

Research review

Plant root mechanisms and their effects on carbon and nutrient accumulation in desert ecosystems under changes in land use and climate

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Summary

Deserts represent key carbon reservoirs, yet as these systems are threatened this has implications for biodiversity and climate change. This review focuses on how these changes affect desert ecosystems, particularly plant root systems and their impact on carbon and mineral nutrient stocks. Desert plants have diverse root architectures shaped by water acquisition strategies, affecting plant biomass and overall carbon and nutrient stocks. Climate change can disrupt desert plant communities, with droughts impacting both shallow and deep-rooted plants as groundwater levels fluctuate. Vegetation management practices, like grazing, significantly influence plant communities, soil composition, root microorganisms, biomass, and nutrient stocks. Shallow-rooted plants are particularly susceptible to climate change and human interference. To safeguard desert ecosystems, understanding root architecture and deep soil layers is crucial. Implementing strategic management practices such as reducing grazing pressure, maintaining moderate harvesting levels, and adopting moderate fertilization can help preserve plant–soil systems. Employing socio-ecological approaches for community restoration enhances carbon and nutrient retention, limits desert expansion, and reduces CO₂ emissions. This review underscores the importance of investigating belowground plant processes and their role in shaping desert landscapes, emphasizing the urgent need for a comprehensive understanding of desert ecosystems.

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Introduction

Arid and hyper-arid landscapes encompass 14.6% and 4.2% of Earth's terrestrial surface, respectively. These regions support significant populations engaged in livestock production for food, fuel, and fibre (Abd El-Ghani *et al.*, 2017). Arid and hyper-arid ecosystems have mean annual precipitations (MAP) below

250 mm, and precipitation to potential evapotranspiration ratios (MAP : PET) below 0.20 and 0.03, respectively, and both are referred as deserts (Holzapfel, 2008). Plants in deserts exhibit unique characteristics as surviving under extreme climates necessitate morphological and physiological adaptations (Holzapfel, 2008; Abd El-Ghani *et al.*, 2017). Despite their ecological significance, these systems, with their distinct biotic communities

and crop wild relatives, often face threats and are frequently overlooked (Zhang *et al.*, 2023). While arid ecosystems span a range of aridity levels, deserts represent the extreme end and are frequently marginalized from a conservation standpoint. Despite hosting fewer species than humid tropics (Safriel & Zafar, 2005), deserts exhibit high functional diversity and endemism. Consequently, the loss of species in these ecosystems can have a more pronounced impact than in wetter and species-rich regions (Maestre *et al.*, 2021). Furthermore, restoring degraded desert ecosystems requires specialized strategies due to their limited capacity for regeneration and growth (Principe *et al.*, 2014). As a result, desert ecosystems hold a unique position and necessitate significant attention due to their heightened vulnerability to climate change and human activities. Furthermore, desertification and the expansion of deserts continue to be viewed as problems, overshadowing the much more nuanced impacts of climate change on desert ecosystems, as well as the distinct impacts of various facets of environmental change on different plant communities. Plants and microorganisms in deserts suffer multiple abiotic stresses, mainly derived from long lapses of low water availability, soil salinity, low nutrient content and mobility, extreme temperatures, high irradiance, and frequent wind and sand storms (Alsharif *et al.*, 2020). The biota in these regions heavily rely on intermittent water pulses that occur at irregular intervals, making rainfall a pivotal factor influencing plant growth and soil microorganismal activity (Saul-Tcherkas & Steinberger, 2009; Collins *et al.*, 2017; Roncero-Ramos *et al.*, 2022; Vikram *et al.*, 2023). Additionally, geochemical cycles operate sluggishly in deserts due to their harsh and water-deprived environments, resulting in limited nutrient availability and mobility in the soil (Tariq *et al.*, 2022a; Maurice *et al.*, 2023). Consequently, diverse desert plant species exhibit unique morpho-physiological adaptations in their leaf, stem, and root architectures to ensure survival. However, while aboveground organs have been extensively studied due to their accessibility, adaptations of root systems and their consequences have largely been neglected (Alsharif *et al.*, 2020; Kirschner *et al.*, 2021). Water acquisition in desert plants primarily occurs through the soil, making distinct root architectures crucial for survival (Lynch, 2022). Root-system architecture (RSA) significantly influences water access, nutrient acquisition, carbon (C) sequestration, and overall plant function (Maeght *et al.*, 2013). Thus, the characteristic root structure of desert plants, whether deep or shallow, impacts C and nutrient stocks, as they give access to groundwater or rainwater, respectively, resulting in differential responses to environmental changes. Recently, the role of groundwater in C storage in deserts has been explored (Li *et al.*, 2016), but there remains a notable gap in understanding how RSA impacts nutrient and C accumulation in desert plant communities.

Plant communities and their specific structures dictate vegetation cover, soil properties, and microbial activities, thereby influencing C stocks and organic matter decomposition (Yang *et al.*, 2022; Lu *et al.*, 2023). Vegetation profoundly influences C accumulation in soil and aboveground and root biomass (Manning, 2008). In desert ecosystems, biomass allocation shifts towards the root system during water deficit conditions; C stocks in deep roots exhibit greater stability and longevity than aboveground

components (Kell, 2011). By contrast, aboveground biomass is more susceptible to land-use changes (such as fire, grazing, harvesting) and climate perturbations, resulting in increased C release into the atmosphere and exacerbating climate change. Additionally, reduced biomass density in deserts can be attributed to both environmental limitations (soil nutrients, seasonal precipitation and temperature distribution) and anthropogenic disturbances, further contributing to lower nutrient and C stocks in the plant–soil system (Houghton *et al.*, 2009).

In addition to natural ecological processes, human management practices (such as harvesting, vegetation burning and grazing) used for agricultural management in deserts negatively impact C and nutrient accumulation and cycling (Marks *et al.*, 2008; Escolano *et al.*, 2018; Tariq *et al.*, 2022a; Geng *et al.*, 2023; Wang *et al.*, 2023). The influence of agricultural and livestock management in arid ecosystems varies depending on the architecture, specifically the root architecture, of the present plant species (Gurrero-campo *et al.*, 2006; Paula & Pausas, 2011). Deep-rooted plants are often capable of resprouting after disturbances maintain stable C and nutrient stocks in the soil, but as shallow-rooted plants depend on sporadic surface water inputs for growth, they change their root system size more frequently and consequently the C and nutrient stocks (Gurrero-campo *et al.*, 2006; Paula & Pausas, 2011). Given the projected increases in aridity (Feng & Fu, 2013; Spinoni *et al.*, 2021) and changes in use, such as resource overexploitation (Hein & De Ridder, 2006; Huang *et al.*, 2019), understanding the vulnerability of various species is crucial to allow management and facilitate sustainable use.

This review primarily aims to dissect the mechanisms influencing C and mineral nutrient accumulation in deserts, specifically focusing on plant morphology, particularly root systems, and how these factors are shaped by human land use and climate change. We gathered information and data using different search engines and databases (Supporting Information Methods S1) to explore three hypotheses: (1) water table depth and the frequency of drought vs rainfall shape plant communities based on various root strategies and architectures, influencing C and mineral nutrient stocks in roots and soil; (2) differing root system architectures shape plant responses to diverse environmental changes; and (3) land-use practices decrease C and nutrient stocks in the soil, a decline that could be further exacerbated by climate change. The ultimate goal of this review is to deepen our understanding of how climate change and land use (and other management changes) impact C and mineral nutrient stocks within plant–soil systems in desert ecosystems. This examination predominantly focuses on plant root architecture and its adaptive capacity while identifying existing knowledge gaps.

Plant root architecture in desert ecosystems

Plants obtain water from various sources in desert environments, including rainfall (Zoccatelli *et al.*, 2019), snowmelt, dew (Matos *et al.*, 2022), and groundwater (Glanville *et al.*, 2023; Liu *et al.*, 2023). Rainfall in deserts is both scarce and unpredictable, characterized by significant year-to-year variability (Li *et al.*, 2016). Hot deserts exhibit spatial variability in rainfall, often confined to

small regions. By contrast, cold deserts receive precipitation in the form of snow, blanketing the entire surface and providing liquid water to plants during the warm growth season (Fan *et al.*, 2014). Dew is an additional water source for plants, particularly in coastal deserts, where it is absorbed by leaves and subsequently transported to drier stems and roots (Kidron & Starinsky, 2019). Moreover, desert plants have the capacity to draw water from the water table and nearby surface water bodies. Yet, given that desert plants predominantly acquire water through their roots from dry soils, the distinctive architectures of their root systems are critical for survival (Lynch, 1995).

We have broadly categorized desert plants into five groups (Fig. 1; Notes S1), which generally align with deep or shallow-rooting strategies, particularly among longer-lived species. Some species may exhibit traits spanning multiple groups or falling in between. Among deep-rooted species, the first group, termed phreatophytes, encompasses trees, shrubs, and several perennial herbs with root systems extending beyond 5 m (Hukin *et al.*, 2005; Cooper *et al.*, 2006; Xu *et al.*, 2007; X. Wang *et al.*, 2015). The second group in Fig. 1, also deep-rooted, comprises trees, palms, shrubs, and herbs with deep roots but restricted to water table near the soil surface (shallower than 5 m) (Otieno *et al.*, 2005; Mata-González *et al.*, 2022). Members of these two groups often exhibit characteristics such as small leaves, photosynthetic stems, thick cuticles, trichomes, finely tuned stomatal control, and encrypted stomata (Šantrůček, 2022) to minimize water loss. Roots and shoots have the capacity to accumulate osmolytes to maintain a potential gradient to water entrance (Nilsen *et al.*, 1984; Arndt *et al.*, 2004a; Silveira *et al.*, 2009). Shallow-rooting species form the third group, which includes cacti and succulents that store substantial water in their roots, stems, or leaves. These plants require relatively frequent rainfall to replenish their water reservoirs (Dubrovsky & North, 2002; Nobel, 2002; Bacilio *et al.*, 2011). When rainfall does occur, they can rapidly develop new roots and store water in their stem or root, preventing loss by embolizing conductor vessels to secure a long-term water supply for ensuing extended drought periods until the next rainfall event (Snyman, 2006; Kim *et al.*, 2018). Roots, leaves and stems of succulents and cacti have a high water capacitance, with aerenchyma and cells with very low matric potential due to the accumulation of mucilage (Su, 2010; Mohanta *et al.*, 2023). The fourth group, also relies on shallow roots, and consists of perennial grasses, herbs, and shrubs that employ metabolic slowdown, osmolytes accumulation, heightened antioxidants, during dry seasons to avoid shoot water stress (Hultine *et al.*, 2018). These plants can resume growth promptly after a rainfall, maintaining root and/or stem viability throughout the dry period and producing leaves when soil moisture becomes available. Resurrection plants are exemplary of this category, retaining dehydrated leaves during dry periods and rapidly resuming photosynthesis upon rainfall. Such plants can remain dormant for extended periods in dry periods, ranging from several months to one or two years, only to swiftly re-engage in photosynthesis when rehydrate (Bechtold, 2018). Finally, the fifth group comprises ephemeral plants characterized by extremely shallow root systems (Lu *et al.*, 2022). These plants germinate or sprout from bulbs following rainfall and complete their life cycle

within a few days due to their rapid growth rate, due to limited duration of rainfalls.

Deep-rooted plants, primarily belonging to group 1, possess the ability to access water and nutrients (Zeng *et al.*, 2013) that percolate through the soil in a vertical manner (Fig. 2). This includes mobile ions such as nitrate, potassium, and sulphate (Lynch, 2022). These plants, prevalent in desert regions, develop roots that extend deep into the subsoil. These deeper roots typically exhibit steeper angles and more developed root cap, which promote vertical exploration (Kirschner *et al.*, 2021). Furthermore, these roots tend to possess reduced root density, particularly in the primary root or crown, aiming to minimize competition among roots and allocate more resources to a smaller number of roots. This strategy stimulates growth and development while enabling exploration of larger soil volumes. However, deep-rooted plants, during dry soil conditions, often develop few and short root hairs (Shishkova & Dubrovsky, 2005). In adverse conditions, these roots often form aerenchyma tissue – air-filled tissue – which serves to counter hypoxia. This adaptation facilitates gas exchange and deep rooting, complemented by the development of xylem vessels to transport water and nutrients (Lynch, 2022). This root architecture strategy is termed ‘steep-cheap-deep’ (SCD) or the herringbone strategy. Plants employing this approach can effectively avoid competition for water and nutrients with shallow-rooted plants in mixed communities, as they are able to reach deeper soil layers.

Contrary to deep-root strategies, shallow-rooted plants generally adopt a rooting strategy that optimally explores the topsoil, where less-mobile nutrients such as phosphate, ammonium, and zinc tend to accumulate (Lynch, 2022). For many species, following rainfall events, shallow roots swiftly emerge horizontally to maximize the uptake of water and nutrients from the topsoil. This enables them to efficiently capitalize on the resource-rich topsoil while avoiding the resource investment required during prolonged dry periods between rainfalls, when soil water is depleted. As a result, these plants channel their resources into root growth only when the benefits outweigh the investment, ensuring effective resource acquisition (Lynch *et al.*, 2012). The angle between the roots tends to be shallower since a broader area of the crown root region needs more roots to provide coverage. Similar to deep-rooted plants, shallow-rooted plants also employ aerenchyma to thrive in challenging environments, enhancing root growth while minimizing associated costs (Lynch, 2007), and develop root cap to protect young root tips from exploring soil (Bhanot *et al.*, 2021; Rüger *et al.*, 2023). However, the aerenchyma and root cap of shallow-rooted plants are less developed compared to the deep-rooted plants. Additionally, shallow-rooted plants develop longer and more abundant root hairs, facilitating nutrient uptake, particularly for phosphorus (P) (York *et al.*, 2013; Lynch, 2019). Low P levels induce root hair formation and elongation, with the degree of response varying among genotypes and species (Bates & Lynch, 1996). This strategy of shallow rooting is often termed ‘topsoil foraging’ (Lynch, 2022). Plants adopting the ‘topsoil foraging’ strategy can utilize the water and nutrients transported by deep-rooted plants from the deeper soil layers to supplement water

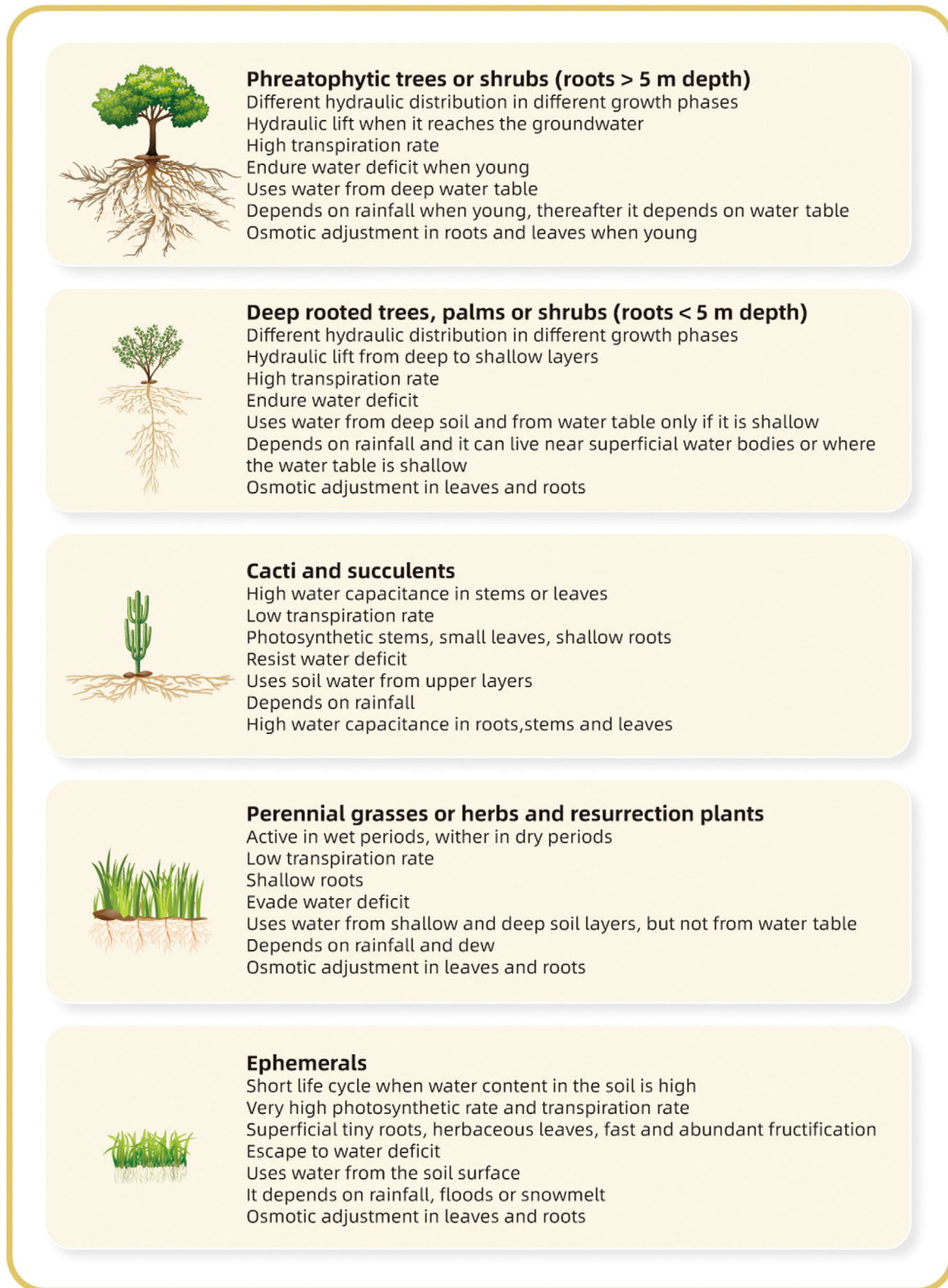


Fig. 1 Summary of the plant types that can be found in deserts.

scarcity caused by prolonged drought (Hultine *et al.*, 2003a,b, 2004; Scholz *et al.*, 2007, 2008, 2010; Barron-Gafford *et al.*, 2017). This strategy sustains the long-term stability of mixed community

structures in arid and nutrient-deficient environments. These contrasting architectures have implications for other root functions, which we will discuss further in this review.

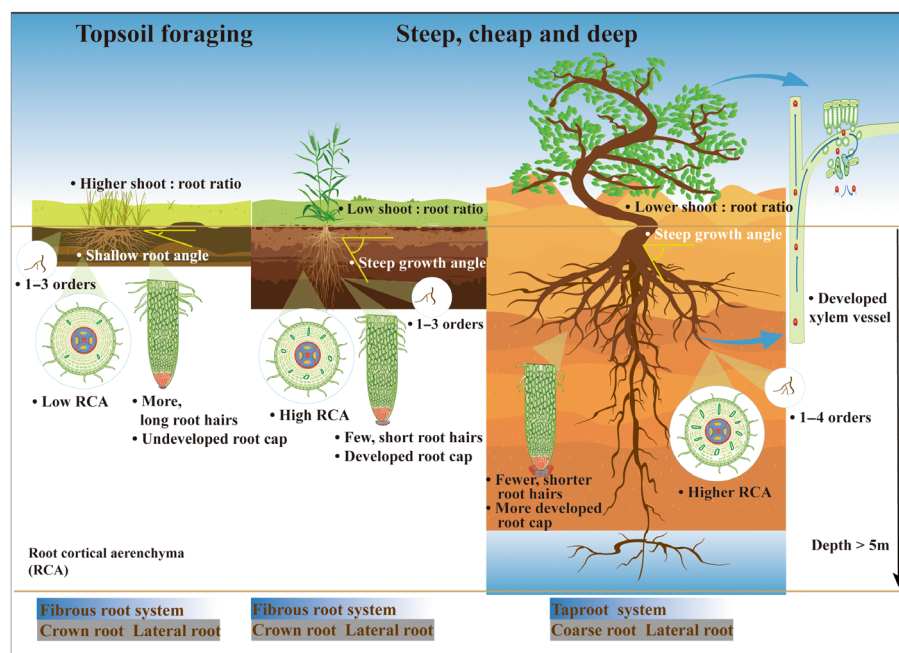


Fig. 2 Conceptual diagram of root architecture strategies of deep and shallow-rooted plants. The RCA stands for 'root cortical aerenchyma'.

Carbon and nutrient stocks in desert ecosystems

Root architecture not only shapes water uptake but also governs C uptake and sequestration. Deserts play a crucial role in C sequestration, encompassing both soil inorganic (SIC) and soil organic (SOC) carbon stocks (Fig. 3). Vegetation significantly influences C accumulation in the soil as well as in aboveground and root biomass (Manning, 2008). Desert soils frequently exhibit elevated concentrations of SIC (Schlesinger, 2017), with SIC stocks being 10 times greater than SOC stocks (L. Wang *et al.*, 2015). Given its greater stability compared to SOC, SIC significantly impacts desert C cycling (McKenna *et al.*, 2022). Desert plants contribute substantially to carbonate formation, enhancing SIC storage. For example, the introduction of deep-rooted pine and poplar trees in the Badain Jaran Desert, China, significantly fostered SIC accumulation (Gao *et al.*, 2017).

Plants also exert a notable influence on soil microorganism activity, which in turn affects C stocks and the decomposition of organic matter, ultimately shaping CO₂ emissions (Yang *et al.*, 2022). Beyond natural ecological processes, anthropogenic practices in deserts influence C accumulation and cycling. Activities such as vegetation burning for agricultural purposes and grazing of aboveground biomass led to significant C outflows from the system and alterations in plant dry mass partitioning. Conversely, irrigation and fertilization have a positive impact on C accumulation and cycling (Zhang *et al.*, 2021a; Yin *et al.*, 2021b).

Plant biomass, the allocation of C within plants, and the duration of C retention postassimilation are influenced by plant type (Fig. 3; Notes S2). Desert phreatophytes, deep-rooted plants, and perennial grasses exhibit higher root-to-shoot dry weight ratios (Zeng *et al.*, 2013) in contrast to cacti and succulents (averaging 12%) (Dubrovsky & Shishkova, 2013). The greater root biomass and long life of perennial grasses and shrubs fosters soil aggregation,

reducing soil erosion and C loss (Balazs *et al.*, 2022). Although the root biomass of cacti and succulents is low, they display extended turnover times once C is fixed through photosynthesis. Resurrection plants, perennial grasses, and herbs exhibit short-lived shoot biomass while maintaining slower root turnover due to their longer root lifespan. Up to 20% of the total biomass in these plant types accumulates as roots in the upper 20 cm of soil (Toledo *et al.*, 2022). By contrast, ephemeral plants exhibit high rates of C fixation over a short period, with the shoot and roots decomposing as the wet season conclude (Dubrovsky & Shishkova, 2013).

Apart from deep roots, fine root biomass also significantly contributes to C accumulation in desert plant communities (Tian *et al.*, 2022), with fine root biomass showing positive correlation with total root biomass, contingent on the seasons. Additionally, dead roots contribute to SOC increases (7–50 g m⁻² yr⁻¹). Furthermore, leaf litter accumulates in patches forming necromass C stocks in deserts. As necromass mixes with wet soil, microbial activity initiates and recirculates C and nutrients through SOC mineralization (Barnes *et al.*, 2015). Microorganisms inhabit the rhizosphere and biocrust, contributing to C fixation (Nara, 2006; Young *et al.*, 2022; Notes S3).

Arbuscular mycorrhizal fungi (AMF) communities are crucial in plant nutrient and water uptake (Notes S3), and exhibit variation among global arid lands (Vasar *et al.*, 2021). The extent of root colonization, fungal diversity, and the presence of AMF in deserts are influenced by micro-environmental factors such as temperature, pH, soil water content (SWC), salinity, and the composition of the plant community (Harrower & Gilbert, 2021). In general, desert ephemerals exhibit lower mycorrhizal associations compared to perennial grasses, shrubs, and trees (Apple, 2010). The symbiotic relationship between plants and AMF incurs a substantial C cost for plants, particularly during the wet season when fungi actively grow.

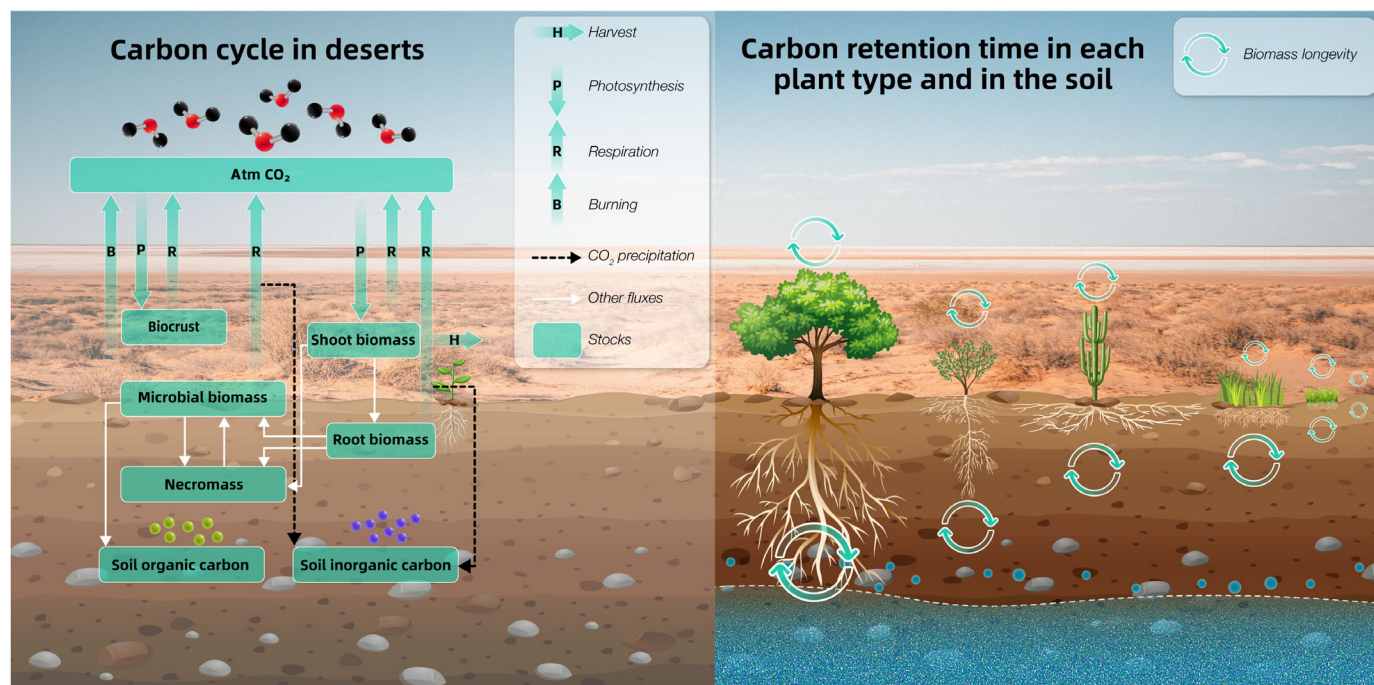


Fig. 3 Carbon cycle in deserts. Plant and soil biocrust photosynthesis incorporates atmospheric CO₂ to the ecosystem. Respiration of all the living organisms returns part of the C fixed by photosynthesis to the atmosphere. Part of the CO₂ from root and soil microorganism respiration can precipitate as carbonate and pass to the soil inorganic C stock through lixiviation. Harvest (anthropic or by animals) removes part of the C storage in plants, mainly in shoot biomass. Burning produces C emissions, from shoots biomass > necromass > soil organic carbon > roots biomass, depending on fire intensity and duration. Soil microorganisms are closely associated with roots, as they need water and organic substances delivered by roots. When plants die, the necromass is used by microorganisms, part is lost to the atmosphere as CO₂ and part becomes stable organic carbon, which increases soil water retention capacity and benefits plant and microorganism life. Biocrusts are not necessarily associated with plants and can grow in bare soil and rocks. Plants in the right panel represent the types described in Fig. 1, where C sequestration in biomass takes varying periods until it transitions to necromass; with longer spans depicted by the larger circular arrows. Ephemerals last for days to a few months, grasses and herbs live for a few years, while cacti, succulents, phreatophytes, and deep-rooted trees and shrubs live for several years (> 10 yr). Atm, Atmospheric.

The AMF hyphal network enhances the root access to water and nutrients during the dry season. Mycorrhizas are relevant in biogeochemical cycles because the increase in soil C relates to major nutrient concentrations particularly nitrogen (N) and P (Bell *et al.*, 2012). At the global level, the estimated storage of C, N, and P in the soil of desert ecosystems was 50.9, 0.3, and 0.6 g kg⁻¹, respectively (Z. Wang *et al.*, 2022).

Nutrient limitations are common in desert plants because following rainfall events water becomes available faster than nutrients, as decomposition is slow (Fig. 4). Decomposition primarily occurs on the soil surface, while roots extend deeper into areas where organic matter is scarce (Carrera *et al.*, 2008). Additionally, desert soils are typically coarse and poorly developed, resulting in low nutrient-holding capacity. Necromass and nutrients can be dispersed haphazardly with runoff, leading to patchy fertility distribution in deserts. Animals also contribute to the nutrient cycling through their faeces, creating ephemeral fertile patches that certain desert plants can exploit (Peek & Forseth, 2003). Hydraulic descent (downward siphoning) plays a significant role in young plants to facilitate root expansion process and redistributes water from shallow soil layers to deeper soil layers away from evaporation zones, while hydraulic redistribution (hydraulic lift) plays a crucial role once the plant reaches water

table to enhance organic matter decomposition and nutrient uptake near the soil surface (Hultine *et al.*, 2003a,b). Shallow-rooted grasses can receive up to 50% of their water from the hydraulic lift facilitated by the deep-rooted shrubs, for example *Artemisia tridentata* in the Great Basin Desert (Chapin *et al.*, 2011). Similarly, in the Taklamakan desert, *Alhagi sparsifolia* roots form symbiotic relationships with nitrogen-fixing bacteria even in saline soils, and the deep roots absorb substantial amounts of N from the water table (Arndt *et al.*, 2004b; Tariq *et al.*, 2022b).

To cope with low nutrient availability, desert plants employ a variety of strategies. Generally, nutrient stocks are closely linked to the overall biomass of plants and their distribution among different organs (B. Zhang *et al.*, 2018). Photosynthetic organs typically contain higher nutrient concentrations than roots; for instance, ephemerals exhibit rapid growth and often possess leaves with the highest nutrient concentration (Yuan *et al.*, 2009). Conversely, phreatophytes demonstrate greater adaptability and employ varied strategies for nutrient acquisition, depending on the nutrient availability in the soil, while still maintaining higher nutrient concentrations in the leaves (Yin *et al.*, 2021a,b; Gao *et al.*, 2023). Moreover, due to the limited mobility of nutrients in desert soils, changes in SWC significantly influence plant nutrient concentrations. Nutrients from parental minerals dissolve in water, becoming

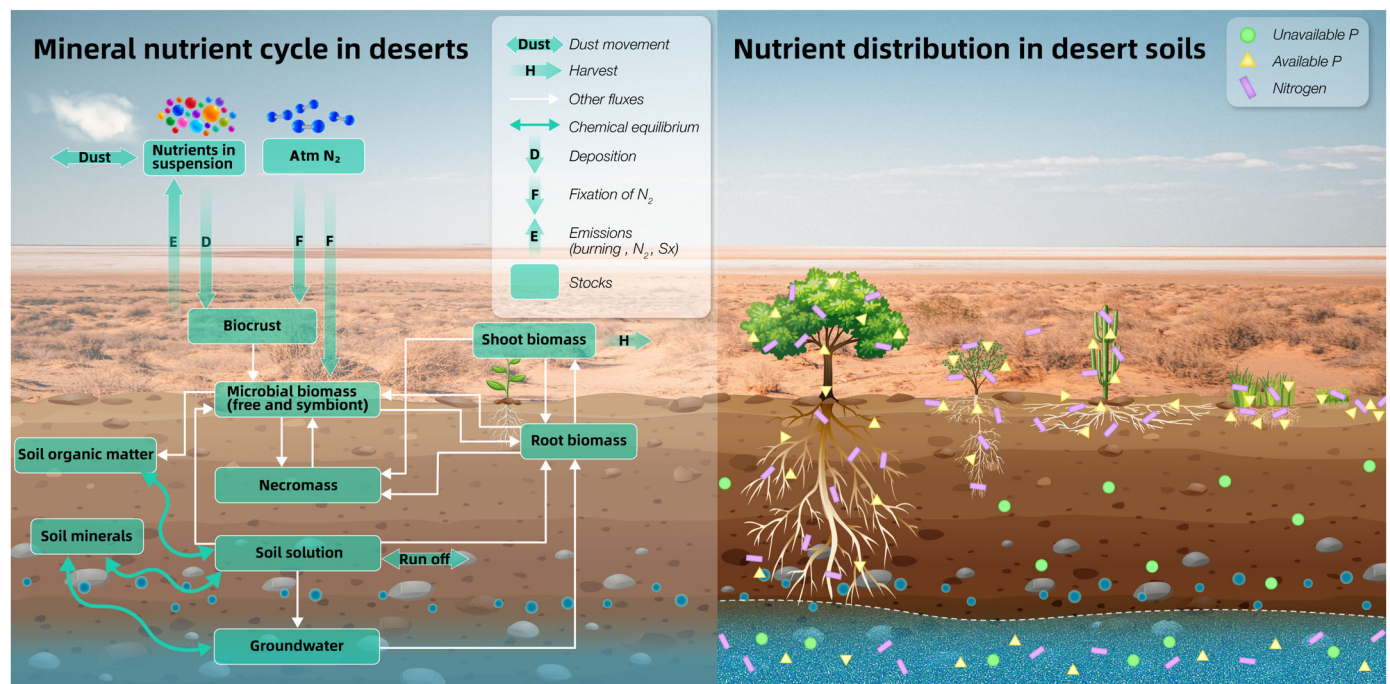


Fig. 4 Desert nutrient cycles. Nutrients arrive and leave by dust deposition or with the runoff of water after rainfall. Soil solution is in equilibrium with parental soil minerals and organic matter through anionic and cationic exchange capacity. Soil minerals also interact with nutrients diluted in the groundwater, which receives some nutrients from the upper layers through lixiviation. Roots and microorganism take up nutrients from the soil. Phreatophytes obtain some nutrients from groundwater. Nutrients taken up by roots are accumulated in stems and leaves (shoot), and the time retained in biomass depends on plant type (see carbon cycle in Fig. 3). When living organisms die, nutrients accumulate as necromass, that when water availability is enough, is used in part by microorganisms and in part is transformed into soil organic matter. Biocrusts intercept dust from air and use the minerals. Some components of biocrusts can fix N_2 from atmosphere, the same as free and root-symbiotic bacteria. Burning releases minerals to the atmosphere by oxidation of biomass, necromass, organic matter, and the ulterior ash blowing. Nutrient losses by fire depend on fire intensity and duration. The activity of soil biota and weather factors in soil organic matter formation, release N_2 , SO_2 , H_2S . Examples of these strategies are shown in Supporting Information Table S1. Plants in the right panel represent a higher stock of nitrogen and phosphorus in plant biomass and in the soil near roots, as nutrient mobility is low due to water scarcity, and organic matter plays a crucial role in nutrient accumulation. Biocrusts on bare soil also accumulate nutrients from dust and through nitrogen-fixing microorganisms. The water table contains nutrients in solution, accessible only for phreatophytes. Roots and microorganisms (primarily mycorrhizas, other fungi, and bacteria) solubilize phosphorus and contribute to the transition from unavailable to available phosphorus, given the low rate of weathering. Atm, Atmospheric.

accessible for phreatophytes near the water table, whereas other plant groups may be unable to reach these nutrients.

In addition, the ground surface of bare soil in desert ecosystems is frequently covered with cyanobacteria, lichens, mosses, and other photoautotrophic organism groups. The primary productivity of these groups can contribute to 1% of the net productivity of terrestrial ecosystems (Elbert *et al.*, 2012; Barger *et al.*, 2016). These groups can bind the surface soil for a few centimetres through cementation using algal filaments, mycelium, moss rhizoid, and secretions, along with soil surface particles, forming a biocrust covering 31% of the surface in arid regions (Rodríguez-Caballero *et al.*, 2018; Su *et al.*, 2020). Within biocrusts, phototrophic groups such as cyanobacteria and mosses play a crucial role in promoting the accumulation of organic matter and regulating soil C, N, and energy cycling processes (Zhou *et al.*, 2020a; Q. Wang *et al.*, 2022). Biocrusts can mineralize and dissolve insoluble inorganic P and organic P in the soil, sometimes forming 'fertile islands' due to their nutrient accumulation function (Pérez *et al.*, 2016; Bunn *et al.*, 2019). In addition to nutrients, biological soil crusts can enhance soil water infiltration and retention due to their high surface roughness, facilitating the germination of annual

short-lived plants in desert ecosystems (Zhang *et al.*, 2006). Thus, biocrusts emerge as a key feature of arid ecosystems, contributing significantly to nutrient and water accumulation and promoting positive succession in desert ecosystems.

Impact of land-use change on desert plant communities and carbon and nutrient stocks

Beyond natural ecological processes, human management practices in desert ecosystems, such as vegetation burning, biomass harvesting, grazing, and fertilization, wield substantial influence over C and nutrient accumulation and cycling by altering the allocation of plant dry mass. This section examines the repercussions of these agronomic practices on C and nutrient dynamics within plant–soil systems (Fig. 5).

Grazing

Grazing can have different impacts on arid ecosystems, affecting the plant community structure and the C sequestration capacity. Overgrazing can lead to biomass degradation, substantial C and

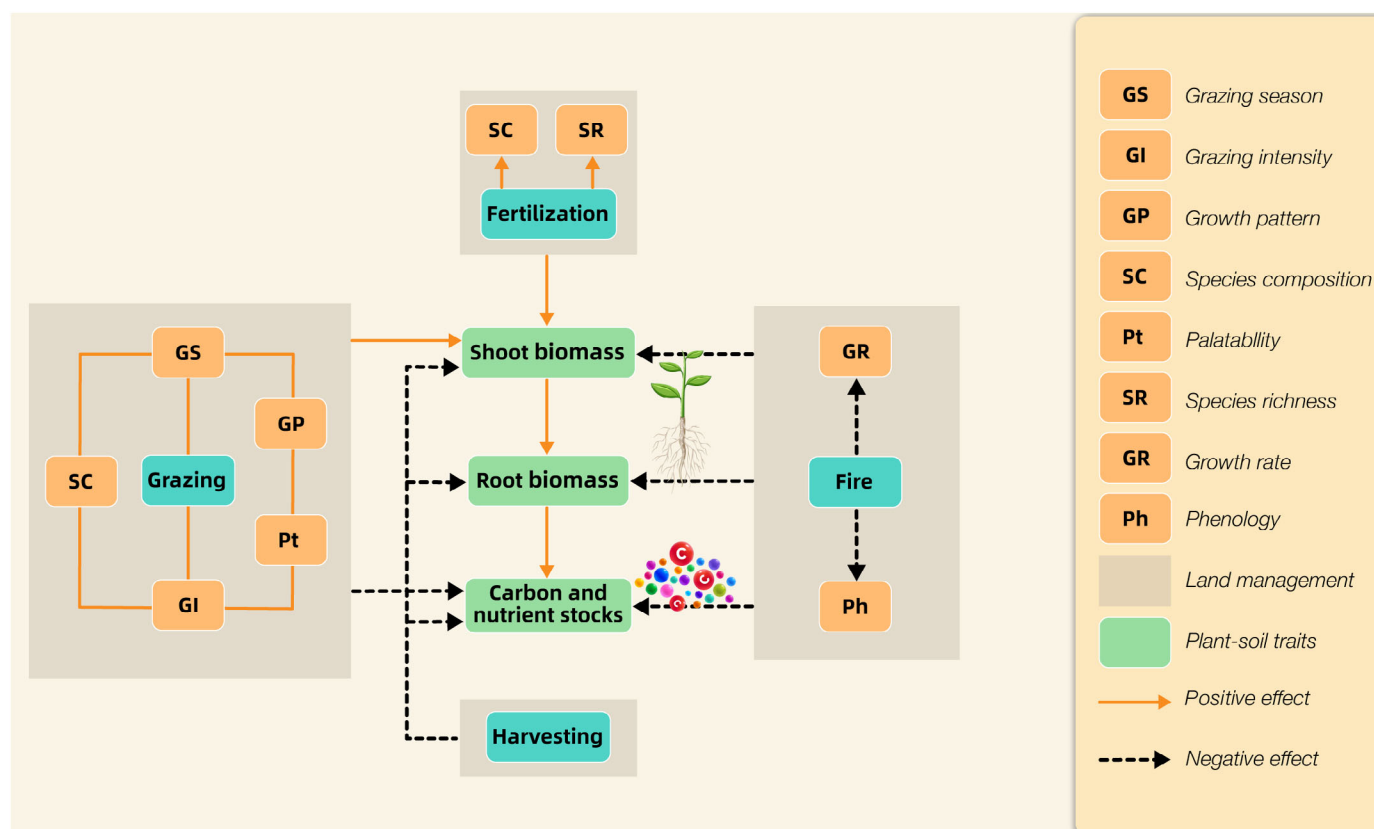
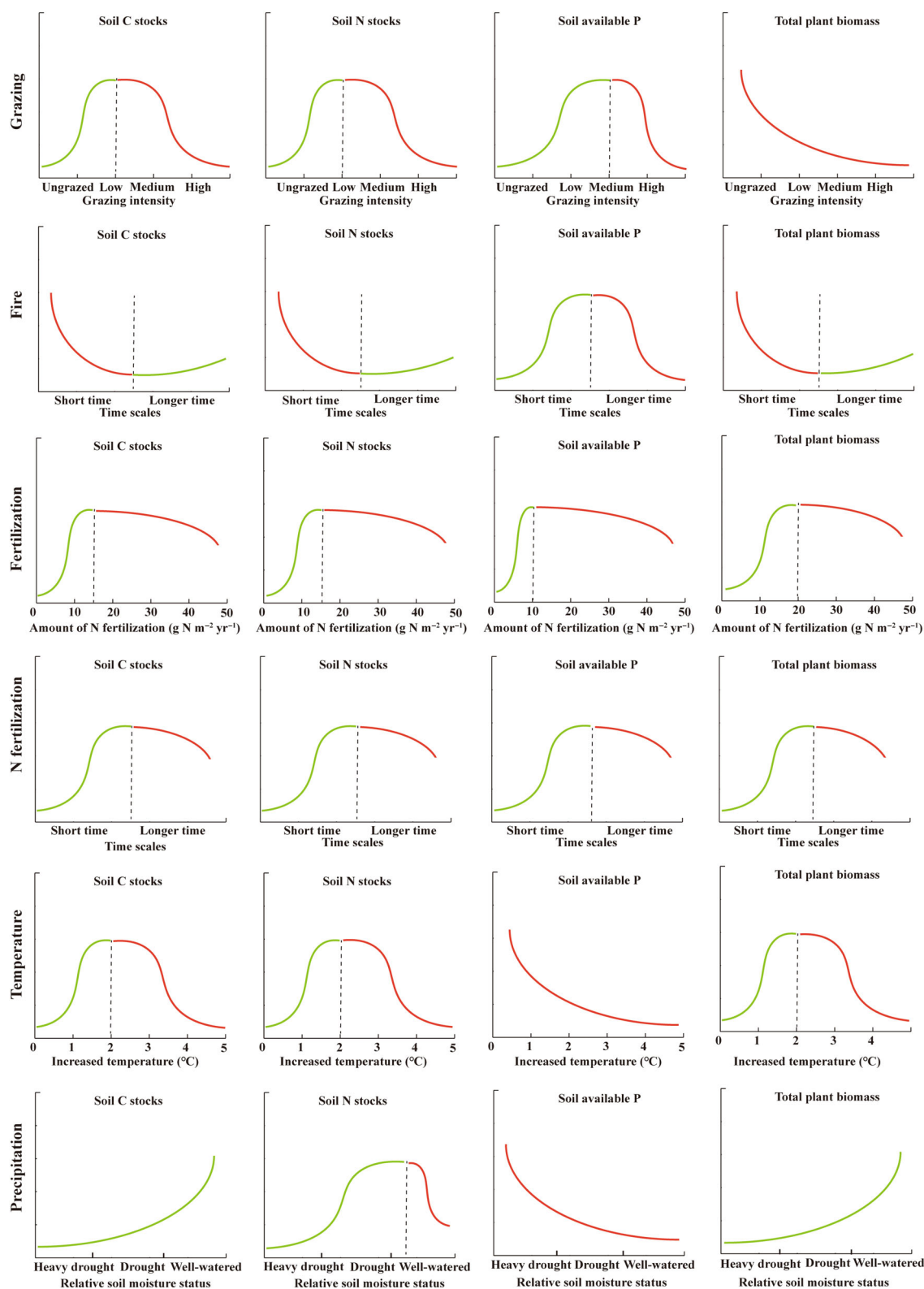


Fig. 5 Impact of land management practices on carbon and nutrient stocks of desert plants. Grazing intensity, grazing season (winter/fall), species palatability, growth pattern, and species composition positively impact plant shoot and root biomass, but they negatively affect the soil mineral and carbon stocks. Fertilization can also improve plant root and shoot biomass, promoting species composition and richness, leading to higher microbial activity and availability of mineral nutrients in the soil. However, fire and harvesting can have a negative impact on the growth and phenology of desert plants, resulting in poor C and nutrient stocks in the soil.

nutrient losses, which demand prolonged recovery (Fig. 5). The consequences of agricultural and livestock management in deserts hinge upon the root architecture of the species present. Deep-rooted plants can resprout postdisturbances and generally maintain more stable C stocks in plant–soil systems than shallow-rooted plants. Globally, increased grazing pressure in drylands generally leads to reduced rates of C storage in plant–soil systems, organic matter deposition, and erosion control. Grazing impacts on soil C and N stocks, P availability, and plant biomass depend on the grazing intensity (Fig. 6; Notes S4). When grazing is not too intense, it reduces total biomass but increases the soil C and

N stocks and P availability. Conversely, when grazing is extreme, it reduces plant biomass to a fraction and decreases soil C and N stocks at a similar level to ungrazed situations. For example, plant biomass and C stocks increased under light to moderate grazing but declined significantly under heavy grazing in the desert steppes of China (Deng *et al.*, 2023). Several studies have reported negative effects of grazing on the biomass and cover of different desert plant species (such as *Bouteloua eriopoda*, *Artemisia spinescens*, and *Aristida* spp.), mostly shallow-rooted plants (Kerley & Whitford, 2000; An & Li, 2015; Lasché *et al.*, 2023; Table S1). Therefore, under low grazing pressure, these systems retain soil

Fig. 6 Effects of diverse land-use practices (grazing, fire, and fertilization) and climate factors (temperature and precipitation) on total plant biomass (including aboveground and belowground biomass) and soil C, N and P stocks. A total of 17 papers related to grazing, 19 papers related to fire, 19 papers related to fertilization, 10 papers related to temperature and 27 papers related to precipitation were reviewed and analysed to design these nonlinear and threshold effects. Soil C and N stocks indicate soil organic matter and total N, respectively; soil P stocks represent soil available P; short time scales (1–5 yr); longer time scales (5–60 yr). Plant biomass and soil C, N and P stocks are influenced not only by individual land-use practices and climate factors but also by interactions and the combined effects of other biotic and abiotic factors. Such as, grazing (grazing years, vegetation coverage, dominant plant species, and seasons); fire (vegetation coverage, precipitation, temperature, and seasons); fertilization (precipitation, temperature, growth period, and soil texture); temperature (precipitation and soil texture); and precipitation (duration of continuous precipitation, plant species, soil texture and temperature). We only considered the general trends of the grazing intensity, postfire time, amount and postfertilization time, increased temperature, and relative soil water moisture status on plant biomass and soil C, N and P stocks. Low grazing intensity: 2–3 livestock density ha^{-1} ; Medium grazing intensity: 4–5 livestock density ha^{-1} ; Soil C and N stocks reach threshold at $15 \text{ g N m}^{-2} \text{ yr}^{-1}$. See 'Supporting Information Notes S4: Nonlinear and threshold effects' for further information.



fertility and potential for recovery. However, intense grazing that strongly reduces biomass reduces capacity for complete recovery. Overall, C and nutrient stocks decrease due to biomass reduction, and long-term overgrazing practices can even alter the community structure.

Dominant and more palatable grass species are particularly affected by overgrazing, displaying a more substantial positive response in biomass accumulation during wetter years than drier ones. For instance, in a desert community (encompassing shrubs, perennial grasses, and annual herbs) within the Chihuahua desert

(North America), low-intensity grazing failed to alter shrub density or the species composition of the annual community (Table S1) (Valone, 2003). Similarly, within the Arizona desert (North America), shoot and root biomass as well as SOC and SIC pools remained largely unaffected by grazing, with climatic conditions playing a predominant role in determining their concentrations (McKenna *et al.*, 2022). In arid polyphytic grasslands, the timing of animal grazing significantly influences biomass accumulation and the prevalence of different plant species (Maestre *et al.*, 2022). For instance, within the Chihuahua desert, grazing during summer resulted in lower biomass accumulation compared to grazing during winter or fall, even during wetter-than-average years (Lasché *et al.*, 2023). Hence, when determining animal stocking rates and grazing intensity, the abundance and growth patterns in varying rainfall conditions, along with the palatability of each species, should be considered. Furthermore, the temporal dynamics of C stocks in aboveground biomass should be considered when assessing anthropogenic land uses.

Plant harvesting

Harvesting plants to feed animals during the winter is a common practice in certain deserts, which exerts significant impacts on C and nutrient cycles. Repetitive foliar harvesting influences soil fertility, composition and biomass of soil biota, as well as the nutritional status of plants (Fig. 5). For example, a long-term experiment spanning 12 yr, conducted in the Taklamakan desert (West China), where *Alhagi sparsifolia* plants were annually cut, demonstrated that plant harvesting induced alterations in soil chemical composition throughout the soil profile (Tariq *et al.*, 2022a; Table S1). This practice also heightened soil microbial activity and led to a reduction in overall foliar nutrition. Similarly, within another arid grassland ecosystem in the Patagonia steppe (South America), intensive foliar harvesting did not markedly alter root or shoot biomass but did have a notable effect on root inoculation by arbuscular mycorrhiza, resulting in a reduction of its presence (Toledo *et al.*, 2022). The decline in mycorrhizal association, due to diminished root biomass, can impede the capacity of perennial desert plants to take up water and nutrients. This is because the symbiotic bond between fungi and roots is pivotal for extending the growing period beyond the wet season. These studies underscore the crucial role of plant management effects on soil biology, which in turn impacts, and is influenced by plant nutrition, ultimately leading to shifts in C and nutrient cycling. These factors merit further exploration in deserts, where nutrient availability can be constrained. This makes the impact of nutrient extraction through harvesting more pronounced when compared to other ecosystems.

Fires

Fires in desert ecosystems can result from various forms of disturbance, accidents, or deliberate management efforts. 0.295 million km^2 of land is burned in desert and xeric shrublands annually, resulting in the combustion of $c. 0.83$ Pg C (Pellegrini *et al.*, 2022). The impacts on the C cycle vary significantly when fire

is utilized as a tool for vegetation management. Fire reduces litter coverage and releases minerals into the soil, with the exception of N and magnesium (Mg), which are mostly lost (Bodí *et al.*, 2014). Phenology and growth rate, rather than diversity, primarily drive the variation in production after a fire (Liu *et al.*, 2022). This makes fire an inappropriate management practice, especially in arid ecosystems (Fig. 5), as it prolongs growing periods and diminishes overall production. It can also spread beyond the intended area and become uncontrollable.

Frequent fire reduces mineral nutrients input due to the combustion of plant biomass, litter, and stable organic matter that negatively affect soil fertility and impacts geochemical cycles and plant nutrition. For instance, in the Taklamakan desert (West China), where *A. sparsifolia* plants were burned annually for 12 yr, fire impacted the chemical composition of the upper soil layers and adversely affected the nutritional status of *A. sparsifolia* (Tariq *et al.*, 2022a), leading to a notable reduction in foliar stocks of N, P, and K. In the Chihuahua desert, prolonged burning decreased shrub density and augmented the number, diversity, and richness of summer herbs (Valone, 2003). Similarly, in the Mojave Desert, fire reduced the abundance, cover, and diversity of shrubs and increased the mortality rate (Horn *et al.*, 2015; Table S1). This resulted in decreased C stocks in long-living deep-rooted shrubs and increased C stocks in short-lived herbs with faster turnover rates. In the Sonoran Desert (North America), where tree and shrub density are low, litter decomposition and C emissions are higher than in communities with denser plant populations. This is due to the absence of plant canopies, which provide protection, allowing high temperatures and UV radiation to degrade lignin, and micro-organisms to more rapidly utilize organic compounds (Predick *et al.*, 2018). Consequently, burning impacts C stocks through alterations in plant population structure, which in turn affects the decomposition of necromass.

Moreover, human activities near desert edges and roads that traverse deserts can introduce nondesert plants from adjacent semi-arid biomes. This poses a threat to native desert species and increases the risk of wildfires by providing additional fuel sources. For instance, the invasion of exotic grasses in the Mojave Desert has heightened the fire risk, endangering the survival of species like *Yucca brevifolia*. The postfire mortality rate is particularly hazardous for succulent desert species such as *Y. brevifolia*, which sporadically regenerate during exceptionally wet summers, often with intervals exceeding 20 yr (DeFalco *et al.*, 2010; Esque *et al.*, 2015). This effect is not solely due to C and N losses during the fire but also stems from changes in the abundance of different plant types within the community and their associated micro-organisms. Quantitative data analysis (Fig. 6) also demonstrated that as fire frequency and/or intensity increase, they can enormously decrease soil C and N stocks and total biomass. Soil C and N are in higher proportion near the soil surface and can be lost by direct combustion or volatilization under fire. However, available P can increase under low-moderate fire frequency. The combustion of organic matter can liberate P from plants and soil organic matter and remain in the less volatile ashes. However, if the frequency increases, the continuous loss of biomass and ash amount makes P availability decrease again.

Beside the effect of fire in shoots and roots, in the Mojave Desert, wildfires significantly reduced the seed bank and decreased shrub cover and density, impeding the regeneration of long-lived species that require shelter and protection (Horn *et al.*, 2015). Thus, fire reduces tree and shrub density, shifting community composition from deep-rooted to shallow-rooted systems, thereby limiting overall access to groundwater for the entire community and resulting in a considerably shorter lifespan of aboveground biomass. However, a more comprehensive mechanistic understanding of the community composition shift in response to fire and its implications for nutrient uptake and conservation within plant–soil systems is necessary.

Fertilization

Although many crops in desert areas are irrigated and fertilized, this review focuses on the analysis of fertilization in deserts without irrigation, where water acts as a limiting factor for nutrient uptake, as explained previously. Nutrient addition in the Negev (East Asia) and Jodhpur desert (Southeast Asia) significantly affected C and nutrient cycles, influencing plant and microbial biomass (Alon & Steinberger, 1999; Singh & Shukla, 2011). However, the positive effect of fertilization on the herbaceous community in the Jodhpur desert was more pronounced when some native trees coexisted with herbs. Deep roots are particularly important for nutrient interception and soil mobilization through hydraulic redistribution.

Timing of nutrient application also has an impact. For example, in the Chihuahu desert grassland, N fertilization applied annually significantly increased aboveground biomass only in high-productivity years with abundant rainfall, while it had no effect during dry years (Ladwig *et al.*, 2012). Thus, if plants are under stress or inactive due to aridity (e.g. ephemerals, resurrection plants, and perennials with no active leaves in the dry season) they cannot effectively take up nutrients, and thus the addition of fertilizer would not impact plant biomass. By contrast, phreatophytes, that remain active despite water scarcity, can benefit from higher nutrient availability, improving their tolerance to drought (Ullah *et al.*, 2022; Tariq *et al.*, 2022b). For instance, phreatophytes such as *A. sparsifolia* and *Calligonum mongolicum* under N fertilization increased root and shoot biomass, antioxidant defence system, osmolytes and nutrients accumulation (Zhang *et al.*, 2020, 2021b; Table S1). Therefore, if fertilization is carried out during the dry season, species that are physiologically active at that time (i.e. deep-rooted species and phreatophytes) will benefit.

However, fertilization does not always increase biomass, as interactions between applied and naturally occurring nutrients can alter plant stoichiometry and other nutrients than those applied can then limit growth (Sardans & Peñuelas, 2012). In desert grassland and shrubs in West China 80% dominated by *Seriphidium korovinii*, N fertilization increased shoot and fine root N concentrations but decreased shoot and fine root P concentration (Li *et al.*, 2017), thereby diluting the concentration of one nutrient linked to the addition of the other. However, when P fertilization was applied along with irrigation, plants responded by increasing their growth. Coexisting shrub responded to N fertilization by increasing growth and leaf N concentration, regardless of

irrigation, indicating the greater water uptake capacity of shrubs from deeper soil layers (Drenovsky & Richards, 2004). In the Sonora desert (North America), N concentration in leaves increased with N fertilization, but in wetter years, biomass production was higher, leading to a decrease in N concentration due to greater allocation to more leaf's biomass production (Hall *et al.*, 2011). This allows accumulation of nutrients in tissues during wetter years. Similarly, in a fertilization trial conducted in ephemeral communities in the Chihuahua desert, only three winter annual species increased canopy cover when fertilized with N or S and irrigated, while no meaningful response was observed in rainfed plots (Ludwig *et al.*, 1989). This demonstrates that responses to increased rainfall and nutrient deposition or fertilization are highly species and site-specific, and the composition and productivity of deserts cannot be easily predicted. Thus, as water dramatically limits mineral movement in arid soil and plant water and nutrient uptake in arid lands, it is necessary to test the responses of desert species in their specific environments, as results from mesic environments cannot be readily applied to deserts.

If fertilization has a positive effect on the growth of active plants, it can drive changes in coverage, dominance, and species richness. For example, an arid steppe in China increased coverage and biomass of perennial grasses but decreased ephemerals and shrubs due to reduced light availability following N fertilization (Zhou *et al.*, 2020b). When annual plants in the Sonora desert community were fertilized with N, the seedling emergence of six native species was higher than unfertilized plots, although the opposite effect was observed in two native species and one perennial exotic grass (Salo *et al.*, 2005).

A quantitative analysis of studies providing data on the effects of N fertilization in function of the intensity/time of application have observed that low doses of N addition can alleviate soil N limitations and promote the accumulation of desert plant biomass (Fig. 6). The increased underground biomass also increased soil C and N stocks in these conditions. In addition, an appropriate amount of N addition can improve soil microbial activity, promoting the release of more enzymes and organic acids by root systems, and reducing soil pH value (Tian & Niu, 2015; Huo *et al.*, 2021; Cui *et al.*, 2023). These changes will improve the bioavailability of soil P. However, excessive and long-term N addition may shift the soil from N limitation to P limitation. Thus, in the short time scales, N addition have shown to decrease soil pH, thus increase P bioavailability in soil. In addition, long-term N addition can cause plants to extract too much nutrients from the soil, especially soil P with low availability and no external supplementation. In desert ecosystems, the decomposition rate of litter is relatively slow, and it takes a long time to supplement the soil C stocks and the turnover of soil P also takes a very long time. Therefore, P limitation may cause plant growth to be inhibited, reducing its biomass and soil C and N stocks. In summary, the nutrient imbalance caused by long-term N addition is frequently the main underlying reason for the decrease in soil C and N stocks and biomass over longer time scales. However, at this moment, current data highlights that a moderate input of N fertilizer can be advisable in some stages of restoration processes to give an impulse to plant growth and soil nutritional improvement (Fig. 6).

Moreover, the effects of fertilization on C and nutrient stocks depend on the roots' capacity to intercept and take up nutrients, the shoot's ability to accumulate nutrients in cases where growth is constrained by other factors (such as water, temperature, light), and the overall increase in plant and microorganism biomass. Further research is necessary to understand the interactions and synergies between nutrient and water-use efficiencies in desert plants and communities and the potential influence of root architecture on this relationship.

Impacts of indirect effects of climate change: Plant winners and losers and the consequences

In response to climatic fluctuations, individuals within desert ecosystems often acclimate by altering their physiology and morphology, and phenotypic changes in a species are common across a spectrum of environmental change. These changes can influence total biomass accumulation and species performance (Andresen *et al.*, 2016; Notes S5 describes the main morpho-physiological strategies of desert plants to cope with dry environments). Climatic shifts can also lead to changes in community composition, affecting the abundance and dominance of different species. In extreme cases, certain species and functional groups might migrate or face extinction, which can subsequently alter species richness (Nevo, 2012). The following discussion delves into the impacts of warming, precipitation changes, and sandstorms as drivers of modifications in carbon (C) stocks within desert environments.

Water table depth and depleting aquifers

In general, higher mean annual precipitation (MAP) can elevate the water table, while lower precipitation can deplete aquifers. However, water table recharge can also occur from distant sources, unaffected by local MAP. Consequently, changes in plant communities and C stocks depend on whether MAP and water table changes occur concurrently or independently. The depth of the water table plays a substantial role in shaping the distribution and biomass of phreatophytes like Acacia trees, which can extend roots to depths of up to 60 m to access the water table. However, even a relatively minor 5-m decline in the water table due to excessive water extraction can cause significant stress and dieback in the branches of these trees (Shadwell & February, 2017). This highlights that despite their adaptation to harsh conditions, desert species can be impacted by relatively small changes in groundwater levels, influencing growth, survival, community composition, and C stocks in biomass (Fig. 7). Conversely, if the water table rises and becomes more accessible to various species, biodiversity might increase, but the frequency of phreatophytes could decline, potentially leading to deep-rooted species becoming more dominant (Mata-González *et al.*, 2022).

However, certain desert species that rely on the water table may allocate fewer resources to roots when SWC is higher. For example, *A. sparsifolia* displays morpho-physiological strategies to survive in harsh conditions and can acclimate to wetter, shaded environments, as evidenced in an experiment where it was grown

under trees in an oasis with high SWC (Tariq *et al.*, 2022b). Species with high phenotypic plasticity and wide ecological niches, like *A. sparsifolia*, could potentially perform better under climate change compared to species with narrower ecological requirements.

Increasing temperatures

In contrast to cold, humid ecosystems (Andresen *et al.*, 2016), warming is anticipated to reduce biomass in desert ecosystems, where water availability is the limiting factor. In hot regions, higher potential evapotranspiration (PET) rates can drive ecosystems from semi-arid to arid and even hyper-arid conditions (Fig. 7). Similar to the association between warming and dryness, a global meta-analysis revealed that warming increases root allocation while decreasing total biomass and ultimately C and nutrient stocks (Zhou *et al.*, 2022). Consequently, warming equalizes shoot-to-root ratios in various plant types. Therefore, warming in the absence of increased precipitation intensifies evaporative demand and dryness. Shallow-rooted plants (e.g. ephemerals, resurrection plants, cacti, and succulents) are particularly susceptible to warming, as higher PET reduces available water. By contrast, temperature increases have less impact on deep-rooted plants and phreatophytes since PET has less influence on deeper water sources. Consequently, warming restricts the distribution of shallow-rooted species to cooler, wetter microenvironments within their natural range (Sweet *et al.*, 2019), leading to an overall reduction in C and nutrient stocks in desert ecosystems. Based on the available quantitative data, it is clear that moderate temperature increases positively impact soil C and N stocks, as well as plant biomass. Moreover, there is a reduction in soil available P concentration, which can be attributed to a rise in plant P uptake. The moderate increase in temperature does not appear to affect the water status of the plant–soil system, which is well-adapted to drought. However, if the temperature increase surpasses a particular threshold, there is a decline in soil C and N stocks and plant biomass. This is likely due to the unfavourable effect of high temperatures on water status and economy in plant–soil systems, specifically in situations where there is a possibility of water loss via evapotranspiration (Fig. 6).

Variation in precipitation

Projections suggest a decrease in MAP in the main arid regions in the coming decades (Miao *et al.*, 2020; Yao *et al.*, 2020). Areas projected to experience increased aridity include the Mojave and Sonoran deserts (North America), northeastern Brazil, northern Bolivia, the Atacama Desert (Chile), the Patagonian steppe (Argentina), the Mediterranean region, the Namib and Kalahari deserts (southern Africa), steppes in Russia, Kazakhstan, and Mongolia, the Thar desert (India), southeastern China, and various semi-arid regions in Australia (Spinoni *et al.*, 2021). Decreased MAP is often accompanied by heat events, and the timing and sequence of hot events and precipitation reductions significantly impact arid ecosystem stability (Mukherjee *et al.*, 2023). Reduced rainfall frequency can particularly affect desert communities, especially ephemeral and resurrection plants.

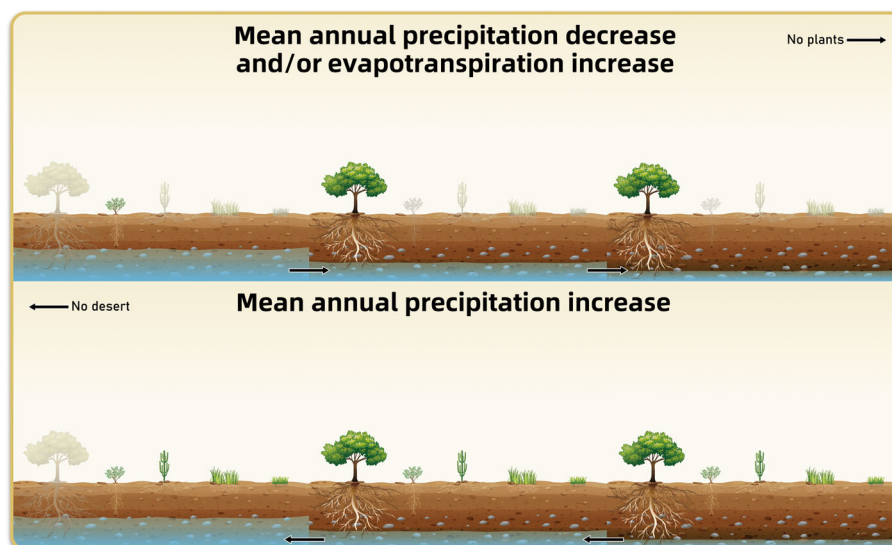


Fig. 7 Hypothesis of plant persistence with changes in the groundwater depth, indicated by a blue line, and modifications in mean annual precipitation. Both variables change together if groundwater recharge happens in the same area, or they modify independently if recharges occur at distant points. All five types of plants are currently present in deserts, and will continue to be present if rainfall increases without changes in water table depth (lower–middle draw). Phreatophytes will be less frequent in deserts with shallow water table, while trees, palms and shrubs with deep roots will prevail (left draws). Succulents, shrubs or grasses with shallow root systems and ephemeral abundance are independent of water table, so they will be affected only by precipitation. As precipitation decreases, the abundance of succulent will be lower, as they need rainfalls to recharge their storage tissues and maintain physiological activity (upper draws). Dormant shrubs and herbs without leaves during dry periods will survive with lower precipitation than succulents, but their growth period will be shorter (upper draws). Ephemerals can stand very sparse rainfalls, as they only have activity when soil is wet, and seeds maintain viability during many years. An increase in precipitation will produce more frequent germination of ephemerals (lower draws). If precipitation increases markedly and feeds the water table that goes upper, the ecosystem will tend to change to a semi-arid land. If precipitation decreases markedly and water table goes deeper as water consumption is higher and no recharge occurs, plant coverage will be sparse and in extreme situations in which roots systems are not able to reach groundwater and rainfalls are so sparse that bank seed is dramatically reduced, no plants will survive.

For instance, in the Gobi Desert, the total biomass of the resurrection plant *Reaumuria soongorica* was significantly lower when precipitation occurred only half as frequently as usual (Geng *et al.*, 2014; Chong *et al.*, 2015; Table S1). However, plant growth remained relatively unaffected when rainfall was 30% higher or lower than the annual mean, as long as the frequency remained consistent (Z. Zhang *et al.*, 2018). This underscores the significance of considering both MAP and the frequency and distribution of rainfall events throughout the year.

Furthermore, reduced MAP will disproportionately affect ephemeral and resurrection plants compared to perennial deep-rooted plants, while phreatophytes will be relatively unaffected (Fig. 7). This change in community composition favours deep-rooted plants and reduces ephemerals, which increases C stored in deep roots and extends the lifespan of C in biomass. However, despite potential increases in root biomass to some extent, plant density and aboveground biomass may decline, contributing to C losses. Yet, high species diversity can significantly enhance productivity and C storage in shrublands (Chen *et al.*, 2018). Quantitative analysis further supported the fact that under extreme drought conditions, soil C and N stocks, soil available P, and plant total biomass decrease compared to less extreme conditions (Fig. 6). Moreover, under water deficit conditions, deep-rooted plants like *Tamarix ramosissima* showed a variety of adaptive responses such as reduced transpiration, increased leaf cuticle thickness, diameters of epidermal and

palisade tissues, cortical thickness (to maintain water retention and photosynthetic efficiency), root growth rate, and hydraulic conductance of xylem, but increasing drought stress and groundwater depth were not conducive to development (Zhuang & Chen, 2006; Table S1).

Conversely, within a desert steppe community, higher MAP has been shown to stimulate the aboveground growth of shrub species without affecting perennial grass species (Ma *et al.*, 2022). This suggests shifts in community composition, favouring shrub dominance over grasses. As a result, C stocks would transition from grasses to shrubs, resulting in increased belowground C stocks and longer root and shoot lifespans (Ma *et al.*, 2022). Therefore, increased rainfall is likely to promote C sequestration in arid ecosystems by boosting shrub abundance while reducing grasses (Fig. 7). This was supported by quantitative analyses of studies that have applied water irrigation in field conditions showing a continuous increase in plant biomass with increasing MAP. This was accompanied by an increasing of soil C and N stocks and a decrease in P availability, potentially linked to the increase of biological production (more litter production and N fixation) and greater P uptake (Fig. 6).

In communities with phreatophytes, the response of roots should be assessed to predict the impact of higher MAP and SWC on desert ecosystems. Four coexisting desert tree species displayed varying responses in dry mass allocation when SWC increased (Biruk *et al.*, 2022). Under higher SWC, two species including a

phreatophyte and a deep-rooted plant increased allocation to shoots, while a shallow-rooted species allocated more to roots, utilizing the additional water for enhanced soil exploration. Other species also demonstrate variations in root allocation across different habitats, underscoring the dichotomy between deep and shallow root systems. For instance, *Prosopis flexuosa* growing in arid dunes possesses deeper roots than the same species growing in more humid valleys (Guevara *et al.*, 2010). Similarly, *Argania spinosa* populations from coastal regions with higher MAP rely less on deep rooting than populations from drier inland sites (Zunzunegui *et al.*, 2018). An interesting example is *A. sparsifolia*, a phreatophyte that develops 2-m deep roots during the first year after germination, but root elongation decreases when SWC rises. Furthermore, when the water table is shallow, these plants develop lateral roots and tillers, leading to increased aboveground coverage (Tariq *et al.*, 2022b). These examples highlight the significance of assessing root allocation in different species and habitats. Therefore, high C accumulation belowground facilitated by phreatophytes could potentially be reduced under high MAP in arid regions, as projected in the Midwest of North America, southern Chad, Hebei and Beijing provinces in China, and central-southern India (Spinoni *et al.*, 2021).

Sandstorms

In many deserts, an increase in the frequency and intensity of sandstorms is expected (Rabbani & Sharifikia, 2023). The depth at which seeds are buried is crucial in ensuring rapid germination when the soil becomes wet after a sandstorm. If sandstorms become more frequent or intense and bury the seed bank deeper, seedling emergence will be delayed (Tao *et al.*, 2022; Copeland *et al.*, 2023). As a result, the presence of ephemeral plants in arid ecosystems will be severely compromised by a combination of sparse rainfall and more frequent sandstorms. In such cases, the C recycling between wet and dry seasons will gradually decrease as few ephemerals complete their active growth and the subsequent necromass decomposition drops. This decline will subsequently reduce the population of microorganisms associated with root activity and organic matter mineralization.

Perspectives for future research

Current knowledge of how roots impact and reflect nutrient accumulation in arid ecosystems, although limited, provides valuable insights into the intricate dynamics of desert ecosystems. However, several unknowns warrant further consideration:

- (1) Desert ecosystems are influenced by multifaceted interactions between climate, soil, and plant communities. The interplay of these factors can be complex and challenging to fully unravel.
- (2) Long-term studies encompassing multiple climatic cycles are essential to understand the resilience and adaptability of desert plant communities over time.
- (3) While this review focuses on climatic and human-induced changes, other factors like soil characteristics and geological processes can also impact C and nutrient cycling.

(4) Though advanced technologies hold promises, their application to desert ecosystems is still evolving, and their full potential in predicting plant responses remains to be seen. Traditional studies of root architecture have involved excavation and careful analysis of roots, advanced technologies like electrical resistance imaging and 3D analysers can aid in predicting desert plant responses to climate change. The structure of the community and plant traits are crucial for understanding the resilience of desert ecosystems to changing climate and management, affecting their roles in nutrient cycling.

So the following future directions are warranted: (1) Initiating and maintaining long-term monitoring studies across diverse desert ecosystems to provide insights into how plant communities respond to changing conditions over extended timeframes, (2) Integrating ecological, physiological, and biogeochemical approaches will enhance our understanding of the holistic impact of changing conditions on C and nutrient cycling, (3) Further research into the intricate interactions between plant root systems and belowground microorganisms is vital to unravel the hidden dimensions of nutrient cycling and plant performance, (4) Scaling up investigations to encompass landscapes and regions will provide a more comprehensive understanding of how different desert ecosystems respond to global change, (5) Developing predictive models that incorporate climatic, physiological, and ecological parameters can enhance our ability to forecast desert ecosystem responses under different global change scenarios, (6) As the anthropogenic footprint expands, incorporating social and economic dimensions into ecological restoration strategies is paramount for long-term success, (7) Global collaborative efforts across disciplines will facilitate the exchange of knowledge and data, contributing to a more nuanced comprehension of plants performance in desert ecosystem dynamics.

Conclusions

Water availability stands as the primary growth-limiting factor in desert ecosystems, prompting plants to rely on various sources for water acquisition, where soil water emerges as the main source. The plant community's makeup is shaped by the depth of the groundwater, discerning between deep-rooted and shallow-rooted plants. The root system of deep-rooted plants adapts according to groundwater depth – phreatophytes accessing groundwater below 5 m and other deep-rooted plants tapping into shallower water tables < 5 m deep. By contrast, shallow-rooted plants like cacti and succulents store water in both aboveground and belowground structures, therefore, their survival tied to frequent rainfall. Resurrection plants keep their leaves dehydrated during dry periods, swiftly resuming growth after rains, so they can stand changes in rainfall frequency. Meanwhile, ephemeral plants with ultra-shallow root systems sprout or germinate from bulbs postrainfall, completing their life cycle within days.

For deep-rooted plants, their root systems grow vertically and with lower density, maximizing water and nutrient absorption in the deep soil. Shallow-rooted plants, on the other hand, exhibit a more horizontal growth pattern. In young plants, particularly phreatophytes, hydraulic descent play a vital role, redistributing water from upper soil layers to deeper ones. This process aids in root

expansion, water-use efficiency, and nutrient mobilization. Hydraulic lift becomes crucial once plant roots reach the groundwater, boosting nutrient uptake near the soil surface and assisting shallow-rooted plants in acquiring water and nutrients.

Human activities, such as vegetation burning, biomass harvesting, and grazing, impact soil fertility, microorganisms associated with roots, and the outflow of carbon and nutrients. Consequently, this can lead to shifts in plant community structure from deep to shallow-rooted plants, reshaping carbon and nutrient stocks. Combined with climatic changes, these disturbances further affect biomass, carbon and nutrient stocks, population structure, and contribute to desert land degradation. Shallow-rooted plants find themselves more susceptible to heightened warming and reduced MAP, limiting their presence to moister microenvironments. While an abundance of deep-rooted plants can somewhat increase carbon stocks, overall biomass might decrease, resulting in losses of carbon and nutrients.

Restoration management can involve fertilization and strategic species composition. Furthermore, carefully regulating grazing and harvesting, or maintaining them at low to moderate levels, can yield positive impacts on carbon, nitrogen and phosphorous (CNP) stocks, biomass, and plant–soil conservation within desert ecosystems. Additionally, avoiding human-induced vegetation burning is essential, given its negative impact on soil fertility, plant nutritional status, and biomass. Practical strategies for livestock feeding and ecosystem restoration should centre around suitable plant species that optimize ecological functions and enhance carbon and nutrient retention within the plant–soil system.

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Competing interests

None declared.

Author contributions

AT, FZ, CG, JS and JP conceptualize and designed the manuscript. The manuscript was written and revised by AT, CG, JS, JP, ACH and FZ. AT, CG, ZA, AU, YG and SA reviewed and gathered the

literature. AT, FZ, CG, JS, ACH and JP organized and structured the information. All authors reviewed and contributed to the text of the manuscript.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Methods S1 Methodology.

Notes S1 Classification of desert plants.

Notes S2 Carbon stocks in desert ecosystems.

Notes S3 Soil biota associated with roots in deserts.

Notes S4 Nonlinear and threshold effects.

Notes S5 Morphological strategies of desert plants to cope with dry environments.

Table S1 Examples of desert plant species responses to different environmental and land-use factors.

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