

BIOECOLOGICAL ADAPTATION MECHANISMS OF CAPPARIS SPINOSA (CAPER) TO EXTREME ARID AND SALINE CONDITIONS IN THE REPUBLIC OF KARAKALPAKSTAN

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ABSTRACT

This article examines the bioecological adaptation mechanisms of Capparis spinosa L. in the arid and saline conditions of Karakalpakstan. The region is marked by extreme heat, low rainfall, and high soil salinity linked to the Aral Sea crisis. The species survives through deep root systems, xeromorphic leaves, facultative leaf shedding, and stem photosynthesis. It regulates water loss via stomatal control, osmotic adjustment, and facultative CAM-idling under drought stress. Salinity tolerance is ensured by ion compartmentalization, antioxidant activity, and salt excretion. Reproductive success is supported by rapid flowering, self-compatibility, and seed dormancy. Clonal growth and mycorrhizal associations further enhance resilience. These integrated strategies allow the species to persist in degraded desert ecosystems and support its value for ecological restoration.

Capparis spinosa L., commonly known as caper, is a perennial shrub that has long fascinated ecologists and botanists due to its remarkable ability to thrive in some of the most extreme arid and saline environments on Earth. In the Republic of Karakalpakstan, a region situated in the northwestern part of Uzbekistan and encompassing the southwestern shores of the rapidly desiccating Aral Sea, C. spinosa presents a compelling case study of bioecological adaptation. The climate here is starkly continental and hyper-arid, with summer temperatures often exceeding 45°C, annual precipitation rarely reaching 100 mm, and soils heavily salinized by decades of irrigation runoff and the retreat of the Aral Sea. Despite these punishing conditions, caper populations not only survive but often dominate the degraded landscapes, forming dense thickets along dry riverbeds, abandoned agricultural fields, and saline depressions. Understanding the mechanisms that underpin this resilience is not merely an academic exercise—it holds practical significance for ecological restoration and sustainable land use in one of the world's most severe anthropogenic deserts [5].

The morphological adaptations of C. spinosa in Karakalpakstan are immediately evident upon inspection. The plant develops an extensive, deep-reaching taproot system that can penetrate more than 10 meters into the soil profile, exploiting groundwater reserves that remain beyond the reach of most competing species. This root architecture is complemented by a network of lateral roots that spread horizontally to capture sporadic surface moisture

from rare rainfall events. The leaves, typically simple, orbicular, and fleshy, are covered with a thick cuticle and often exhibit a waxy bloom that reduces cuticular transpiration. In the Karakalpak populations, leaf size is notably reduced compared to Mediterranean ecotypes, a classic xeromorphic response that minimizes water loss by reducing the surface area-to-volume ratio. Stomata are sunken and partially occluded by trichomes, creating a boundary layer that slows water vapor diffusion. However, perhaps the most striking morphological feature is the plant's ability to shed a significant portion of its leaves during the most intense drought periods, effectively entering a state of facultative deciduousness. This leaf abscission is not a sign of stress-induced mortality but a controlled strategy to conserve water; the stems, which remain green and photosynthetic, assume the role of primary carbon fixation. These photosynthetic stems contain chlorenchyma in the cortex, allowing continued assimilation with greatly reduced water loss due to the lower stomatal density on stem surfaces compared to leaves [2].

At the physiological level, C. spinosa in Karakalpakstan employs a suite of drought-avoidance and drought-tolerance strategies that operate in concert. Stomatal regulation is extremely sensitive: the plant closes its stomata early in the day when vapor pressure deficit rises, often before midday, thereby avoiding the peak evaporative demand. This conservative water-use behavior is coupled with an osmotic adjustment mechanism that accumulates compatible solutes such as proline, glycine betaine, and soluble sugars in the cytoplasm. Field measurements from populations near the dried bed of the Aral Sea show that proline concentrations in leaf tissues can rise to over 20 μmol g^{-1} fresh weight during the hottest months, lowering osmotic potential and enabling water uptake from saline or drying soils. Additionally, the plant maintains a high root-to-shoot ratio, investing a disproportionate amount of biomass underground. This allows it to extract water from deeper, more stable reservoirs while minimizing the aerial surface that loses water. Another critical physiological adaptation is the ability to perform Crassulacean Acid Metabolism (CAM) as a facultative strategy. While C. spinosa is primarily a C3 plant, studies in the Central Asian populations have shown that under severe drought stress, it shifts to a weak CAM-idling pattern: stomata open at night to fix CO_2 into malate, which is decarboxylated during the day for photosynthesis. This nocturnal CO_2 uptake reduces daytime transpiration by up to 80%, a critical advantage in the hyperarid Karakalpak summer [1].

Salinity is perhaps an even greater challenge than drought in this region. The soils of the southern Aral Sea region have become hypersaline, with electrical conductivity values exceeding 20 dS m^{-1} in many areas. C. spinosa demonstrates a remarkable halophytic tendency, tolerating salt concentrations that would kill most glycophytes. The mechanisms include selective ion uptake and compartmentalization. Sodium and chloride ions are sequestered into vacuoles, while potassium is preferentially retained in the cytosol to maintain enzymatic function. The plant also synthesizes salt-stress-specific proteins and upregulates antioxidant enzymes such as superoxide dismutase, catalase, and ascorbate peroxidase to combat the oxidative damage that accompanies ionic imbalance. In Karakalpak populations, the activity of these enzymes shows a two- to threefold increase during the summer salinity peak, correlating with a reduction in lipid peroxidation products. Furthermore, the plant has a well-developed system of salt glands on its leaves and young

stems, though these are not as conspicuous as in some true halophytes. Microscopic examination reveals that epidermal cells can excrete salt crystals onto the leaf surface, which are then washed off by rare rains or simply accumulated until leaf abscission removes them entirely [4].

Reproductive biology also reflects adaptation to the harsh environment. C. spinosa flowers in late spring to early summer, coinciding with a brief window when soil moisture from snowmelt is still available and pollinator activity is highest. The large, showy white-pink flowers are short-lived, opening for only one day, but they produce copious nectar that attracts a variety of bees and flies. In Karakalpakstan, where pollinator diversity is low, the plant compensates with a high degree of self-compatibility, ensuring seed set even in the absence of cross-pollinators. Fruit development proceeds rapidly, and the berries mature within six to eight weeks, releasing seeds that are coated with a mucilaginous layer. This mucilage serves multiple adaptive functions: it delays germination until sufficient moisture is available, it protects the seeds from desiccation, and it may even facilitate myrmecochory—ant dispersal—as observed in some populations. Seeds exhibit physical dormancy due to a hard seed coat, which requires scarification by mechanical abrasion or passage through an animal's digestive tract to germinate. In the field, germination is therefore staggered, ensuring that not all seeds germinate in a single unfavorable year. This bet-hedging strategy is crucial in an environment where rainfall is not only scarce but highly unpredictable.

At the biochemical level, C. spinosa in Karakalpakstan synthesizes a rich array of secondary metabolites that confer multiple adaptive advantages. Flavonoids, particularly rutin and quercetin, accumulate in high concentrations in leaves and flower buds. These compounds act as UV screens, protecting photosynthetic tissues from the intense solar radiation that characterizes the Aral Sea region. They also function as antioxidants, scavenging reactive oxygen species generated by drought and salinity stress. Glucosinolates and their hydrolysis products, isothiocyanates, are present in all plant parts and serve as deterrents against herbivores and pathogens; in the degraded Karakalpak landscapes, where grazing pressure from livestock is high, this chemical defense is likely a key factor in the plant's persistence. Moreover, the alkaloid capsaicin (structurally distinct from the chili pepper compound) and other nitrogen-containing compounds found in caper have been shown to inhibit the growth of soilborne fungi, possibly providing a competitive advantage in the rhizosphere. The synthesis of these metabolites is energetically costly, but in a low-competition environment where the main stressors are abiotic, the investment pays off by reducing biotic pressure.

The population dynamics of C. spinosa in Karakalpakstan reveal an additional layer of ecological adaptation. The species exhibits a clonal growth form, with horizontal roots producing adventitious shoots that can establish new ramets several meters from the parent plant. This vegetative propagation allows the population to expand rapidly after disturbance events, such as plowing or grazing, and to persist in sites where sexual reproduction fails. Genetic studies of Karakalpak populations show a high degree of clonal diversity, indicating that both sexual and asexual reproduction contribute to population structure. The ability to regenerate from root fragments also makes caper highly resilient to mechanical damage. In areas subjected to repeated grazing, the aboveground biomass may be removed entirely, but

the root system survives, and resprouting occurs within weeks after the first rainfall. This resprouting capacity is supported by large starch reserves stored in the root cortex, which can constitute up to 30% of root dry weight during the dormant season [3, 684-686].

Interactions with soil microbiota play an underappreciated role in the plant's adaptation. Mycorrhizal fungi, particularly arbuscular mycorrhizae (AMF), form extensive associations with C. spinosa roots in the Karakalpak soils. These fungi enhance phosphorus and nitrogen uptake from the nutrient-poor, alkaline soils and also contribute to drought tolerance by improving water transport through the hyphal network. In return, the plant supplies the fungi with carbohydrates. Recent surveys in the Muynak district, near the former Aral Sea coastline, found that root colonization rates exceed 80% during the growing season, with Glomus and Rhizophagus species being the most abundant genera. The association is so tight that the plant's performance in saline soils is significantly reduced when mycorrhizae are experimentally eliminated. Additionally, nitrogen-fixing bacteria, though not in root nodules (since caper is not a legume), have been isolated from the rhizosphere, suggesting that associative nitrogen fixation may contribute to the plant's nitrogen budget in these nitrogen-limited soils.

Climate change projections for the Aral Sea region indicate further warming and aridification, with a predicted increase in the frequency of extreme drought events. C. spinosa appears well-equipped to cope with these trends due to its already extreme adaptations. However, the species may face challenges from changing precipitation patterns: if winter snowfall decreases, the spring moisture pulse that triggers germination and early growth will diminish. On the other hand, the plant's deep root system and facultative CAM pathway provide a buffer against more erratic rainfall regimes. The capacity for clonal spread also ensures that established populations can persist even if seedling recruitment becomes episodic. In a broader context, C. spinosa represents a model organism for understanding the limits of plant resilience in desert environments. Its success in Karakalpakstan—a region that has experienced one of the most dramatic anthropogenic ecological catastrophes of the 20th century—offers a powerful example of how life can persist, adapt, and even flourish under conditions that push the very boundaries of terrestrial habitability. The bioecological mechanisms detailed here are not isolated traits but an integrated network of morphological, physiological, reproductive, and biochemical strategies that operate synergistically. Their deep analysis not only illuminates the inner workings of a remarkable plant but also provides a blueprint for identifying and perhaps even engineering crops and restoration species capable of sustaining productivity in a rapidly warming world.

Conclusion. The bioecological adaptations of Capparis spinosa in Karakalpakstan form an integrated system—deep roots, facultative leaf shedding, CAM-idling, osmotic adjustment, salt tolerance, clonal propagation, and symbiotic associations—that enables it to dominate the extreme hyperarid, saline conditions of the retreating Aral Sea basin. This resilience makes the species a valuable model for ecological restoration and sustainable land use in degraded desert environments worldwide.

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