronically drought-stressed landscapes, where many commonly used restoration species fail to establish. This directly addresses a major gap in southern African restoration, where species selection typically relies on general species lists, availability of nursery material, or local familiarity rather than on physiological drought-adaptive strategies.

The trait–environment analyses showed that the three woody forage species investigated in Chapter 4 rely on distinct drought-response strategies. These findings underscore that TBR must account for both trait stability and trait plasticity, rather than assuming that co-occurring species respond similarly along climatic gradients. This has practical implications. Species such as *C. mopane*, which maintain conservative, stable traits, are likely to tolerate prolonged multi-year droughts, whereas species like *T. prunioides*, which rely heavily on plasticity, may only perform well under variable but not persistently extreme conditions. This distinction may help explain observed woodland mortality patterns in Namibia. For example, the disproportionately high mortality of *T. prunioides* relative to *C. mopane* during the prolonged drought at Ongava Research Center (V. De Cauwer, personal communication, November 18, 2025). Plasticity allows rapid short-term adjustment, but it does not necessarily confer resilience under sustained, chronic water limitation, whereas conservative, stress-tolerant species such as mopane maintain performance through long-term trait stability (Grime et al., 1986; Krug, 2017; Matthews et al., 2024).

Together, these insights position functional strategies, such as CAM and conservative drought-tolerant traits, as operational tools for dryland restoration, offering clearer guidance than current practice for matching species to specific climatic and environmental contexts.

5.5.2 Advancing plant functional ecology in African drylands

African drylands remain underrepresented in global trait databases, limiting the development of generalisable ecological theory for arid systems (Funk et al., 2024). By generating new field-based trait measurements for ecologically important woody species, this study contributed regionally novel data and provided the first mechanistic comparison of drought-response strategies for these taxa in Namibia. These empirical data fill a long-standing gap and move dryland trait ecology in the region beyond descriptive accounts toward a more functional and predictive understanding of species performance.

The evidence of trait stability in *C. mopane* aligns with ecological models suggesting that widespread savanna dominants often rely on conservative, slow-turnover traits to buffer against climatic variability (Sarmiento et al., 1985; Wigley et al., 2016). In contrast, *T. prunioides* exhibited strong plasticity, particularly in specific leaf area and stomatal density, revealing an opportunistic strategy centred on rapid trait adjustment to shifting water availability. Meanwhile, the weak relative water content response in *C. alexandri* suggested reliance on deciduousness and structural defences rather than continuous physiological regulation of water status. These contrasting strategies demonstrated that co-occurring dryland species achieve drought tolerance through multiple mechanistic pathways. Some through water-saving conservatism, others through opportunistic water spending, and others through phenological strategies such as seasonal leaf shedding.

This diversity of drought adaptations explains key patterns in Namibian woodland dynamics. For example, the disproportionately high mortality of *T. prunioides* during the prolonged drought is

consistent with its plastic, opportunistic strategy, which facilitates short-term adjustment but provides limited buffering during extended, multi-year drought. In contrast, *C. mopane*'s conservative trait stability aligns with its well-documented drought resilience and lower mortality under severe climatic stress. Thus, the trait evidence presented here helps mechanistically explain mortality patterns and strengthens ecological understanding of woodland responses to extreme drought.

The novelty of this contribution lies not in showing that multiple drought strategies exist, already recognised globally, but in quantifying these strategies for Namibian woody species for the first time, and in demonstrating how these traits vary along environmental gradients. This provided a functional, mechanistic basis for predicting performance under increasing aridity. Furthermore, the study offered a significant advance over the generalised or anecdotal knowledge commonly used in restoration in Africa (see chapter 2).

Practically, these findings have direct implications for restoration planning. Species with conservative, stable traits, such as *C. mopane,* are better suited for hyper-arid or chronically water-limited sites, whereas species with higher plasticity, such as *T. prunioides*, may be more appropriate for variable or moderately stressed environments. Structural strategists like *C. alexandri* are ideal for sites where deciduousness and seasonal shedding confer an advantage. These data allow for more nuanced species–site matching than current restoration practice, which typically does not differentiate species based on mechanistic drought-response strategies (see chapter 2).

5.5.3 Linking physiological and functional insights to resilience theory

Resilience theory emphasises the ability of ecosystems to absorb disturbance while maintaining function (Gunderson, 2000). The findings of this study provided complementary evidence for resilience in drylands across two temporal scales. The broad distribution of CAM identified in Chapter 3 reflected an evolutionary dimension of resilience, where long-standing physiological strategies enable species to persist under chronic aridity and episodic water scarcity. In contrast, the trait–environment patterns documented in Chapter 4 illustrated an ecological dimension of resilience, showing how woody species differ in their capacity to adjust functional traits in response to contemporary climatic gradients.

These dual dimensions clarify that resilience in Namibian drylands is not built on a single mechanism but emerges from the coexistence of contrasting strategies. Species with conservative, stable traits that buffer against prolonged drought, species with plastic traits that respond to short-term variability, and CAM species whose metabolic efficiency allows them to operate under extreme water limitation. For restoration, this means that the most robust assemblages will be those that intentionally combine these different resilience pathways, enabling sites to withstand both predictable seasonal stress and extreme, prolonged drought events. Integrating species with complementary resilience strategies, therefore, offers a practical framework for designing restoration interventions capable of sustaining ecosystem function under intensifying climatic pressures.

5.6 Emerging themes and conceptual insights

Across the three chapters, several overarching themes emerged that collectively advance understanding of drought adaptation and restoration potential in Namibia's drylands and beyond. First, this study emphasised that drought tolerance in Namibian flora is inherently multidimensional. Species persisted not through a single mechanism, but through diverse combinations of metabolic

pathways, structural investments, phenological strategies, and physiological adjustments. This diversity, ranging from CAM in succulents to conservative hydraulic traits in *C. alexandri* and high leaf-level plasticity in *T. prunioides*, challenges simplified views of dryland adaptation. They also highlighted the need for restoration frameworks that explicitly account for multiple ecological strategies.

Second, the CAM distribution patterns revealed in Chapter 3 highlighted the strong influence of microclimatic heterogeneity and environmental filtering on physiological strategy. Fine-scale gradients such as fog zones, coastal humidity corridors, and topographic variation create microhabitats where CAM taxa can persist despite severe water limitation. The enriched representation of CAM in Namibia relative to global averages underscored the long-term stability of succulent biomes and the importance of fog-dependent environments in shaping drought-adaptive metabolism. In the context of climate change, rising atmospheric CO_2 may further shift the relative advantages among photosynthetic pathways. Because CAM plants take up CO_2 at night when stomata are open (Kluge & Ting, 1978; Osmond et al., 1982; Winter, 1985), they already minimise transpiration losses under extreme aridity. Elevated CO_2 could enhance this advantage by increasing the diffusion gradient for nocturnal CO_2 uptake, improving carbon gain without additional water loss. Although higher CO_2 generally boosts water-use efficiency across C_3, C_4, and CAM pathways (Wang & Feng, 2012), CAM species begin from a position of strong drought resilience due to their temporal separation of gas exchange and assimilation. Under future climates characterised by hotter and drier conditions, CAM species are therefore likely to become even more suitable for restoration, combining inherent drought tolerance with improved carbon assimilation under elevated CO_2.

Third, the functional trait analyses in Chapter 4 demonstrated that environmental gradients exert strong selective pressures on trait expression, but species respond to these pressures in fundamentally different ways. *T. prunioides* adjusts leaf traits dynamically with shifting moisture regimes, *C. mopane* maintains stable traits across broad gradients, and *C. alexandri* relies on structural and life-history strategies such as deciduousness. These contrasting strategies reinforced the importance of recognising interspecific variation in drought responses, even among co-occurring species. This further illustrated how environmental filtering interacts with species' evolutionary histories to produce different adaptive outcomes.

A final theme concerns the persistent scarcity of African trait data and the implications of this gap for restoration planning. Chapter 2 showed that restoration initiatives across the continent often operate without the mechanistic information needed to inform species selection. This thesis contributed directly to addressing that deficit by generating new physiological (CAM) and functional trait data for Namibian species. Together, these insights revealed that effective restoration in Namibia requires integrating drought-tolerant strategies and environmental filtering into a cohesive decision-making framework grounded in local ecological realities. This integrated perspective offers a more ecologically realistic and climate-resilient foundation for dryland restoration in Africa than current practice, which rarely differentiates species based on mechanistic drought-response pathways.

5.7 Conclusion and Implications for Practice and Policy

This study set out to advance understanding of drought adaptation in one of the world's most water-limited environments. The study integrated a continent-level evaluation of restoration practice with new functional strategies and traits evidence from Namibian flora. I argued that effective dryland restoration in Africa must be grounded in a mechanistic understanding of how species persist under

chronic aridity. The combined findings show that drought tolerance arises from multiple, interacting strategies, including metabolic pathways such as CAM, conservative structural traits, phenological adjustments, and plastic physiological responses, and that these strategies vary across species. This research further illustrated how these functional mechanisms can be operationalised within restoration planning. The CAM assessment expanded the pool of native species with inherent water-use efficiency suited to drylands or fog-dependent systems. On the other hand, the trait–environment analyses provided a basis for matching woody species to sites according to whether long-term trait stability, phenological flexibility, or rapid plasticity is required. Together, these insights move species selection beyond reliance on general species lists or availability of nursery material, offering a more diagnostic, evidence-based approach that aligns functional strategies with local environmental constraints. The unified contribution of this study is the establishment of a scientifically grounded framework for trait-informed dryland restoration in Namibia. One that integrates evolutionary, physiological, and ecological dimensions of drought adaptation. By providing new CAM and functional trait datasets, clarifying how drought strategies differ among co-occurring species in Namibia, and demonstrating their practical relevance for species–site matching, this work strengthened the foundation for restoration approaches that are ecologically realistic and increasingly climate-resilient. Future progress will depend on field trials that test the performance of species with contrasting drought strategies, further expansion of trait datasets for underrepresented African taxa, and stronger integration of Indigenous and scientific knowledge systems. Such developments will be essential for ensuring that restoration interventions succeed both ecologically and socially as climate change intensifies pressures on dryland landscapes.

Implications for Restoration Practice

The findings of this thesis provided several practical insights for improving dryland restoration outcomes in Namibia and comparable arid systems.

- **Prioritise trait-based species–site matching.** Restoration planning should move beyond traditional species lists and place stronger emphasis on functional traits, including specific leaf area (SLA), leaf dry matter content (LDMC), stomatal characteristics, relative water content (RWC), and CAM physiology, to ensure that species are matched to the environmental conditions where they are most likely to persist.
- **In extremely arid environments, incorporate CAM-performing succulents.** CAM species can persist under severe moisture limitation and may play stabilising roles by maintaining minimal cover, reducing erosion, and buffering microhabitats that support later colonisers. Their value lies in complementing, rather than replacing, other life-forms in highly water-limited settings.
- **Adopt microsite-based planting strategies.** Targeted placement of plants in run-on patches, soil cracks, sheltered slopes, rock crevices, and other moisture-accumulating microsites can significantly enhance establishment success compared with uniform seeding approaches.
- **Use framework or facilitation shrubs strategically.** Drought-adapted species such as *Aloe* and *Euphorbia* may act as nurse plants by moderating microclimates, improving soil conditions, and facilitating recruitment of additional native species when introduced at low densities.
- **Support trait-based selection with continuous monitoring.** Long-term monitoring of plant survival, physiological performance, and functional traits is essential for refining species

choice, adjusting restoration strategies, and improving predictive understanding of species–environment relationships over time.

- **Recognise variation among woody species.** Differences in drought-response strategies, such as the plasticity of *Terminalia prunioides*, the structural drought tolerance of *Catophractes alexandri*, and the trait stability of *Colophospermum mopane*, highlight the importance of selecting woody species according to the specific aridity regime and restoration objective.

Implications for Policy

The research also identified several policy-level opportunities to strengthen restoration efforts in African drylands:

- **Embed trait-based criteria in restoration guidelines.** National and regional restoration frameworks would benefit from explicitly incorporating functional-trait information into species selection protocols and planning tools.
- **Invest in expanding African trait datasets.** Limited availability of trait data for native species remains a major barrier. Expanding national and regional trait databases, particularly for dryland taxa, would support more evidence-informed decision-making.
- **Promote co-production of knowledge.** Effective restoration should integrate scientific trait data with Indigenous and Local Ecological Knowledge (IEK). This combination improves species–site matching, enhances community ownership, and aligns restoration choices with long-standing land-use understandings.
- **Ensure funding structures support long-term outcomes.** Restoration programmes should prioritise long-term monitoring and adaptive management rather than short-cycle projects focused primarily on planting targets.

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