

Integrated drought tolerance strategies in Cerrado plants and their agricultural implications

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Abstract: Drought tolerance in plants arises from coordinated interactions among morphological, hydraulic, and physiological processes that regulate water acquisition, transport, and conservation under water-limited conditions. This study aimed to synthesize and critically evaluate functional strategies associated with drought tolerance in Cerrado plants and their implications for agricultural systems. An Integrative literature review was conducted following PRISMA-based guidelines, using Web of Science, Scopus, ScienceDirect, and SciELO. Studies published between 2004 and 2024 were considered, resulting in 28 selected articles after screening and eligibility assessment. The results indicate that deep root systems, hydraulic safety mechanisms, stomatal regulation, and osmotic adjustment are key components of drought responses. Trade-offs between hydraulic efficiency and safety, and between water conservation and carbon assimilation, were consistently reported. Environmental factors, particularly soil properties and climatic seasonality, strongly modulate these responses. This study demonstrates that drought tolerance depends on functional coordination rather than isolated traits, providing a more integrative framework for understanding plant resilience under climate change.

Keywords: Plant Ecophysiology; Hydraulic Architecture; Water-Use Efficiency; Tropical Savanna; Physiological Plasticity; Functional Integration.

1. Introduction

Water availability is a key determinant of plant physiological performance, directly regulating processes such as gas exchange, stomatal conductance, and water-use efficiency. In the context of climate change, marked by increasingly frequent and severe drought events, understanding the mechanisms underlying tolerance to water deficit has become essential for both ecosystem ecology and the sustainability of agricultural systems (Tardieu et al., 2018; Qiao et al., 2024). Despite substantial empirical advances, the literature still lacks mechanistic syntheses capable of integrating structural, hydraulic, and physiological responses into a unified framework.

The Brazilian Cerrado provides a valuable context

for this investigation due to its strong seasonal water limitation. In this biome, woody species exhibit recurrent combinations of traits that sustain functioning during the dry season, including adjustments in hydraulic architecture, stomatal regulation, and investment in deep root systems (Oliveira et al., 2005; Bucci et al., 2008; Franco et al., 2005). However, these attributes are often studied in isolation, limiting the understanding of how their interactions support resistance to water stress.

Access to deep soil water has been identified as a key mechanism for plant persistence in the Cerrado, allowing exploitation of relatively stable water reserves and supporting processes such as hydraulic redistribution (Moreira et al., 2003). Although recent

studies confirm the importance of deep roots in mitigating drought effects, they also show that their contribution to transpiration is variable, depending on soil properties, atmospheric demand, and water recharge dynamics (Kühnhammer et al., 2023; Pinheiro et al., 2021). This variability indicates that drought responses cannot be explained by single traits alone.

In this context, edaphic and geomorphological factors play a central role in modulating resource availability and shaping the expression of functional traits (Martins et al., 2022). However, their incorporation into ecophysiological analyses remains limited. This gap is particularly relevant given ongoing land-use changes, which alter hydrological regimes and impose new constraints on plant communities (Fushimi et al., 2024).

At the physiological level, responses to water stress involve coordinated hydraulic and biochemical processes, including osmotic adjustment, stomatal control, and variation in water-use efficiency (Blum, 2017; Bertolino et al., 2019; Takahashi et al., 2020). Trade-offs between water security and water-use efficiency have been identified as key drivers of these responses (Yan et al., 2020; Blackman et al., 2019). However, the generality of these patterns across ecological contexts remains uncertain, particularly in heterogeneous systems such as the Cerrado.

In agricultural systems, similar mechanisms regulate productivity under water deficit, directly affecting photosynthesis, growth, and water-use efficiency (Du et al., 2018; Qiao et al., 2024). Nevertheless, knowledge from agronomic studies remains largely disconnected from ecological research, limiting the identification of general principles governing plant responses to drought.

Overall, the main limitation in this field lies not in the lack of data, but in the persistence of conceptual fragmentation. The predominance of reductionist approaches, in which traits are analyzed independently, restricts the understanding of plant responses as integrated and context-dependent processes.

Therefore, this study proposes that tolerance to water deficit should be understood as a functional outcome of coordinated structural, hydraulic, and physiological processes, modulated by environmental conditions. By integrating evidence from the Cerrado with recent advances in plant ecophysiology and agronomy, this work aims to provide a more mechanistic and unified framework for understanding drought resistance. This approach contributes to advancing ecological theory while supporting the

development of more resilient agricultural strategies under climate change.

2. Material and Methods

2.1. Study Design

This study is an integrative literature review with an analytical and interpretive approach, aimed at synthesizing and critically evaluating mechanisms of drought tolerance in plants, with emphasis on both natural systems in the Cerrado and agricultural systems.

The review was structured to integrate evidence across multiple levels of biological organization, morphological, hydraulic, and physiological, allowing the identification of functional patterns and supporting a mechanistic interpretation of plant responses to water limitation.

To ensure transparency, reproducibility, and methodological rigor, the study followed principles adapted from the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines. Although not a formal systematic review, structured procedures for search, screening, eligibility assessment, and study inclusion were applied to reduce selection bias and increase analytical consistency.

2.2. Literature Search Strategy

The literature search was conducted between April 2022 and June 2025 using major scientific databases with broad international coverage, including Web of Science, Scopus, ScienceDirect (Elsevier), and SciELO.

Publications from 2004 to 2024 were considered, encompassing both recent studies and foundational works relevant to plant ecophysiology.

English-language keywords were combined using Boolean operators (AND, OR), including:

- “drought stress,” “Cerrado,” “tropical savanna,” “plant functional traits,” “hydraulic architecture,” “deep roots,” “water use efficiency,” and “plant ecophysiology.”

Search strategies were adapted to the specific structure of each database to maximize retrieval of relevant studies. In addition, backward and forward citation tracking were applied to identify studies not captured in the initial search.

2.3. Study selection process

The study selection followed PRISMA-based procedures, including identification, screening, eligibility

assessment, and inclusion, ensuring transparency and reproducibility.

The initial search yielded 132 records. After removing duplicates, 104 studies remained and were screened based on titles and abstracts. Studies not addressing water deficit, not involving plants, or lacking a functional or ecophysiological focus were excluded at this stage, resulting in 47 potentially relevant studies.

Full-text evaluation was then conducted using predefined eligibility criteria. Nineteen studies were excluded due to absence of functional attribute analysis (n = 8), exclusively agronomic focus (n = 5), insufficient methodological clarity (n = 4), or lack of full-text availability (n = 2).

A total of 28 studies met all criteria and were included

in the qualitative synthesis. The final selection prioritized methodological consistency and relevance to the mechanistic understanding of drought tolerance, ensuring a balance between analytical depth and representativeness.

The selection process is summarized in the PRISMA flow diagram (Figure 1).

The final number of studies (n = 28) reflects a deliberate balance between representativeness and analytical depth. Rather than aiming for exhaustive coverage, priority was given to studies providing consistent and mechanistic evidence across morphological, hydraulic, and physiological dimensions, which is consistent with integrative review approaches.

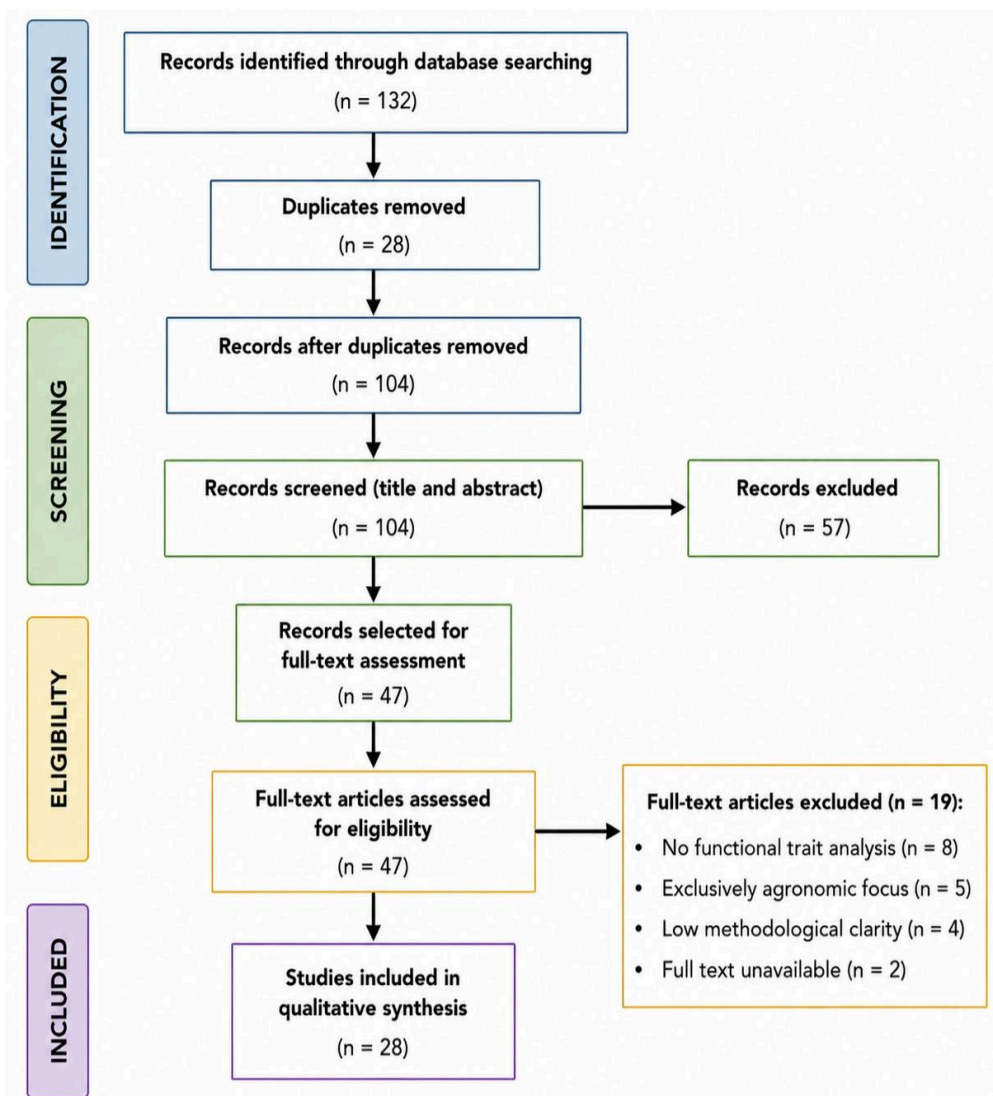


Figure 1. Flowchart of the process for identifying, screening, assessing eligibility, and including the studies analyzed in

the review, prepared in accordance with the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) guidelines. Source: Author 2026

2.4. Inclusion and Exclusion Criteria

Explicit criteria were defined to guide study selection.

Inclusion criteria:

- i. Studies conducted in Cerrado environments, tropical savannas, or ecologically comparable seasonal systems;
- ii. Experimental, observational, or mechanistic review studies;
- iii. Studies addressing functional attributes related to drought tolerance (morphological, hydraulic, or physiological);
- iv. Articles published in peer-reviewed and indexed journals;
- v. Studies conducted under natural or controlled water-limiting conditions.

Exclusion criteria:

- i. Studies without full-text access;
- ii. Studies with exclusively agronomic focus lacking ecophysiological analysis;
- iii. Studies not directly addressing drought tolerance mechanisms;
- iv. Studies with insufficient methodological clarity or scientific consistency.

The final selection prioritized studies providing consistent and integrable evidence, rather than purely descriptive approaches.

2.5. Data Extraction and Functional Classification

Relevant information was systematically extracted from the selected studies, focusing on functional attributes associated with drought tolerance.

For analytical purposes, data were organized into three categories:

- Morphological and structural attributes: root depth and architecture, specific leaf area, biomass allocation;
- Hydraulic attributes: hydraulic conductivity, vulnerability to cavitation, hydraulic safety margin, and water transport strategies;
- Physiological attributes: photosynthetic rate, stomatal conductance, leaf water potential, and water-use efficiency.

Environmental variables, including soil

characteristics, climatic seasonality, and land-use changes, were also considered due to their influence on plant functional responses.

2.6. Data Analysis and Integrative Approach

Data analysis followed a qualitative, interpretive, and comparative approach, focusing on identifying recurring patterns, functional relationships, and trade-offs among plant attributes. Rather than evaluating traits independently, the analysis considered their interactions within a functional system operating across multiple scales. No formal meta-analysis was conducted due to the heterogeneity among the selected studies.

Key relationships examined included:

- water-use efficiency versus hydraulic safety;
- root depth versus water availability;
- stomatal regulation versus carbon assimilation.

These relationships were compared across studies to identify convergences, divergences, and context-dependent patterns.

The interpretation was guided by established frameworks in plant ecophysiology, including the leaf economic spectrum and hydraulic trade-offs, supporting a mechanistic understanding of drought tolerance strategies.

2.7. Quality assurance and scientific consistency

To ensure analytical robustness, only studies published in peer-reviewed and indexed journals were included. The reliability of the synthesis was strengthened through evidence triangulation, comparing patterns across species, ecological contexts, and methodological approaches.

This approach reduces the influence of isolated findings and supports the identification of consistent patterns. In addition, study quality was assessed qualitatively based on methodological clarity, experimental design, consistency of results, and relevance to the objectives of this review. Studies lacking sufficient methodological detail or presenting inconsistent or non-reproducible results were excluded during the eligibility stage.

Although no formal scoring system was applied, this structured qualitative assessment ensured that the synthesis was based on robust and comparable

evidence.

2.8. Limitations of the Approach

Despite the methodological rigor, this study has limitations inherent to integrative reviews, including:

- methodological heterogeneity among studies;
- variation in spatial and temporal scales;
- diversity of species and environmental contexts;
- lack of standardization in ecophysiological metrics.

In addition, although PRISMA-based procedures increase transparency, the interpretive nature of the synthesis may introduce some degree of subjectivity. Nevertheless, the emphasis on identifying consistent patterns and functional relationships helps mitigate these limitations.

3. Results

3.1. Overview of selected studies

The analysis of the 28 selected studies revealed consistent patterns in plant responses to water deficit across both natural and agricultural systems. Most studies focused on Cerrado species, while a subset included comparative analyses with other tropical seasonal ecosystems and cultivated species.

Despite methodological differences, the literature converges on three main functional axes underlying drought responses: (i) morphological and structural traits, (ii) hydraulic characteristics, and (iii) physiological processes. These axes are consistently interconnected, indicating that plant responses to water limitation are governed by coordinated trait networks rather than isolated mechanisms.

This convergence suggests that, although experimental approaches vary, similar functional principles underlie plant performance under drought. The distribution of studies, including their main approaches and key findings, is summarized in Table 1.

Table 1. A representative subset of the 28 studies analyzed on mechanisms of water-deficit tolerance in natural and agricultural systems

| Author/Year | Environment | Study type | Key variables | Key findings |
|------------------------|--------------|---------------|--|---|
| Oliveira et al. (2005) | Cerrado | Experimental | Sap flow, root depth | Deep roots maintain water flow during drought |
| Bucci et al. (2008) | Cerrado | Observational | Water use | High dependence on water in deep layers |
| Choat et al. (2012) | Global | Comparative | Hydraulic conductivity | Trade-off between efficiency and security |
| Hoffmann et al. (2005) | Cerrado | Experimental | Specific Leaf Area, biomass allocation | Predominance of conservative strategies |
| Chaves et al. (2009) | Agricultural | Review | Stomatal conductance | Stomatal regulation as a central mechanism |
| Klein (2014) | Cerrado | Experimental | Stomatal conductance | High variability among species |
| Tardieu et al. (2018) | Agricultural | Experimental | Water use efficiency | Increased under moderate stress |
| Qiao et al. (2024) | Agricultural | Experimental | Photosynthesis | Marked reduction under severe drought |
| Bartlett et al. (2016) | Global | Review | Hydraulic traits | Attribute |

| | | | | |
|--------------------------|--------------|--------------|-------------------------|---|
| Yan et al. (2020) | Global | Comparative | Hydraulic safety margin | integration is essential Important predictor of survival |
| Blum (2017) | Agricultural | Review | Osmotic adjustment | Maintains cellular function under stress |
| Zandalinas et al. (2017) | Global | Experimental | Combined stress | Drought + heat intensify impacts |

Source: Author, 2026.

3.2. Morphological and structural traits

Morphological traits are consistently associated with drought tolerance across the analyzed studies, particularly the development of deep and extensive root systems. Several studies indicate that deep roots enable access to water stored in subsurface layers, sustaining plant activity during prolonged dry periods (Oliveira et al., 2005; Bucci et al., 2008). Similarly, Kühnhammer et al. (2023) reported that deep rooting buffers drought impacts by maintaining water uptake under limiting conditions.

However, the contribution of this trait varies substantially across studies. While some authors emphasize the central role of deep roots in sustaining transpiration during drought (Oliveira et al., 2005), others report that their contribution to overall plant water balance may be limited or highly variable depending on soil properties and water recharge dynamics (Kühnhammer et al., 2023; Pinheiro et al., 2021). This contrast indicates that root depth alone is insufficient to explain drought performance and must be interpreted in relation to environmental constraints and other functional processes.

At the leaf level, variation in traits such as specific leaf area and biomass allocation reflects contrasting resource-use strategies along a continuum from acquisitive to conservative (Hoffmann et al., 2005; Wright et al., 2004). Species with lower specific leaf area generally exhibit more conservative strategies, reducing water loss and increasing leaf longevity, whereas acquisitive strategies may enhance carbon gain under favorable conditions but increase vulnerability under drought.

Nevertheless, the relationship between leaf traits and drought performance is not consistent across studies. While some authors support the predictive value of these traits, others show that similar morphological configurations may lead to distinct physiological responses depending on environmental context (Cianciaruso et al., 2013; Reis et al., 2022). This inconsistency suggests that morphological attributes do not function as reliable proxies for plant performance

under water deficit, particularly in heterogeneous systems such as the Cerrado.

Overall, these findings highlight an important gap in the literature: although morphological traits are widely used as indicators of drought tolerance, their functional significance remains context-dependent and often insufficient when considered in isolation. This limitation reinforces the need for approaches that explicitly account for interactions between structural traits and hydraulic and physiological processes.

3.3. Hydraulic traits

Hydraulic characteristics were consistently identified as central components of plant responses to water deficit. Most studies report substantial variation in hydraulic conductivity, vulnerability to cavitation, and hydraulic safety margins, reflecting different strategies of water transport and resistance to hydraulic failure.

A recurrent pattern across the literature is the trade-off between hydraulic efficiency and safety. Species with higher water transport capacity tend to be more vulnerable to cavitation, whereas species with greater resistance to hydraulic failure generally operate with lower transport efficiency.

However, this relationship is not consistent across all studies. While several authors describe this trade-off as a fundamental organizing principle (Choat et al., 2012; Blackman et al., 2019), others report deviations depending on environmental conditions and species-specific traits. These findings suggest that hydraulic strategies are not fixed constraints, but flexible responses shaped by environmental variability and phenotypic plasticity.

In this context, the hydraulic safety margin remains an important parameter for understanding plant persistence under severe drought, although its predictive value depends on its interaction with other functional traits.

3.4. Physiological responses to water deficit

Physiological responses to water deficit are primarily associated with changes in stomatal conductance, photosynthetic activity, and water-use efficiency, with stomatal regulation acting as a central control mechanism across studies (Chaves et al., 2009; Bertolino et al., 2019). Most studies report that reductions in stomatal conductance under drought conditions limit water loss and help maintain plant water status.

However, the consequences of this response vary markedly among studies. While some authors report that increased water-use efficiency under moderate stress enhances plant performance (Tardieu et al., 2018), others show that under severe or prolonged drought, stomatal closure leads to substantial reductions in photosynthesis and growth (Qiao et al., 2024). This contrast reflects a fundamental trade-off between water conservation and carbon assimilation, whose outcome depends on stress intensity and duration.

Variability in stomatal sensitivity among species

further complicates these patterns. Klein (2014) demonstrated that species differ widely in their stomatal regulation thresholds, indicating that distinct physiological strategies may result in similar ecological outcomes. In addition, mechanisms such as osmotic adjustment can sustain cellular function under water deficit (Blum, 2017; Takahashi et al., 2020), although their relative importance varies across species and environmental contexts.

Together, these findings indicate that physiological responses to drought are highly dynamic and context-dependent. Although stomatal regulation is consistently identified as a key mechanism, its effects on plant performance depend on interactions with other physiological processes and environmental conditions. The main physiological traits associated with these responses and their ecological roles are summarized in Table 2.

Table 2. Major functional traits associated with water-deficit tolerance and their respective ecological roles in plants from natural and agricultural environments.

| Category | Functional trait | Ecological function | Drought response |
|---------------|---------------------------------|--|--|
| Morphological | Deep root system | Access to water in subsurface layers | Increases tolerance to water deficit |
| Morphological | Low specific leaf area (SLA) | Resource conservation and increased leaf longevity | Reduces water loss |
| Morphological | High allocation of root biomass | Greater soil penetration | Improves water uptake |
| Hydraulic | High hydraulic conductivity | Efficient water transport | Increases the risk of cavitation |
| Hydraulic | Resistance to cavitation | Greater hydraulic safety | Increases resistance to hydraulic failure |
| Hydraulic | Hydraulic safety margin | Prevention of water-conducting system failures | Protection under severe drought conditions |
| Physiological | Low stomatal conductance | Reduced transpiration | Limits photosynthesis |
| Physiological | High water-use efficiency | Optimization of the carbon-to-water ratio | Advantage under moderate stress |
| Physiological | Osmotic adjustment | Maintenance of cell turgor | Sustains metabolic activity |

Source: Author, 2026.

A major gap emerges from this analysis: despite the recognition of multiple physiological mechanisms, few studies explicitly integrate these processes into a unified framework, limiting the development of predictive

models of plant responses to water deficit.

3.5. Influence of environmental factors

Environmental factors were consistently identified as

key drivers modulating plant responses to water deficit. Soil characteristics, particularly depth, texture, and water retention capacity, strongly influence water availability and the expression of functional traits.

Climatic seasonality, especially the pronounced dry season in the Cerrado, is associated with recurrent adjustments in morphological, hydraulic, and physiological processes throughout the annual cycle. These adjustments reflect adaptive strategies to predictable fluctuations in water availability.

In addition, land-use changes alter hydrological regimes and impose new constraints on plant functioning, modifying both resource availability and plant responses.

These findings indicate that plant responses to drought cannot be understood independently of environmental context. Instead, environmental conditions shape both the

expression and effectiveness of functional traits.

3.6. Integration of functional traits

Taken together, the analyzed studies indicate that drought responses arise from the coordination among multiple functional attributes rather than from the isolated action of individual traits. Evidence consistently shows that plant performance under water deficit is governed by interactions among soil conditions, root systems, hydraulic transport, and stomatal regulation.

This coordination sustains water flux across the soil–plant–atmosphere continuum, even under limiting conditions. The conceptual model presented in Figure 2 synthesizes these relationships.

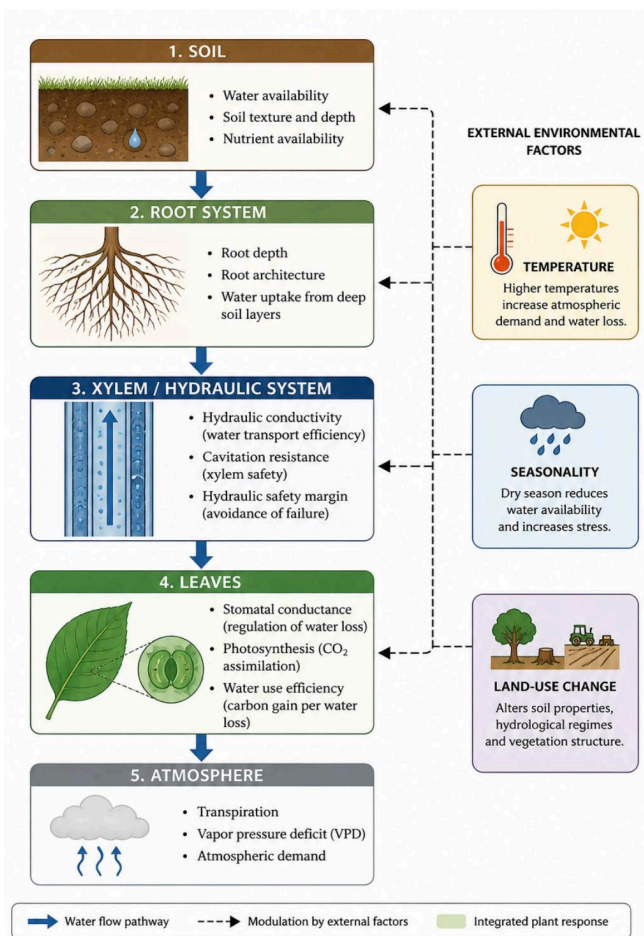


Figure 2. A conceptual model illustrating the integration of morphological, hydraulic, and physiological characteristics underlying plant responses to water deficit. The diagram represents the soil-plant-atmosphere continuum, highlighting the coordinated role of root systems, hydraulic transport, and stomatal regulation in maintaining water flow under drought conditions. External environmental factors, such as temperature, climatic seasonality, and changes in land use, modulate these interactions. Source: Author 2026.

The model highlights that plant performance depends on the balance among functional processes operating at different levels of organization. Importantly, the effectiveness of this coordination is modulated by environmental conditions, indicating that functional integration, rather than trait specialization alone, drives drought responses.

A mechanistic interpretation emerges when considering how these processes interact. Deep root systems enhance access to subsurface water, sustaining hydraulic conductivity and delaying stomatal closure, which allows continued carbon assimilation under moderate stress. Conversely, restricted water access increases hydraulic vulnerability, accelerates stomatal closure, and reduces photosynthetic activity.

These interactions demonstrate that plant responses to drought result from causal linkages among structural, hydraulic, and physiological processes. In this context, the contribution of any given trait depends on its coordination with other functional components and environmental conditions.

4. Discussion

The synthesis of the analyzed studies indicates that drought tolerance cannot be explained by isolated functional traits, but depends on the coordination among morphological, hydraulic, and physiological processes operating across the soil–plant–atmosphere continuum. This perspective challenges traditional trait-based approaches that assume direct and universal relationships between individual traits and plant performance, emphasizing instead the context-dependent nature of plant responses to water deficit.

A key implication is that widely reported structural traits, such as deep root systems, should not be interpreted as independent predictors of drought resistance. Although deep roots are frequently associated with access to subsurface water and the maintenance of plant activity during dry periods (Oliveira et al., 2005; Bucci et al., 2008; Kühnhammer et al., 2023), their effectiveness varies across environmental conditions. While some studies highlight their central role in sustaining water uptake, others indicate that their contribution may be limited under low soil water recharge or restrictive substrates (Kühnhammer et al., 2023; Pinheiro et al., 2021). This contrast suggests that root depth alone is insufficient to explain drought performance and must be interpreted in relation to environmental constraints.

Variation in leaf traits reflects positioning along a continuum of resource-use strategies, ranging from acquisitive to conservative approaches (Hoffmann et al., 2005; Wright et al., 2004). However, their predictive

value remains limited when considered in isolation. Empirical evidence shows that similar morphological configurations may result in contrasting physiological responses depending on environmental conditions (Cianciaruso et al., 2013; Reis et al., 2022). This inconsistency indicates that structural traits do not function as universal proxies for adaptive strategies in heterogeneous systems such as the Cerrado.

From a hydraulic perspective, the trade-off between water transport efficiency and hydraulic safety provides a useful framework for interpreting plant responses to drought (Choat et al., 2012; Blackman et al., 2019). However, deviations from this pattern across studies suggest that this trade-off is not a fixed constraint. Instead, hydraulic behavior appears to be modulated by environmental variability, phenotypic plasticity, and ontogenetic factors. In this context, the hydraulic safety margin remains a relevant parameter (Yan et al., 2020), although its predictive value depends on its interaction with other functional attributes.

Physiological responses further highlight the dynamic nature of drought tolerance. Stomatal regulation acts as a central control point, mediating the balance between water conservation and carbon assimilation (Chaves et al., 2009; Bertolino et al., 2019). While increased water-use efficiency under moderate stress may enhance performance (Tardieu et al., 2018), other studies show that under severe or prolonged drought, stomatal closure leads to substantial reductions in photosynthesis and growth (Qiao et al., 2024). This contrast reflects a fundamental trade-off whose outcome depends on stress intensity and duration. In addition, variability in stomatal sensitivity (Klein, 2014) and the role of mechanisms such as osmotic adjustment (Blum, 2017; Takahashi et al., 2020) reinforce the importance of physiological plasticity in determining plant performance.

A mechanistic interpretation clarifies how these processes interact. Deep root systems increase access to subsurface water, sustaining hydraulic conductivity and delaying stomatal closure, which allows continued carbon assimilation under moderate drought. Conversely, restricted water access increases hydraulic vulnerability, accelerates stomatal closure, and reduces photosynthetic activity. These interactions show that plant responses are driven by coordinated functional processes rather than isolated traits.

Environmental factors play a central role in modulating these interactions. Soil properties and geomorphological processes influence water availability and nutrient dynamics (Martins et al., 2022; Alves et al., 2018), while climatic seasonality imposes predictable constraints that shape adaptive strategies. In addition, land-use changes alter hydrological regimes and impose

new pressures on plant communities (Fushimi et al., 2024). Despite their relevance, these factors remain insufficiently incorporated into functional analyses, representing a critical gap in current research.

In agricultural systems, these limitations become more evident. Cultivated species generally exhibit reduced access to deep water and lower functional plasticity compared to native Cerrado species, increasing their vulnerability to drought. This suggests that incorporating functional strategies observed in natural ecosystems may improve the resilience and sustainability of agricultural systems under water-limited conditions.

Furthermore, the interaction between drought and other stressors, particularly high temperatures, tends to amplify negative effects on plant functioning (Zandalinas et al., 2017). However, these combined stress responses remain poorly explored within integrative frameworks, highlighting an important direction for future research.

Overall, the main limitation in this field lies not in the lack of data, but in the persistence of conceptual fragmentation. The predominance of reductionist approaches limits the identification of broader patterns and constrains the development of predictive models of plant responses to environmental stress.

Based on this synthesis, three main hypotheses can be proposed: (i) drought tolerance is maximized at intermediate levels of hydraulic efficiency and safety, rather than at extreme values of either strategy; (ii) the effectiveness of deep root systems depends strongly on soil water recharge dynamics and may be constrained under limited subsurface water availability; and (iii) physiological plasticity, particularly in stomatal regulation and water-use efficiency, may be a stronger predictor of drought resilience than structural traits alone.

Advancing this field will require experimental approaches capable of simultaneously evaluating multiple functional attributes across environmental gradients. Such approaches are essential for developing more mechanistic and predictive frameworks of plant responses to water deficit, with direct implications for ecological theory and the sustainability of agricultural systems.

5. Conclusion

This study advances the field by demonstrating that drought tolerance is not determined by isolated traits, but by coordinated interactions among morphological, hydraulic, and physiological processes modulated by environmental context. This framework moves beyond reductionist approaches and provides a more mechanistic basis for understanding plant responses to water deficit.

The results indicate that plant performance under

drought depends on the balance among structural, hydraulic, and physiological processes, rather than on the optimization of individual traits. This perspective helps explain variability in plant responses across environmental gradients and underscores the limitations of single-trait approaches.

From an applied perspective, incorporating functional strategies observed in Cerrado species may improve the resilience and sustainability of agricultural systems under increasing climatic variability.

Overall, this study contributes to bridging ecological theory and agricultural practice by offering a conceptual basis for more predictive approaches to plant drought tolerance. Future research should prioritize experimental designs that capture interactions among functional processes across environmental gradients.

6. Acknowledgement

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Author's Contributions

The author conceived and designed the study, collected and analyzed the data, interpreted the results, drafted the manuscript, and approved the final version for publication.

Ethics

The author declares that this manuscript complies with current ethical standards. The study did not involve experimentation on humans or animals. All data used

were obtained and utilized in accordance with applicable standards and guidelines. The author assumes responsibility for clarifying and resolving any ethical issues that may arise following publication.