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Review Paper

# Drought-Induced Shifts in Biomass Allocation and Carbon Sequestration in Arid Zone Tree Species

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**ABSTRACT**

A rapidly growing population demands greater access to food, feed, and shelter, increasing the strain on natural resources. Human activities, such as converting forests into arable lands and increasing $CO_2$ emissions, intensify atmospheric $CO_2$ concentrations. After a significant rise in atmospheric carbon levels, global temperatures have surged, resulting in the frequent occurrence of droughts worldwide. Drought, a protracted episode of unusually low rainfall, has a detrimental effect on ecosystems in dry zones. Reduced growth, changed phenology, and higher mortality of trees are a result of the physiological and ecological changes. The present review focuses on shifts in allocation between aboveground (leaves, stems) and belowground (roots) biomass, as well as within aboveground components. It assesses how these drought-induced changes impact overall tree growth, carbon storage capacity, and long-term resilience. This review aims to identify patterns and knowledge gaps to understand how arid zone forests respond to and influence the global carbon cycle under increasing drought conditions.

## INTRODUCTION

Due to a significant rise in atmospheric carbon levels, global temperatures have surged, resulting in more occurrences of droughts worldwide (World Meteorological Organization, 2025). $CO_2$ is an important greenhouse gas (GHG) that accelerates climate change (Rehman et al. 2021). Current atmospheric $CO_2$ concentration reaches beyond 420 ppm compared to the pre-industrial revolution level of 280 ppm in 1750 AD (World Meteorological Organization 2025; Berry 2019). There is about a 47 % increase in $CO_2$ levels since 1970 and the concentration of other GHGs is also increasing with time, this trend leads to an increment in average global temperature at the rate of 0.17°C per decade (IPCC 2023; IPCC 2007). $CO_2$ is a well-mixed gas and there are only minor spatial or temporal variations in the concentration of $CO_2$ across the globe, these small fluctuations are due to the local weather pattern and biological activity of plants and soil (Chahine et al. 2008). $CO_2$ concentration at the end of this century will be expected between 550 to 1000 ppm, depending on how we achieve our emission reduction targets, leading to an average global air temperature increase of 1 – 3.7 °C (Ciais et al. 2014; Jain et al. 2024). However, the global increase in temperature is not influenced by these small variations, higher latitudes will be warmer by 10°C and tropics 3-4°C by 2100 AD (Ciais et al. 2014; Khan 2024). The increase in greenhouse gas since 1970 is mainly due to anthropogenic activities, which are accelerated by the increase in the human population and depend on factors like economic status and population size and degree of urbanization (IPCC 2023). A growing population demands greater access to food, feed, and shelter, increasing the strain on natural resources. This strain manifests through activities such as deforestation for local development, forest fires (Agbeshie et al. 2022), and overgrazing (Han et al. 2021). The change in land use was limited till the mid-$19^{th}$ century, but it rapidly increased after the early 1980s, and 60% of all land use and land cover modifications can be attributed directly to anthropogenic activities (IPCC 2023).

Sequestration of atmospheric $CO_2$ cuts down its atmospheric concentration and helps combat climate change (Al-Wabel et al. 2020). The process of carbon sequestration involves capturing and storing atmospheric carbon dioxide for a long period in plants, soils, oceans, and geologic formations (Mondal et al. 2024). The primary mechanisms for carbon sequestration involve geological sequestration, wherein $CO_2$ is stored in underground geologic formations, and biological sequestration (Eigbe et al. 2023). The global carbon cycle is significantly influenced by terrestrial ecosystems, primarily due to their capacity to acquire carbon through photosynthesis and release it through respiration. In the period from 1990 to 2021, the terrestrial biosphere (mainly forests) acted as a net sink, absorbing approximately 21% of the carbon dioxide emitted from fossil fuel combustion, emphasising their role in the mitigation of global warming (Gulev et al. 2021; Boukhris et al. 2024).

Plants absorb atmospheric $CO_2$ through the process of photosynthesis, convert it into organic carbon, and store it as biomass while releasing oxygen into the atmosphere (Dusenge et al. 2019). Several earlier studies have observed the net photosynthesis rates or employed dynamic growth models to assess the carbon sequestration of individual plants. Findings indicate that the efficiency of carbon sequestration varies among different plant species (Kaul et al. 2010; Gratani et al. 2016). No notable correlations were identified between net photosynthetic rates and tree size but trees with larger total leaf area have a higher carbon sequestration efficiency (Wang et al. 2021). Approximately 30% of the earth's land surface, equivalent to nearly 4 billion hectares, is covered by forests. These forests play a crucial role in providing valuable ecosystem services and goods, serving as habitats for a diverse array of flora and fauna. The total carbon content of forests, estimated at 638 Gt for the year 2005, surpasses the amount of carbon present in the entire atmosphere (FAO 2005). Recognizing the crucial role of forests in mitigating climate change, nations are investigating their forest carbon budgets and initiating assessments to enhance and maintain the carbon sequestration of their forest resources. The global potential for afforestation and reforestation activities from 1995 to 2050 is estimated to range between 1.1 and 1.6 Pg (Peta gram) carbon annually, with 70% of this potential occurring in the tropics (Schlamadinger 2000). Afforestation and reforestation are viewed as promising mitigation approaches, given their ability to combine wood production and carbon storage. The United Nations Framework Convention on Climate Change (UNFCCC) has acknowledged the significance of plantation forestry as a viable option for mitigating greenhouse gas emissions.

Meteorological drought, a protracted episode of unusually low rainfall, has a detrimental effect on arid ecosystems that are already marked by a lack of water (Dai 2011; IPCC 2014). Reduced growth, changed phenology, and higher mortality are observed in trees of drought-prone areas (Breshears et al. 2005; Allen et al. 2010). These modifications interfere with the way the ecosystem functions, impacting species interactions, carbon sequestration, and nutrient cycling (Smith et al. 2000; Cramer et al. 2001). Comprehending the subtleties of the effects of drought is essential for forecasting the future paths of ecosystems and providing guidance for sustainable land management in arid areas (IPCC 2021).

Comprising about 40% of the world's land area, arid and semi-arid regions act as natural carbon sinks and are found as shrublands, farmlands, and rangelands (Jia et al. 2021). They have a significant potential for carbon sequestration that can be achieved by utilizing compatible species, predominantly woody plants that demonstrate adaptability to low moisture levels and elevated soil salinity. Global assessments indicate that these lands can sequester up to one billion tons of carbon (Sadeghi & Raeini 2016). The continuously rising concentration of atmospheric $CO_2$ increases the water use efficiency (WUE) of photosynthesis in most plant species. This results in enhanced water accessibility for plants, promoting accelerated growth and enabling quicker carbon sequestration (Grünzweig et al. 2003). Afforestation efforts in these areas will lead to increased absorption and storage of $CO_2$.

Soil stands out as a primary carbon sink on Earth, mainly due to its substantial organic matter content (Keenan & Williams 2018). Soil organic carbon (SOC) plays a crucial role in sustaining soil fertility. The alteration and management of the natural environment into a developed setting, known as a land use system, encompasses activities like cultivating woodlands, pastures, forests, and arable fields that affect the sequestration potential. Sequestering carbon in the soil involves efficiently integrating carbon into the soil.

This comprehensive review investigates how drought stress alters biomass allocation in arid zone trees and the subsequent effects on carbon sequestration. A wide range of studies were analysed, examining how trees prioritize resource allocation under water-limited conditions. The present review assesses how these drought-induced changes impact overall tree growth, carbon storage capacity, and long-term resilience. For this comprehensive review, relevant papers highlighting drought stress adaptations in plants of semi-arid and arid regions were identified using keywords like biomass allocation, drought stress, climate change, arid region, carbon sequestration, carbon storage, drought response, and drought adaptations. Databases like the Web of Science, ScienceDirect, Scopus, and JStore, etc. were referred to. In the next step, the studies relevant to our objectives were identified and thoroughly analysed to compile the gathered information and data.

## 2. DROUGHT-INDUCED SHIFTS IN BIOMASS ALLOCATION AMONG ARID ZONE TREES

A vital aspect of plant growth and survival is biomass allocation, which is a strategic allocation of resources across various plant parts (Poorter et al. 2012). It exhibits a complex equilibrium between the acquisition and use of resources, impacted by environmental cues as well as genetic predisposition (McConnaughay & Coleman 1999). Broadly, plants have two main allocation strategies. First is the optimal partitioning theory, which posits that plants allocate resources to maximize their growth rate by prioritizing organs that acquire the most limiting resource (Bloom et al. 1985). For example, to improve nitrogen uptake in nutrient-poor soils, a higher percentage of biomass may be sent into the roots. On the other hand, to maximize light interception, plants may invest more in their leaves when growing in shade (Poorter & Nagel 2000). The second allocation strategy is functional equilibrium theory, which states that plants maintain a balanced pattern of allocation to fulfill the needs of various organs in a way that ensures overall fitness (Davidson 1969). This method puts stability and adaptability ahead of maximizing growth under any given circumstance.

Allocating biomass is not static. It is a dynamic process that adapts to environmental fluctuations and a plant's life cycle. The way arid zone trees allocate their resources, like water and nutrients, is a carefully balanced process influenced by a complex interplay of genetic, phenotypic, and environmental factors. A specific mechanism in trees mediated by the enzyme hexokinase allows them to quantify carbohydrates and allocate resources to various organs as required (Chaves et al. 2003).

The genetic makeup of a tree species profoundly influences its inherent biomass allocation strategy. Evolutionary pressures in arid environments have been selected for specific traits that enhance survival and reproduction under water-limited conditions. For instance, some species exhibit a predisposition towards greater root allocation, facilitating access to deeper soil moisture (Schenk & Jackson 2002; Lopez et al. 2021). Others might prioritize investment in thick, waxy leaves to minimize water loss through transpiration (Lambers 2022). These genetic adaptations provide a baseline for biomass allocation patterns, but they are not immutable.

Phenotypic plasticity, the ability of an individual plant to modify its traits in response to environmental cues, adds another layer of complexity to biomass allocation (Valladares et al. 2014). This adaptability allows trees to fine-tune their resource distribution to match prevailing conditions. For example, in the face of drought, a tree might decrease its leaf area to reduce transpiration while simultaneously increasing root growth to explore deeper soil layers for moisture (Anderegg & Anderegg 2013). This flexibility is critical for survival in the unpredictable environments of arid zones. However, on exposing saplings of *Pinus edulis* and *Juniperus osteosperma* to drought conditions, it was found that their branches showed severe hydraulic impairment as compared to mature trees due to restricted root networks in saplings and cavitation of xylem tissues (Anderegg & Anderegg 2013).

Environmental factors exert a powerful influence on biomass allocation, often overriding genetic predispositions. Water scarcity is perhaps the most potent driver of biomass allocation shifts in arid-zone trees. Drought stress typically activates a reallocation of resources from aboveground organs (leaves, stems) to belowground roots, enhancing water uptake capacity (Lombardini & Rossi 2019). However, the extent and timing of this response vary among species and depend on drought severity and duration. Temperature extremes, both high and low, can significantly alter biomass allocation. Elevated temperatures often accelerate growth rates, leading to a greater allocation to aboveground biomass, particularly leaves, to maximize photosynthetic capacity (Korner 2003). Conversely, freezing temperatures can damage leaves and stems, prompting a shift in allocation toward storage organs and protective tissues (Bhattacharya 2022). Light availability plays a pivotal role in determining the balance between leaf and root investment. In sun-drenched environments, trees tend to allocate more resources to leaves to optimize photosynthesis, while in shaded conditions, a greater proportion might be directed toward stem elongation to reach sunlight (Valladares & Niinemets 2008). Biomass allocation in arid-zone trees involves the calculated distribution of acquired resources across four key components: roots, stems, leaves, and reproductive structures. Each component plays a crucial role in plant survival, growth, and reproduction, and their relative allocation reflects a delicate balance between competing demands for resources (Poorter et al. 2012).

Drought stress triggers a cascade of physiological responses in arid zone trees aimed at mitigating the detrimental effects of water scarcity and maintaining essential functions. These responses involve intricate adjustments at the cellular, tissue, and organ levels, encompassing a wide range of biochemical, physiological, and morphological changes. The physiological responses to drought vary significantly among tree species, reflecting their diverse evolutionary histories and adaptive strategies. Some adaptive strategies of arid zone trees have been summarised in Table 1.

**Table 1:** Physiological Adaptations to Drought Stress in Select Arid Zone Tree Species

| Tree Species | Drought Response | References |
|---|---|---|
| *Acacia aneura* (Mulga) | Increased root shoot ratio, osmotic adjustment, reduced leaf area | Bartlett et al. 2012; Peters 2019 |
| *Prosopis juliflora* (Mesquite) | Deep root growth, reduced stomatal conductance, leaf shedding | Oliveira et al. 2017 |
| *Pinus edulis* (Pinyon Pine) | Reduced photosynthesis, increased antioxidant production, and hydraulic adjustments | Breshears et al. 2005; Anderegg & Anderegg 2013 |
| *Quercus ilex* (Holm Oak) | Osmotic adjustment, antioxidant production, reduced stomatal conductance | Flexas & Medrano 2002 |
| *Juniperus monosperma* (One-seed Juniper) | Increased root growth, reduced leaf area, stem dieback | McDowell et al. 2008; Atia et al. 2014 |
| *Eucalyptus camaldulensis* (River Red Gum) | Deep root growth, reduced leaf area, and hydraulic adjustments | Duursma et al. 2011 |
| *Olea europaea* (Olive) | Osmotic adjustment, reduced stomatal conductance, leaf shedding | Chaves et al. 2003; Bacelar et al. 2007 |
| *Erythrina velutina* | Downregulates photosynthesis, reduced leaf gas exchange, improved water use efficiency | Leite et al. 2022 |
| *Poincianella pyramidalis* | Reduced photosynthetic activity | Leite et al. 2022 |

### 2.1. Adaptation strategies in roots and stems

Roots serve as the anchors of trees, providing stability and access to water and nutrients from the soil. In arid environments, where water scarcity is a major constraint, root systems often exhibit specialized adaptations to maximize water uptake. These adaptations are displayed as deep root systems, shallow root systems, or root symbioses. Many arid zone trees develop extensive root systems that penetrate deep into the soil to tap into groundwater reserves (Schenk & Jackson 2002), ensuring a reliable water source during prolonged droughts. In contrast, some species have shallow, widespread root systems that efficiently capture water through infrequent rainfall events (Ehleringer & Dawson 1992). Some arid zone trees form mutualistic associations with mycorrhizal fungi, which enhance nutrient uptake, particularly phosphorus, in exchange for carbohydrates (Smith & Read 2010; Ma et al. 2018). The allocation of biomass to roots can vary significantly among species and in response to environmental cues. Drought stress typically triggers an increased allocation to roots at the expense of aboveground organs, reflecting the priority of water acquisition under water-limited conditions (Anderegg & Anderegg 2013; Ma et al. 2018).

Stems provide structural support for leaves and reproductive organs, ensuring optimal positioning for photosynthesis and reproduction. They also serve as conduits for the transport of water, nutrients, and carbohydrates between roots and leaves. In arid environments, stem adaptations may include: Thick bark that protects against fire damage, a common threat in dry ecosystems, and reduces water loss through evaporation (Rossatto et al. 2009). Some species have succulent stems that store water, providing a buffer against drought. For example, *Pachycormus discolour* and *Bursera microphylla* are tree species found in Mexico's arid regions that show stem succulence (Bashan et al. 2006; Nobel 2009). A less branched architecture can minimize water loss by reducing the surface area for transpiration (Bhattacharya 2022). Biomass allocation to stems is generally lower than that to roots and leaves, but it can increase in response to light competition, where trees need to grow taller to reach sunlight (Valladares & Niinemets 2008; Poorter et al. 2012).

### 2.2. Alteration in the root shoot ratio

The root shoot (RS) ratio, representing the relative allocation of biomass to roots versus aboveground organs (stems and leaves), is a critical indicator of plant resource allocation strategies and their adaptation to environmental conditions, especially drought stress in arid zone trees (Poorter et al. 2012). Drought-induced changes in the RS ratio are a fundamental aspect of plant acclimation to water scarcity. Under drought conditions, trees often increase their allocation to roots, enhancing their capacity to access water from deeper soil layers while reducing the demand for water by decreasing leaf area (Anderegg & Anderegg 2013; Ma et al. 2018). This shift in resource allocation is mediated by complex signaling pathways involving plant hormones (e.g., abscisic acid) and hydraulic signals, which communicate the water status from roots to shoots (Gargallo-Garriga et al. 2014). However, the magnitude and timing of RS ratio adjustments vary considerably among species and depend on factors like drought intensity, duration, soil properties, and the tree's developmental stage (Poorter et al. 2012). Some species exhibit a rapid and pronounced increase in RS ratio under drought, while others show a more gradual or limited response. Additionally, the plasticity of RS ratio can differ among genotypes within a species, reflecting their inherent drought tolerance (Padilla et al. 2007).

The implications of changes in RS ratio extend beyond water acquisition and plant survival. An increased RS ratio can enhance drought resistance by improving water uptake, reducing water loss through transpiration, and increasing access to nutrients in deeper soil layers (Volaire 2018). However, it may also come at a cost to aboveground growth and carbon sequestration, as resources are diverted from leaves and stems (Wiley & Helliker 2012). The optimal RS ratio for a given species in a particular environment is a dynamic equilibrium that balances the need for water and nutrient acquisition with the demands for growth and reproduction. Understanding these trade-offs is crucial for predicting the responses of arid zone trees to future climate change scenarios, which are expected to exacerbate drought stress in many regions. By elucidating the mechanisms and consequences of RS ratio adjustments, we can develop more effective strategies for managing and conserving these vulnerable ecosystems.

### 2.3. Alterations in Leaf Morphology and Physiology

Arid zone trees face the constant challenge of water scarcity, necessitating intricate adaptations to survive and reproduce. In arid environments, leaf adaptations may include reduced leaf area that helps reduce water loss through transpiration (Wright et al. 2004). A thick, waxy cuticle or compact trichome layer on leaves minimizes water loss and reflects excess sunlight, reducing heat stress. Some species have stomata sunken into pits or are covered with hairs to reduce water loss (Larcher 2003). Leaf allocation can vary depending on water availability, light intensity, and nutrient levels.

Leaves, the primary sites of photosynthesis, are particularly vulnerable to drought stress. Drought stress triggers profound alterations in leaf morphology, physiology, and reproductive output, showcasing the remarkable plasticity of these resilient plants. Physiologically, drought stress disrupts photosynthesis by limiting carbon dioxide uptake and impairing the photosynthetic machinery. Trees exhibit several morphological adaptations to reduce the area for transpiration and mitigate water loss. Under drought, trees often shed leaves, exhibit leaf curling, or reallocate reserves from older leaves to new leaves or stem to conserve water (Chaves et al. 2003). Conversely, increased light availability may promote greater investment in leaves to maximize photosynthesis (Anderegg et al. 2015). Reduced leaf area is a common morphological response, achieved through smaller leaf size or leaf shedding altogether (Anderegg et al. 2015; Li et al. 2019). Some species develop thicker leaves with denser cell layers, enhancing water storage capacity and reducing vulnerability to dehydration (Blackman et al. 2014).

Stomatal closure, a primary defence mechanism against water loss and the most immediate response to drought, restricts gas exchange and reduces carbon assimilation (McDowell et al. 2008). Stomata, the tiny pores on leaves, regulate gas exchange, including the uptake of carbon dioxide for photosynthesis and the release of water vapor through transpiration. Under drought conditions, trees close their stomata to conserve water, but this also reduces carbon uptake, limiting growth and potentially leading to carbon starvation (Grossiord et al. 2014; McDowell et al. 2016). To compensate, some species exhibit osmotic adjustment, accumulating solutes like proline and sugars in their cells to lower water potential and maintain turgor pressure, which is essential for cell expansion and growth (Bartlett et al. 2012; Geilmann et al. 2022). However, prolonged stomatal closure can lead to photoinhibition, where excess light energy damages the photosynthetic apparatus. To counteract this, trees activate photoprotective mechanisms, such as dissipating excess energy as heat or producing antioxidants to scavenge harmful reactive oxygen species (Flexas & Medrano 2002; Niinemets 2014). For instance, permanent photoinhibition occurred in *Acacia melanoxylon*, *Actinostrobus acuminatus* and *Eucalyptus tenuiramis* due to increased intracellular $CO_2$ and reduced stomatal activity, however, *Acacia aneura* had anisohydric reaction towards water stress and kept stomata open with better ability to balance carbon (Wujeska-Klause et al. 2014).

### 2.4. Other Physiological Adjustments

In addition to stomatal regulation and osmotic adjustment, arid zone trees employ other physiological strategies to cope with drought. These include:

- Antioxidant production: Drought stress leads to the accumulation of reactive oxygen species (ROS) that can damage cellular components. Trees counteract this by producing antioxidants like ascorbate and glutathione, which scavenge ROS and protect cells from oxidative damage (Das & Roychoudhury 2014).

- Hydraulic adjustments: Trees can modify their hydraulic architecture to maintain water transport under drought conditions. This may involve increasing root growth to access deeper water sources, reducing leaf area to minimize water loss, or altering the properties of xylem vessels to prevent embolism (Choat et al. 2012; Anderegg & Anderegg 2013).

- Changes in photosynthesis: Drought stress can disrupt photosynthesis, reducing carbon fixation and impacting growth. However, some species exhibit drought-induced photosynthetic acclimation, involving changes in leaf biochemistry and physiology to maintain or even enhance photosynthetic rates under water-limited conditions (Flexas & Medrano 2002; Niinemets 2014).

- Anisohydric water-spending strategy (Uni et al. 2023): A study conducted on *Acacia* species showed that despite growing in regions with low atmospheric and soil humidity, these trees show more stomatal activity and increased transpiration rates, mainly to cool down in extreme temperature conditions (around 40°C). This strategy allowed them to survive in extremely hot and dry conditions when other tree species cannot survive. However, the trees in semi-arid and Mediterranean forests like *Pinus halepensis* and *Quercus calliprinos* show water-conserving strategies with nearly zero transpiration rates and adopted conduction to reduce the canopy temperature.

### 2.5. Impacts on Reproductive Output

Reproductive structures, including flowers, fruits, and seeds, are essential for the continuation of a species. Reproduction is a resource-intensive process for trees, requiring substantial energy and nutrient investment. In arid environments, reproduction is often synchronized with periods of favorable conditions, such as rainfall events, to ensure seedling establishment. The allocation to reproductive structures can be highly variable, depending on the species' life history, strategy, and environmental conditions. Under drought stress, this investment is often curtailed to prioritize survival. Trees may reduce flower production, abort developing fruits, or produce smaller seeds with lower viability due to stomatal closure and subsequent restricted carbon availability. This may cause die-off in some important species, as reported in the case of *Cedrus atlantica* of North Algeria in extreme drought conditions (Allen et al. 2010). However, reduced reproductive output can have long-term consequences for population dynamics and genetic diversity (Jump & Penuelas 2005). Some species prioritize reproduction even under stress, while others delay reproduction until conditions improve (Felton & Smith 2017). Overall, these strategies conserve resources for essential maintenance processes and enhance the chances of survival during prolonged drought.

## 3. IMPACT OF DROUGHT INDUCED SHIFT ON CARBON SEQUESTRATION

Trees allocate the carbon they acquire through photosynthesis to various functions, including growth, maintenance, defence, and reproduction. Carbon storage occurs primarily in woody tissues (stems, branches, roots), where it contributes to the long-term carbon sink of forests (Ciais et al. 2014). However, drought stress can alter these allocation patterns, shifting resources away from growth and towards survival mechanisms. Trees prioritize survival strategies above growth as the length of the drought rises, depleting their energy stores. There is less carbon available for storage in long-lived tissues as a result of this change in allocation patterns, which lowers carbon sequestration (McDowell et al. 2008). Drought severity can further hasten this process by causing water stress quickly, which makes it more difficult for trees to allocate resources to growth and carbon storage. The ability to sequester $CO_2$ can be made worse by the combined effect of drought duration and intensity, which can seriously impair a tree's ability to absorb carbon.

### 3.1. Impact of drought on photosynthesis and carbon uptake

Drought stress impairs photosynthesis through multiple mechanisms. Stomatal closure, a primary response to water deficit, limits $CO_2$ uptake, while reduced leaf area decreases the overall photosynthetic capacity (Grossiord et al. 2014). Additionally, drought can disrupt the photosynthetic machinery within leaves, leading to decreased efficiency of light energy conversion and carbon fixation (Niinemets 2014). These impacts collectively reduce the amount of carbon a tree can acquire from the atmosphere, thus diminishing its carbon sequestration potential.

### 3.2. Changes in Respiration Rates

Respiration, the process by which trees release $CO_2$ as they break down stored carbohydrates for energy, is also affected by drought stress. While initial drought conditions may lead to decreased respiration due to reduced metabolic activity, prolonged or severe drought can increase respiration rates as trees struggle to maintain essential functions under stress (Rowland et al. 2015). This increased respiration further reduces the net carbon gain of trees, offsetting the carbon sequestered through photosynthesis.

### 3.3. Effects on Wood Density and Carbon Content

Drought stress can alter the wood density and carbon content of trees. Under drought, trees often produce denser wood with lower water content, which can increase the carbon density per unit volume (Marques 2023). However, the overall effect on carbon storage depends on the balance between wood density and total wood production. If drought significantly reduces growth, the increased carbon density may not compensate for the lower overall wood volume (Anderegg et al. 2015).

### 3.4. Overall Impact on Carbon Sequestration Potential

The combined effects of drought on carbon allocation, uptake, respiration, and wood properties ultimately determine its overall impact on carbon sequestration potential. While individual responses can vary among species and drought severity, a general trend of reduced carbon sequestration under drought stress is evident across arid ecosystems (Table 2).

**Table 2:** Impact of Drought Intensity on Carbon Sequestration in Selected Tree Species

| | Tree Species | Drought Intensity | Change in Carbon Sequestration | Reference |
|---|---|---|---|---|
| 1. | *Pinus edulis* | Moderate | -25 % | Anderegg & Anderegg 2013 |
| 2. | *Quercus ilex* | Severe | -40 % | Gargallo-Garriga et al. 2014 |

### 3.5. Species-Specific Responses and Adaptation Strategies

Tree species have evolved a remarkable array of responses and adaptation strategies to thrive in water-limited environments. These strategies are shaped by their evolutionary history, genetic makeup, and the specific environmental conditions they encounter. A range of drought tolerance and resilience are revealed by comparing different species, highlighting the variety of strategies used to deal with water constraints.

Arid zone tree species exhibit a wide range of drought tolerance and resilience, reflected in their physiological, morphological, and ecological traits. Some species, known as drought avoiders, minimize water loss through strategies like rapid stomatal closure, leaf shedding, and deep root systems (Chaves et al. 2003). Others, known as drought tolerators, possess physiological mechanisms that allow them to withstand low water potentials and maintain function under severe drought stress (Bartlett et al. 2012). These mechanisms include osmotic adjustment, antioxidant production, and hydraulic adjustments (Choat et al. 2012; Gargallo-Garriga 2014) that are depicted in Table 3.

**Table 3:** Drought Adaptation Strategies in Selected Arid Tree Species

| Species | Strategy | Adaptations | References |
|---|---|---|---|
| *Pinus edulis* | Avoidance | Increased water-use efficiency | Anderegg & Anderegg 2013 |

| | | | |
|---|---|---|---|
| *Quercus ilex* | Tolerance | Osmotic adjustment, antioxidant production, reduced stomatal conductance | Flexas & Medrano 2002; Gargallo-Garriga et al. 2014 |
| *Olea europaea* | Tolerance | Osmotic adjustment, reduced stomatal conductance, leaf shedding | Chaves et al. 2003; Bacelar et al. 2007 |
| *Populus euphratica* | Avoidance, | Increase in soluble sugars, decrease in peroxidase activity | Chen et al. 2022 |
| | Resistance | Increase in abscisic acid, decreased cytokinin | |

## 4. EVOLUTIONARY ADAPTATIONS TO ARID ENVIRONMENT

The remarkable diversity of drought responses observed in arid zone trees is a testament to millions of years of evolutionary adaptation to a water-limited environment (Choat et al. 2012). Natural selection has favoured traits that enhance survival and reproduction under arid conditions, resulting in a diverse array of morphological, physiological, and phenological adaptations (Anderegg et al. 2015).

Drought Deciduousness: A common strategy in arid zones is drought deciduousness, the shedding of leaves during periods of water scarcity. This reduces transpirational water loss and conserves resources for essential maintenance processes (Anderegg & Anderegg 2013). Species like *Acacia aneura* (mulga) and some *Prosopis* species exhibit this adaptation, allowing them to persist through prolonged droughts.

Leaf Modifications: Trees have evolved distinctive leaf modifications to thrive under high temperatures and irradiance. Smaller leaves reduce the surface area for transpiration, as seen in *Acacia* and *Eucalyptus* species (Li et al. 2019). Thick, waxy cuticles, as seen in *Olea europaea* (olive) and *Quercus ilex*, serve as a barrier against water loss and reflect excess sunlight, reducing heat stress (Peguero-Pina et al. 2020). Furthermore, the presence of sunken stomata and leaf hairs creates a humid microclimate around the leaf surface, minimizing the vapor pressure gradient and thus reducing transpiration (Oliveira et al. 2017). These adaptations collectively enable arid zone trees to optimize photosynthesis while minimizing water loss in harsh environments.

Root Adaptations: The root systems of arid zone trees have evolved diverse architectures to maximize water acquisition in challenging environments. Some species, like *Prosopis* and *Eucalyptus*, have developed extensive taproots capable of reaching deep groundwater sources (Oliveira et al. 2017). Conversely, other species, such as Acacia and certain grasses, have opted for shallow, widespread root systems that efficiently capture infrequent rainfall events near the surface (Ehleringer & Dawson 1992). These contrasting strategies highlight the adaptability of arid zone trees in securing water resources, ensuring their survival in water-limited ecosystems.

Physiological Mechanisms: Arid zone trees employ various physiological mechanisms to mitigate drought stress. They accumulate compatible solutes like proline, polyols and sugars, facilitating osmotic adjustment to maintain turgor and cell function under water deficit conditions (Bartlett et al. 2012). These compatible solutes help maintain osmotic pressure of the cell, protect the plants from stressors like heat waves, cold, drought, salt stress, and regulate cellular enzymatic activity and scavange harmful reactive oxygen species (ROS), acts as for cell membrane stabilizer. Furthermore, these trees counteract the increased production of damaging reactive oxygen species during drought stress by producing antioxidants such as ascorbate and glutathione (Das & Roychoudhury 2014). Additionally, they modify their xylem structure to reduce the risk of embolism, ensuring water transport under drought conditions (Anderegg & Anderegg 2013; Choat et al. 2012). These physiological adaptations collectively enhance the resilience of arid zone trees in coping with water scarcity.

## 5. ADAPTIVE STRATEGIES FOR ARID AND SEMI-ARID TREES OF INDIA

India's arid and semi-arid regions, characterized by low rainfall, high temperatures, and erratic precipitation patterns, present significant challenges for plant growth and survival. These regions comprise about 48% of the country's geographical area, and about 700 million rural communities reside here (Singh & Chudasama 2021). The arid and semi-arid regions that include the Thar Desert, parts of Rajasthan, Gujarat, Madhya Pradesh, and the Deccan Plateau, are home to a diverse range of indigenous tree species that have evolved remarkable adaptations to cope with these harsh conditions.

Deep Root Systems: Many species, such as *Prosopis cineraria* (Khejri) and *Acacia nilotica*, have developed extensive root systems that can penetrate deep into the soil, reaching groundwater sources and providing stability (Bhansali 2010). *Acacia* species have efficient strategies to adapt and survive in arid and stressful environments, which is a positive indication for carbon sequestration in the current changing climate, frequent drought episodes, and drier environment (Uni et al. 2023).

Reduced Leaf Area: Small, leathery leaves with reduced stomatal density minimize water loss through transpiration. *Z. nummularia* a prominent desert tree found in the western plains of India, that exhibits several features to combat drought stress like reduction in leaf area and size, rolling of leaves and leaf shedding to prevent water loss (Sivalingam et al. 2021).

Succulence: Some species, like *Ziziphus lotus* and *Ziziphus mauritiana* (Ber), store water in their stems and leaves, serving as a reservoir during dry periods. *Z. lotus* adapts to oxidative stress by accumulating solutes (i.e., soluble sugars, proline) in leaves to compensate for reduced photosynthetic rates (Maraghni et al. 2011).

Nitrogen Fixation: Certain species, including *Prosopis* and *Acacia* species, form symbiotic relationships with nitrogen-fixing bacteria, enhancing nutrient availability in nutrient-poor soils (Tak & Gehlot 2019). Root symbiosis with rhizobium has been hypothesized to lead to increased stomatal activity, allowing the plant to conduct photosynthesis and gaseous exchange even in extreme water stress (Uni et al. 2023). Several rhizobia have been isolated from tree species like *Vachellia*, *Senegalia*, and *Prosopis*, restricted to specific tree species (Tak & Gehlot 2019).

Phenological Adaptations: Many species exhibit flexible phenological patterns, adjusting their flowering and fruiting times to coincide with periods of favourable moisture availability.

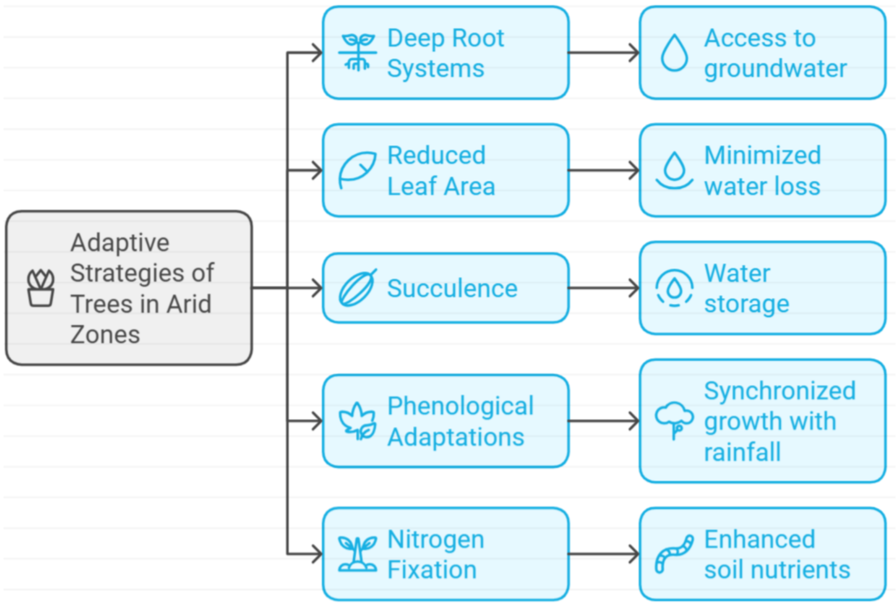


**Fig. 1**: Adaptive Strategies of Trees in Arid Zones

The intricate interplay between biomass allocation and carbon sequestration in arid zone trees highlights the delicate balance between survival, growth, and environmental constraints. The shift in biomass from aboveground organs to roots, while crucial for water acquisition, can compromise carbon storage and overall ecosystem productivity. The diverse array of physiological and morphological adaptations observed across species reveals the remarkable resilience of arid zone trees to water scarcity (Fig. 1). However, the growing risk of climate change, with its potential to exacerbate drought frequency and intensity, raises concerns about the long-term sustainability of these ecosystems.

## 6. CONCLUSION

Understanding the nuances of species-specific responses to drought is essential for developing efficient conservation and management strategies. While some species exhibit remarkable drought tolerance, others may be more vulnerable to prolonged or severe water deficits. Identifying the thresholds at which drought-induced shifts in biomass allocation become detrimental to carbon sequestration is crucial for predicting the future trajectory of arid ecosystems under a changing climate.

In conclusion, this comprehensive review explores the intricate relationship between biomass allocation and carbon sequestration in arid zone trees. Our review underscores the dynamic nature of resource allocation in response to drought stress. Drought stress triggers a cascade of responses, including shifts in resource allocation, modifications in leaf morphology and physiology, and impacts on reproductive output. These changes have profound implications for the carbon sequestration potential of arid ecosystems, with possible consequences for global carbon cycling and climate change mitigation efforts. By delving into the diverse strategies employed by arid zone trees to cope with water scarcity, we gain a deeper insight for their resilience and adaptability. However, the escalating threat of climate change underscores the urgency of understanding the complex interplay between biomass allocation, carbon sequestration, and drought stress. Continued research in this field is essential for developing evidence-based conservation and management practices that can safeguard these vulnerable ecosystems and their critical role in mitigating climate change. The review does not fully address how drought interacts with other stressors (e.g., rising temperatures, $CO_2$ levels, soil salinity) to alter biomass allocation and carbon storage. The review emphasizes root biomass shifts but lacks detailed insights into root exudation, microbial interactions, and their role in soil carbon storage under drought. Most studies focus on individual trees; scaling these findings to ecosystem-level carbon budgets under climate change scenarios is limited.

Future research should focus on investigating the complex mechanisms underlying biomass allocation decisions in arid zone trees, particularly the interplay between genetic predisposition, phenotypic plasticity, and environmental cues. Investigating the molecular and physiological pathways involved in drought responses can provide valuable insights into the adaptive potential of these species. Furthermore, integrating field studies with modeling approaches can help predict the long-term consequences of drought on carbon sequestration and ecosystem dynamics.

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