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CONVERGENT EVOLUTION OF SUCCULENCE ACROSS ANGIOSPERMS: FORM, FUNCTION AND GENOME

SUMMARY

Succulence has evolved independently across numerous angiosperm lineages in response to water limitation, representing a prominent example of convergent evolution. This review integrates morphological, physiological, and genomic evidence to identify the principal mechanisms underlying this convergence. Across distantly related lineages, similar adaptive outcomes repeatedly involve water-storage tissues, reduced water loss, enhanced water-use efficiency, and, in many species, Crassulacean acid metabolism (CAM). At the genomic level, convergence appears to depend primarily on regulatory reprogramming, gene duplication, and the recruitment of conserved genetic networks rather than identical genetic changes. Overall, succulence emerges as a flexible evolutionary strategy in which diverse developmental and molecular pathways converge on comparable functional solutions to drought. Understanding these mechanisms provides important insights into the predictability of plant adaptation and resilience to increasing water limitation under global climate change.

Keywords: Convergent evolution, succulence, crassulacean acid metabolism, climate change, ornamental plants

INTRODUCTION

Convergent evolution is the independent acquisition of similar phenotypic, structural, or functional traits in phylogenetically distinct lineages as a

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consequence of comparable selective pressures. Thus, convergence does not necessarily imply that similar traits arise through identical developmental or genetic mechanisms; rather, different evolutionary pathways may generate analogous adaptive outcomes. In plants, this process is particularly evident in extreme environments, where similar ecological constraints repeatedly favor comparable solutions to environmental stress (Stayton, 2015; Edwards *et al.*, 2012). Within this framework, succulence can be defined as a structural and functional syndrome characterized primarily by the presence of specialized tissues containing enlarged, highly vacuolated cells capable of storing substantial quantities of water and making this water available during periods of limited external supply. Succulence may occur in leaves, stems, roots, or combinations of these organs and is commonly associated with additional traits that reduce water loss and maintain physiological activity during drought (Fradera-Soler *et al.*, 2022; Males, 2017). Therefore, in this review, the term succulence refers not simply to tissue thickness or a fleshy appearance, but to an integrated water-storage strategy that contributes to plant persistence under conditions of intermittent or chronic water limitation.

Succulence has evolved independently numerous times across angiosperms, making it one of the most compelling examples of convergent adaptation to arid and semi-arid environments. Despite the large phylogenetic distances separating succulent lineages, many exhibit strikingly similar morphological and physiological characteristics, illustrating how comparable environmental pressures can repeatedly shape analogous adaptive solutions. The evolution of succulence is closely associated with environmental factors such as low precipitation, high evapotranspiration rates, and episodic water availability. These conditions impose strong selective pressures on traits that enhance water storage and reduce water loss. Consequently, succulent plants typically develop specialized water-storage tissues, often accompanied by reduced leaf surface area, thick cuticles, and altered stomatal behavior (Fradera-Soler *et al.*, 2022; Becklin *et al.*, 2016). These features occur across diverse angiosperm families, including Cactaceae, Crassulaceae, Euphorbiaceae, and Aizoaceae, illustrating the repeated emergence of similar adaptive solutions (Thompson *et al.*, 2024; Males, 2017).

Succulence does not represent a single evolutionary innovation but rather a suite of traits that together constitute a functional syndrome. These traits may arise in different organs depending on lineage-specific developmental pathways. For instance, stem succulence predominates in cacti, whereas leaf succulence is more common in families such as Crassulaceae (Vásquez-Cruz *et al.*, 2025). This diversity highlights that convergent evolution can produce analogous outcomes through distinct anatomical routes, reflecting both developmental flexibility and evolutionary constraints.

In addition to morphology, physiological adaptations play a crucial role in the success of succulent plants. A key innovation associated with many succulents is crassulacean acid metabolism (CAM), a modified photosynthetic pathway that enhances water-use efficiency by temporally separating carbon

fixation from photosynthesis. In CAM plants, stomata open primarily at night, allowing CO₂ uptake when evaporative demand is lower, and close during the day to conserve water (Lüttge, 2010; Töpfer *et al.*, 2020). This adaptation has evolved independently numerous times across angiosperms, further exemplifying the recurrent nature of this convergence (Scossa *et al.*, 2026). However, not all succulents utilize CAM, and some species exhibit facultative CAM, switching between photosynthetic modes depending on environmental conditions (Qiu *et al.*, 2023).

The repeated evolution of succulence and CAM raises important questions regarding the genetic and molecular mechanisms underlying convergence. Advances in comparative genomics and transcriptomics have revealed that similar phenotypes often arise through modifications of shared genetic toolkits rather than through identical mutations. In the case of succulence, genes involved in stress response, circadian regulation, and carbon metabolism are frequently co-opted and reprogrammed to support new functional roles (Pereira and Kohlsdorf, 2023; Wagner and Mitchell-Olds, 2011). This suggests that evolutionary innovation may rely heavily on regulatory changes, including shifts in gene expression timing and intensity, rather than the emergence of novel genes.

Gene duplication has also been implicated as a key driver of succulent evolution, providing the raw genetic material for functional diversification. Duplicated genes can acquire new roles or partition existing functions, facilitating the development of complex traits such as CAM photosynthesis (Shepherd *et al.*, 2023; Uebbing *et al.*, 2024). Network-level changes in gene regulation may enable coordinated responses to environmental stress, integrating multiple physiological processes into a cohesive adaptive strategy.

While convergent evolution often emphasizes similarity, it is equally important to recognize variation among succulent species. Differences in habitat, life history, and evolutionary history can lead to distinct combinations of traits, even among plants occupying similar ecological niches. For example, some succulents primarily rely on water storage, whereas others emphasize drought avoidance or tolerance mechanisms (Artur and Kajala, 2021; Wei *et al.*, 2026). This variability highlights that convergence operates within a framework of ecological and evolutionary constraints, producing a spectrum of adaptive outcomes rather than a single optimal solution.

Recent phylogenetic studies have illuminated the evolutionary history of succulence, revealing multiple independent origins and complex patterns of diversification. These analyses suggest that the evolution of succulent traits is often associated with shifts in habitat and climate, particularly during periods of global aridification (Sackton and Clark, 2019; Pelegrin *et al.*, 2023). These findings underscore the importance of environmental context in shaping evolutionary pathways and highlight the dynamic interplay between climate change and plant adaptation.

Understanding the convergent evolution of succulence has broad implications for plant biology and ecology. As global climate change intensifies,

insights into plant adaptation to water scarcity may inform efforts to improve crop resilience and ecosystem management. Moreover, succulents provide a valuable model system for exploring fundamental questions in evolutionary biology, including the predictability of adaptation, the role of genetic constraints, and the relationship between form and function. In this review, we synthesize current knowledge on the convergent evolution of succulence across angiosperms, focusing on the integration of morphological, physiological, and genomic perspectives. By examining how similar functional traits arise independently through diverse evolutionary pathways, we aim to provide a comprehensive framework for understanding one of the most remarkable examples of plant adaptation to extreme environments.

MATERIAL AND METHODS

Literature Search Strategy

This review was conducted as a semi-systematic integrative literature review designed to synthesize evidence from multiple complementary fields relevant to the convergent evolution of succulence in angiosperms. The semi-systematic approach was considered appropriate because the topic encompasses heterogeneous evidence from plant morphology, anatomy, physiology, ecology, evolutionary biology, phylogenetics, genomics, transcriptomics, and molecular biology. Accordingly, the objective was not to perform a quantitative meta-analysis or a formal systematic review of a narrowly defined intervention or outcome, but to identify, critically evaluate, and integrate the principal lines of evidence explaining the repeated evolution of succulent traits across phylogenetically distinct angiosperm lineages.

Literature searches were performed using Web of Science, Scopus, ScienceDirect, Google Scholar, and PubMed, covering publications primarily from January 2000 to 2026. Earlier publications were retained when they represented seminal contributions necessary for interpreting the historical, physiological, anatomical, or evolutionary foundations of succulence and crassulacean acid metabolism (CAM). The literature search was updated during manuscript preparation to incorporate recent studies available in 2025 and 2026.

Searches were conducted using combinations of terms describing the focal trait, evolutionary process, physiological mechanisms, environmental context, and molecular basis of adaptation. Representative Boolean combinations included: “succulence” AND “convergent evolution”; “succulent plants” AND (“evolution” OR “adaptation”); “succulence” AND (“drought adaptation” OR “water-use efficiency”); (“succulence” OR “succulent plants”) AND (“crassulacean acid metabolism” OR “CAM photosynthesis”); “CAM photosynthesis” AND (“evolution” OR “convergent evolution”); “succulence” AND (“comparative genomics” OR “transcriptomics”); (“succulent plants” OR “CAM plants”) AND (“gene duplication” OR “gene regulation” OR “regulatory networks”); “succulence” AND (“epigenetic regulation” OR “stress tolerance”); and (“angiosperms” AND “arid environments”) AND (“plant adaptation” OR

“drought adaptation”). Searches were adapted when necessary to the syntax and search functions of the individual databases. Additional combinations of the keywords *succulence*, *convergent evolution*, *crassulacean acid metabolism*, *CAM photosynthesis*, *drought adaptation*, *water-use efficiency*, *plant evolution*, *comparative genomics*, *gene duplication*, *epigenetic regulation*, *stress tolerance*, *angiosperms*, *arid environments*, and *plant adaptation* were used to broaden or refine retrieval.

Studies were considered eligible when they addressed at least one of the principal dimensions examined in this review: (i) independent evolutionary origins or phylogenetic patterns of succulence; (ii) anatomical or morphological adaptations associated with water storage and water conservation; (iii) physiological mechanisms related to drought tolerance, hydraulic regulation, stomatal behaviour, or water-use efficiency; (iv) evolution, regulation, or ecological significance of CAM photosynthesis; (v) genomic, transcriptomic, regulatory, or epigenetic mechanisms potentially associated with succulent adaptations; or (vi) ecological and evolutionary consequences of succulence in arid and semi-arid environments. Peer-reviewed original research articles and review papers constituted the principal evidence base, while relevant book chapters and scientific reports were considered when they provided important conceptual or historical information.

Publications were excluded when they were unrelated to angiosperm succulence or did not provide information relevant to the morphological, physiological, ecological, evolutionary, or genomic questions addressed in the review. Studies dealing exclusively with unrelated forms of drought tolerance without a clear connection to succulence, CAM, or the evolutionary mechanisms discussed here were not prioritized. Publications lacking sufficient scientific information to evaluate their relevance to the objectives of the review were also excluded from the principal synthesis.

Search results obtained from the different databases were compared on the basis of title, authorship, publication year, and bibliographic information. Duplicate records retrieved from more than one database were retained only once for subsequent evaluation. Screening was conducted sequentially. First, titles and abstracts were examined to determine their correspondence with the scope of the review. Publications considered potentially relevant at this stage were subsequently evaluated through examination of the full text. Full-text assessment focused on whether each study provided evidence directly contributing to one or more of the structural, physiological, ecological, evolutionary, or genomic dimensions of convergent succulence considered in the manuscript.

The relevance of the selected literature was evaluated according to its direct contribution to the objectives of the review, the appropriateness of the experimental or comparative approach, the clarity of the evidence presented, and its contribution to understanding the evolution or function of succulent traits. Particular weight was given to comparative and phylogenetic studies involving multiple lineages, experimental investigations of CAM and drought-related traits,

and genomic or transcriptomic studies capable of identifying molecular mechanisms potentially associated with convergent evolution. Recent studies were prioritized where appropriate, while seminal publications were retained when necessary to establish fundamental concepts or mechanisms.

Backward reference searching was also performed by examining the bibliographies of particularly relevant articles and reviews. Publications identified through this procedure were subjected to the same relevance criteria used for database-derived studies. This complementary procedure was used to reduce the likelihood of excluding influential studies that might not have been retrieved because of differences in terminology or database indexing.

The literature was subsequently organized into thematic categories corresponding to the major dimensions of the review, including structural and morphological convergence, physiological adaptations and CAM, genomic and molecular mechanisms, ecological and biogeographical implications, and future research priorities. Evidence across these categories was then comparatively synthesized to identify recurring adaptive patterns as well as lineage-specific evolutionary solutions.

Because the objective was an integrative synthesis across heterogeneous biological disciplines, this study was not designed as a formal PRISMA-based systematic review or meta-analysis. Therefore, a prospective quantitative record-flow protocol was not established, and exact numbers of records retrieved, duplicates removed, and studies excluded at each screening stage were not recorded in a manner that would permit reliable retrospective reconstruction. These values are consequently not reported to avoid introducing artificial precision. The methodological description provided here is intended to transparently define the scope, search logic, eligibility criteria, screening procedure, and evidence-evaluation framework used in this semi-systematic review.

RESULTS AND DISCUSSION

Functional and evolutionary integration of succulence across angiosperms

The repeated emergence of succulent traits across angiosperms reflects not only morphological convergence but also deep functional integration between structure, physiology, and environmental response. In water-limited ecosystems, plants face simultaneous constraints on carbon acquisition, hydraulic stability, and thermal balance. Succulence addresses these challenges through coordinated modifications that operate across multiple biological levels, enabling plants to persist under extreme drought conditions and fluctuating resource availability (Griffiths and Males, 2017; Maynard *et al.*, 2022). Central to this integration is the coupling between water storage capacity and metabolic flexibility, which allows succulents to buffer temporal variability in the water supply while maintaining photosynthetic activity (Ogburn and Edwards, 2012; Luján *et al.*, 2023). A defining feature of many succulents is the evolution of crassulacean acid metabolism, which represents a key physiological innovation that enhances

water-use efficiency. CAM enables nocturnal CO₂ uptake and daytime carbon assimilation, significantly reducing transpirational water loss (Males and Griffiths, 2017; Borland *et al.*, 2009). This metabolic shift is tightly linked to anatomical traits, such as large vacuoles for malic acid storage and reduced intercellular air spaces, demonstrating the interplay between form and function (Leverett *et al.*, 2023; Herrera, 2020). Importantly, CAM is not a uniform trait but exists along a continuum, ranging from weak or facultative expression to strong obligate forms, reflecting adaptation to local environmental conditions (Winter *et al.*, 2008; Messerschmid *et al.*, 2026). The hydraulic architecture of succulent plants plays a critical role in their ecological success. Water storage tissues act as internal reservoirs that stabilize the plant water status during prolonged droughts, thereby reducing reliance on immediate soil moisture availability (Pérez-López *et al.*, 2023; Imperiale *et al.*, 2025). This capacity is often complemented by shallow root systems that rapidly absorb water following infrequent rainfall events (Paz *et al.*, 2015). At the same time, succulents must balance water storage with mechanical stability and nutrient transport, leading to unique anatomical configurations such as mucilaginous tissues and specialized vascular arrangements (Mauseth, 2006). Thermal regulation is another critical aspect of succulent function. Many succulents inhabit environments with high solar radiation and temperature extremes, necessitating the development of strategies to avoid overheating and photoinhibition. Compact growth forms and reflective surfaces help reduce the heat load, whereas CAM metabolism allows stomatal closure during the hottest parts of the day (Chetti and Nobel, 1987). Additionally, the high-water content of succulent tissues provides thermal inertia, buffering internal temperatures against rapid fluctuations (Charrier *et al.*, 2015). These features collectively enhance survival in harsh climatic conditions. At the molecular level, the convergence of succulent traits is underpinned by regulatory changes in gene expression rather than identical genetic mutations. Comparative genomic studies have indicated that genes associated with circadian rhythms, stress signaling, and carbon metabolism are consistently recruited during the evolution of CAM and related traits (Chomthong and Griffiths, 2023; Liu *et al.*, 2025). This suggests that convergence often involves the reorganization of existing genetic networks, enabling similar functional outcomes to arise in different lineages (Alvarado *et al.*, 2025; Xiao and Wang, 2025). Furthermore, epigenetic mechanisms may contribute to the dynamic regulation of these pathways, particularly in facultative CAM species that respond plastically to environmental cues (Miryeganeh, 2025; Tan and Chen, 2023). Gene duplication has emerged as a recurrent theme in succulent plant evolution. Duplicated genes provide opportunities for subfunctionalization or neofunctionalization, facilitating the development of novel traits such as enhanced acid metabolism or stress tolerance (Panchy *et al.*, 2016; Birchler and Yang, 2022). In several lineages, the expansions of gene families involved in key metabolic processes have been linked to the optimization of CAM and water storage strategies (Groot Crego *et al.*, 2024; Boxall *et al.*, 2020). However, the extent to which gene duplication versus regulatory modification drives convergence remains an active area of research. Despite their broad similarities, important differences persist among succulent lineages, reflecting their diverse evolutionary histories and ecological

contexts. For example, stem succulence in cacti is associated with extensive cortical storage tissues and reduced leaves, whereas leaf succulence in Crassulaceae involves modifications of mesophyll cells and leaf architecture (Aros-Mualin and Kessler, 2024; Franco *et al.*, 2022). Similarly, the degree of CAM expression and reliance on water storage can vary widely, even among closely related species (Heyduk *et al.*, 2020; Zotz *et al.*, 2023). These variations illustrate that convergent evolution produces functionally analogous but not identical solutions. To better capture the multidimensional nature of convergence in succulents, an integrative framework can be proposed that links trait origin, functional outcome, and genomic mechanism (Table 1).

Table 1. Integrative convergence matrix linking structural innovation, physiological function, and genomic mechanism in succulent angiosperms (Griffiths and Males, 2017; Winter *et al.*, 2008; Lüttge, 2010)

Evolutionary axis	Structural innovation	Physiological consequence	Genomic mechanism	Degree of convergence
Water economy	Enlarged vacuolated cells	Long-term water storage	Upregulation of aquaporins, osmotic regulators	High (repeated across families)
Carbon acquisition	Nocturnal stomatal opening	CAM photosynthesis	Circadian gene rewiring, enzyme regulation	Very high (multiple origins)
Surface minimization	Reduced or modified leaves	Lower transpiration rates	Developmental gene modulation	High
Thermal buffering	Compact growth forms	Reduced heat stress	Stress-response gene networks	Moderate to high
Rapid resource uptake	Shallow, extensive roots	Efficient rainfall exploitation	Root development gene expansion	Moderate

This table summarizes the principal dimensions of convergent evolution in succulent angiosperms by linking structural innovations with their physiological consequences, underlying genomic mechanisms, and relative degree of convergence across independent lineages. The matrix highlights recurrent adaptive solutions associated with water economy, carbon acquisition, reduction of transpirational losses, thermal buffering, and rapid resource uptake.

As shown in Table 1, convergence in succulents is not limited to isolated traits but involves coordinated shifts across multiple biological systems. This integrative perspective highlights how similar ecological pressures can repeatedly

shape complex trait syndromes through diverse yet functionally equivalent evolutionary pathways.

Genomic basis of convergent succulence: mechanisms, evolutionary trajectories and evidence

Understanding genomic convergence in succulent angiosperms requires distinguishing between similarity in phenotype, similarity in biological pathways, and identity of the underlying genetic changes. Current evidence indicates that distantly related succulent lineages generally do not depend on identical mutations to produce comparable adaptive phenotypes. Instead, convergence appears to occur predominantly through recurrent recruitment and reorganization of pre-existing genetic components involved in carbon metabolism, circadian regulation, water relations, development, and stress responses (Artur and Kajala, 2021; Allard and Kumar, 2026; Perron *et al.*, 2024; Xu *et al.*, 2026). This distinction is important because similar functional outcomes may be generated through different combinations of molecular changes. Genomic convergence in succulents should therefore be interpreted primarily as repeated modification of shared functional systems rather than as strict molecular identity among independent lineages.

Which molecular components are repeatedly recruited?

The clearest evidence of recurrent molecular recruitment concerns the regulation of carbon metabolism associated with crassulacean acid metabolism (CAM). In CAM species, genes controlling CO₂ fixation, malate synthesis, decarboxylation, stomatal function, and associated metabolic processes exhibit coordinated diel expression. Changes in the timing and magnitude of gene expression enable nocturnal carbon fixation and daytime decarboxylation without requiring the evolution of an entirely novel metabolic machinery (Yang *et al.*, 2017; Li *et al.*, 2024). Regulatory modifications involving promoter activity, transcription factors, and circadian control therefore provide a plausible mechanism through which existing pathways can be reorganized into CAM-related functions (Rijo-Ferreira and Takahashi, 2019; Maderazo *et al.*, 2022).

This interpretation is consistent with evidence that CAM is not a discrete and uniform state but can range from weak or facultative expression to strongly constitutive forms. Reversible transcriptional changes during CAM induction further demonstrate that substantial physiological reorganization can occur through changes in gene expression rather than through alterations of protein-coding sequences (Brillhaus *et al.*, 2016; Qiu *et al.*, 2023). Consequently, temporal regulatory reprogramming represents one of the more strongly supported molecular components of CAM evolution.

Water transport and cellular osmotic regulation constitute another recurrent molecular component. Aquaporins regulate water movement across cellular membranes, whereas genes involved in osmolyte synthesis and vacuolar function contribute to the maintenance of cellular turgor under water limitation (Chaumont and Tyerman, 2014; Ghosh *et al.*, 2021; Li *et al.*, 2022). Altered expression of these functional categories is consistent with the requirements imposed by large water-storage tissues. However, these mechanisms are widespread among plants

and are not unique to succulent taxa. Their occurrence in succulent tissues therefore supports their physiological importance but does not by itself demonstrate that they were causal innovations in the evolutionary origin of succulence. Comparative analyses involving succulent species and their closely related non-succulent relatives remain essential for distinguishing mechanisms specifically associated with the origin of succulence from general plant responses to drought.

The recurrent recruitment of stress-response, circadian, metabolic, and water-transport pathways therefore suggests the existence of a broadly conserved genetic toolkit from which succulent adaptations can evolve. Nevertheless, different taxa appear to use different components or regulatory configurations of this toolkit (Gilman *et al.*, 2022; Heyduk *et al.*, 2023). Molecular convergence is consequently more evident at the level of functional pathways than at the level of individual genes.

Which genomic mechanisms may generate convergent outcomes?

Gene-regulatory reprogramming is one of the principal mechanisms proposed to explain repeated functional convergence. Changes in transcriptional timing, expression intensity, and tissue specificity can modify existing physiological processes without requiring new genes. This mechanism is particularly relevant to CAM because the pathway depends strongly on temporal coordination among circadian regulation, stomatal behaviour, carbon fixation, and malate metabolism (Yang *et al.*, 2017; Chomthong and Griffiths, 2023). Network-level reorganization may similarly alter interactions among circadian, metabolic, developmental, and stress-response pathways, allowing relatively limited molecular changes to produce coordinated physiological effects (Sackton and Clark, 2019; Stanley *et al.*, 2022).

Gene duplication represents a second potential source of evolutionary innovation. Whole-genome, segmental, tandem, and other duplication events generate redundant gene copies that may subsequently undergo subfunctionalization or neofunctionalization (He and Zhang, 2005; Kaltenecker *et al.*, 2018). Expansion of gene families associated with CAM has been documented in some lineages, supporting the hypothesis that duplication can facilitate metabolic specialization (Groot Crego *et al.*, 2024). Duplicated genes involved in stress responses, carbohydrate metabolism, and ion transport may similarly increase the evolutionary flexibility available for adaptation to water limitation (Du *et al.*, 2023; Yang *et al.*, 2019).

However, gene duplication should not be regarded as a universal requirement for the evolution of succulence. Independent succulent lineages have different genome-duplication histories, yet they can produce comparable adaptive phenotypes. Duplication is therefore more appropriately viewed as a mechanism that can increase evolutionary opportunity rather than as a single causal explanation for convergent succulence. In some lineages, gene-family expansion may have facilitated functional innovation, whereas in others regulatory modification of existing genes may have been sufficient.

Epigenetic regulation provides an additional potential mechanism for generating physiological flexibility. DNA methylation, histone modifications, and chromatin remodelling can alter gene accessibility and expression without modifying the underlying DNA sequence (Miryeganeh, 2025; Petroll *et al.*, 2025; Casamassimi and Ciccodicola, 2019). Such mechanisms are particularly relevant to facultative CAM, in which photosynthetic behaviour can change in response to environmental conditions. The reversible transcriptional response observed during CAM induction supports the broader concept that regulatory plasticity is important for metabolic transitions (Brilhaus *et al.*, 2016; Winter and Holtum, 2024).

Table 2. Molecular mechanisms underlying convergent evolution of succulence in angiosperms

Molecular level	Key mechanism	Functional role	Example processes	Evolutionary significance	References
Gene regulation	Temporal and spatial expression changes	Coordinates metabolism and stress responses	Diel regulation of CAM genes	Enables adaptation without coding changes	(Greenwald <i>et al.</i> , 2010)
Gene duplication	Genome and local duplications	Provides genetic redundancy	Expansion of metabolic and stress-related genes	Promotes functional diversification	(Storz <i>et al.</i> , 2013)
Epigenetic control	DNA methylation and histone modification	Modulates environmentally responsive gene activity	C ₃ -CAM switching	Enhances phenotypic plasticity	(Vaissière <i>et al.</i> , 2008)
Water transport genes	Aquaporin regulation	Controls cellular and tissue water movement	Enhanced expression in succulent tissues	Improves water storage and drought tolerance	(Chaumont and Tyerman, 2014)
Metabolic pathway rewiring	Carbon–osmotic pathway integration	Links carbon fixation with water conservation	CAM malate metabolism	Supports efficient resource use	(Heyduk <i>et al.</i> , 2021)
Regulatory networks	Circadian, stress, and metabolic interactions	Coordinates environmental responses	Circadian stomatal regulation	Integrates adaptive traits	(Xu <i>et al.</i> , 2023)

Nevertheless, the evolutionary significance of epigenetic mechanisms requires more cautious interpretation. Evidence that epigenetic regulation contributes to environmentally responsive gene expression does not necessarily demonstrate that epigenetic modifications caused the independent evolutionary origins of succulence. Their strongest established role may currently concern short-term plasticity and environmental responsiveness, whereas their contribution to long-term evolutionary fixation remains less certain. The principal molecular mechanisms proposed to contribute to the convergent evolution of succulence, together with their functional roles and evolutionary significance, are summarized in Table 2.

This table summarizes the principal molecular mechanisms contributing to the convergent evolution of succulence in angiosperms. It highlights how different genomic levels ranging from gene regulation to network interactions collectively shape adaptive responses to drought. These mechanisms demonstrate that similar phenotypic outcomes can arise through diverse but functionally equivalent molecular pathways, emphasizing the flexibility of evolutionary processes.

How strong is the evidence for genomic convergence?

The evidence supporting genomic mechanisms of convergent succulence is heterogeneous. Temporal regulation of CAM-related metabolism is supported by physiological, transcriptional, and functional studies and represents one of the strongest examples of molecular reorganization associated with succulent adaptation (Yang *et al.*, 2017; Boxall *et al.*, 2020). By contrast, broader claims concerning gene-family expansion, epigenetic mechanisms, or regulatory-network rewiring often rely more heavily on comparative genomic or transcriptomic associations (Lyu *et al.*, 2025).

This distinction is particularly important when interpreting differential gene expression. The observation that genes associated with water transport, stress responses, osmotic regulation, or carbon metabolism are differentially expressed in succulent plants does not establish that these changes initiated the evolution of succulence. Some molecular patterns may represent downstream consequences of succulent anatomy or environmental exposure rather than causal evolutionary innovations. Similarly, the presence of duplicated stress-related genes does not demonstrate that duplication itself was responsible for the origin of the phenotype. Functional validation is therefore necessary to separate causal mechanisms from genomic correlates (Hartmann *et al.*, 2021).

Comparisons among lineages further indicate that phenotypic convergence does not require identical genomic trajectories. Some succulent groups show expansions of particular gene families, whereas others appear to rely more strongly on modifications in gene expression and network regulation (Franco *et al.*, 2022; Artur and Kajala, 2021; Heyduk *et al.*, 2023). This variation argues against a single genomic model of succulence. Instead, several molecular routes may lead to similar physiological outcomes, with the route available to each

lineage influenced by its ancestral genome, developmental architecture, and ecological history.

The relationship between anatomy and molecular regulation illustrates this complexity particularly well. Genes controlling organ development interact with metabolic pathways to generate water-storage tissues and associated physiological characteristics. However, analogous anatomical solutions can originate through different developmental modifications, as illustrated by the contrast between stem succulence and leaf succulence among independent angiosperm lineages. Genomic convergence therefore occurs within lineage-specific developmental constraints rather than independently of them.

Recent advances in high-throughput sequencing, comparative genomics, transcriptomics, and functional genomics provide increasingly powerful approaches for testing these hypotheses (Goche *et al.*, 2025; Ramzan *et al.*, 2026). Nevertheless, genomic resources remain unevenly distributed across succulent diversity, and conclusions based on a relatively small number of well-characterized taxa should not automatically be generalized to all independent origins of succulence. Broader phylogenetic sampling and direct functional comparisons between succulent and non-succulent relatives will be required to determine which molecular mechanisms are repeatedly causal and which represent lineage-specific associations.

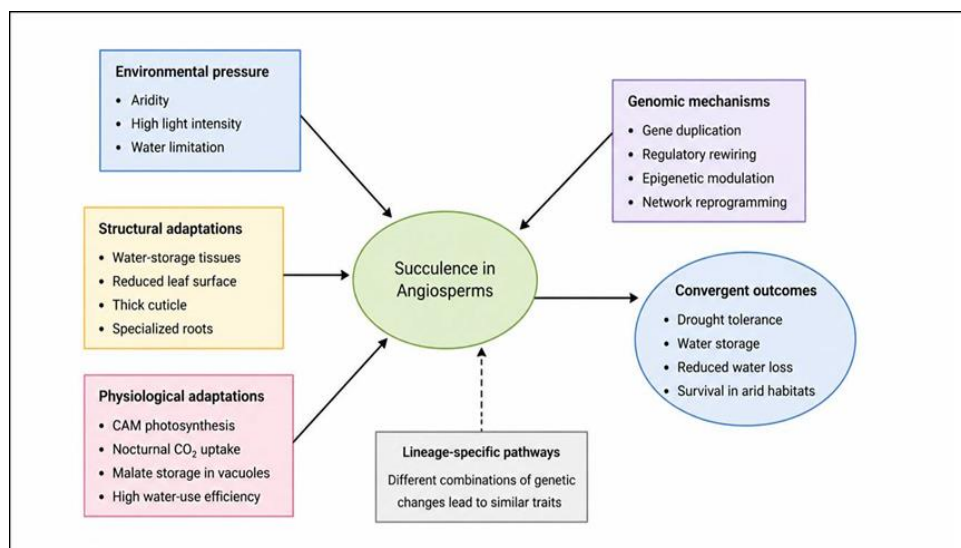


Figure 1. Schematic representation of the convergent evolution of succulence in angiosperms, integrating environmental drivers, structural and physiological adaptations, and genomic mechanisms. Original illustration by the authors.

Overall, current evidence supports a hierarchical interpretation of genomic convergence. The strongest convergence occurs at the functional and pathway levels, where independent lineages repeatedly recruit mechanisms associated with carbon metabolism, circadian regulation, water relations, and stress tolerance.

Convergence at the level of individual genes, mutations, duplication events, or epigenetic modifications is considerably less uniform. Thus, the genomic architecture of succulence is best understood as a balance between conservation and innovation: evolution repeatedly draws upon conserved genetic toolkits, but reorganizes them through lineage-specific combinations of regulatory changes, gene duplication, metabolic coordination, and developmental modification. This framework explains how phylogenetically distant angiosperms can achieve similar drought-adapted phenotypes without following identical molecular evolutionary trajectories. The integration of these structural, physiological, and genomic processes provides a conceptual framework for understanding how similar environmental pressures can generate convergent functional outcomes through partially distinct evolutionary pathways. The relationships among environmental drivers, phenotypic adaptations, physiological responses, and underlying genomic mechanisms are summarized in Figure 1.

The genomic architecture of succulence reflects a balance between conservation and innovation. While similar environmental pressures drive the repeated evolution of comparable traits, the underlying genetic mechanisms remain diverse and flexible. This combination of predictability and variability underscores the complexity of convergent evolution and reinforces the value of succulents as a model system for studying plant adaptation at multiple biological scales.

Ecological, biogeographical and evolutionary implications of convergent succulence

The repeated emergence of succulence across angiosperms has far-reaching ecological and biogeographical consequences, influencing not only individual plant performance but also broader ecosystem structure and function. In arid and semi-arid environments, succulent species often act as ecosystem modifiers by stabilizing soils, altering microclimates, and buffering temporal variability in water availability (Ding *et al.*, 2025; Mircea *et al.*, 2025). Their capacity to store water in specialised tissues enables them to maintain physiological activity during prolonged droughts, which in turn supports associated organisms, such as microbes, insects, and small vertebrates (Haghpanah *et al.*, 2024; Nieves-Cordones *et al.*, 2019). Through these interactions, succulents contribute to the formation of localized resource islands that enhance biodiversity and promote ecological resilience (Valencia *et al.*, 2015). From a biogeographical perspective, succulent lineages have diversified independently across multiple dryland regions, including the Americas, southern Africa, Madagascar, and Australia. These radiations often coincide with periods of climatic drying and the expansion of open habitats, creating ecological opportunities for drought-adapted plants (Holtum, 2023; Arakaki *et al.*, 2011). Fossil and phylogenetic evidence indicate that many succulent clades originated during the Cenozoic, when declining atmospheric CO₂ and increasing seasonality intensified the selection for water-use efficiency (Pittermann *et al.*, 2012; Sage *et al.*, 2023). The convergence of

similar growth forms and physiological strategies in geographically distant regions illustrates how environmental filtering can repeatedly produce analogous and adaptive solutions (Domagal-Goldman *et al.*, 2016). Ecological interactions have played a significant role in shaping the evolution and persistence of succulence. For example, herbivory has driven the development of defensive traits, such as spines, toxic compounds, and tough epidermal layers, in many succulent species (Wininger and Rank, 2017; Jameel *et al.*, 2025). These defences not only reduce tissue loss but also influence species interactions and the dynamics of the community. Pollination systems in succulents are equally diverse, ranging from specialised relationships with nocturnal pollinators, such as bats, to more generalised systems involving insects and birds (Chitchak *et al.*, 2024; Diniz *et al.*, 2025). Seed dispersal strategies, including wind, water, and animal-mediated transport, further contribute to the spatial distribution and colonization success of succulent plants (Rubalcava-Castillo *et al.*, 2025). Together, these biotic interactions demonstrate that succulence is embedded within complex ecological networks, rather than functioning as an isolated trait. At larger spatial and temporal scales, the evolution of succulence has contributed to patterns of diversification and endemism in dryland flora. Some lineages exhibit rapid adaptive radiations following the acquisition of succulent traits, suggesting that these adaptations can act as key innovations that open up new ecological niches (Vanschoenwinkel *et al.*, 2025). In contrast, other groups show more gradual diversification, indicating that the evolutionary impact of succulence can vary depending on lineage-specific factors, such as genetic background and ecological opportunity (Hernández-Hernández *et al.*, 2014; Jaramillo, 2023). This heterogeneity highlights the interplay between deterministic environmental pressures and historical contingencies in shaping evolutionary outcomes. The physiological strategy of crassulacean acid metabolism further enhances the ecological success of many succulents by enabling efficient carbon assimilation under water-limited conditions. CAM plants can maintain a positive carbon balance while minimising water loss, allowing them to occupy habitats that are inaccessible to many other plant types (Heyduk, 2022; Chomthong and Griffiths, 2023). This advantage not only influences species distribution but also affects ecosystem-level processes, such as primary productivity and nutrient cycling. In some ecosystems, CAM plants contribute disproportionately to carbon fluxes during dry periods, thereby stabilising ecosystem function under climatic stress (Zhang *et al.*, 2026; Talbot *et al.*, 2018). The evolutionary significance of convergent succulence extends beyond individual lineages to broader questions in the field of evolutionary biology. The repeated origin of similar trait combinations across unrelated taxa provides strong evidence for the predictability of adaptation to consistent environmental pressures (Speed and Arbuckle, 2017). However, the diversity of underlying genetic and developmental pathways demonstrates that multiple routes can lead to similar phenotypic outcomes, emphasising the role of this evolutionary flexibility. This duality of predictable phenotypes arising from

diverse mechanisms represents a central theme in the study of convergence. Finally, understanding the ecological and evolutionary dynamics of succulence has important implications for conservation and for global change biology. Many succulent-rich regions are biodiversity hotspots that are increasingly threatened by habitat degradation, climate change, and overexploitation (Pereira and Kohlsdorf, 2023; James *et al.*, 2021). The traits that enable succulents to survive in extreme environments may provide insights into plant resilience under future climatic scenarios. Identifying the mechanisms that underlie drought tolerance and resource-use efficiency can inform strategies for ecosystem restoration and the development of climate-resilient crops (Fradera-Soler *et al.*, 2022). The ecological, biogeographical, and evolutionary implications of convergent succulence highlight its importance as a key adaptive strategy for angiosperms. By linking organismal traits to ecosystem processes and large-scale evolutionary patterns, succulence provides a powerful framework for understanding how plants respond to environmental challenges across space and time (Figure 2).

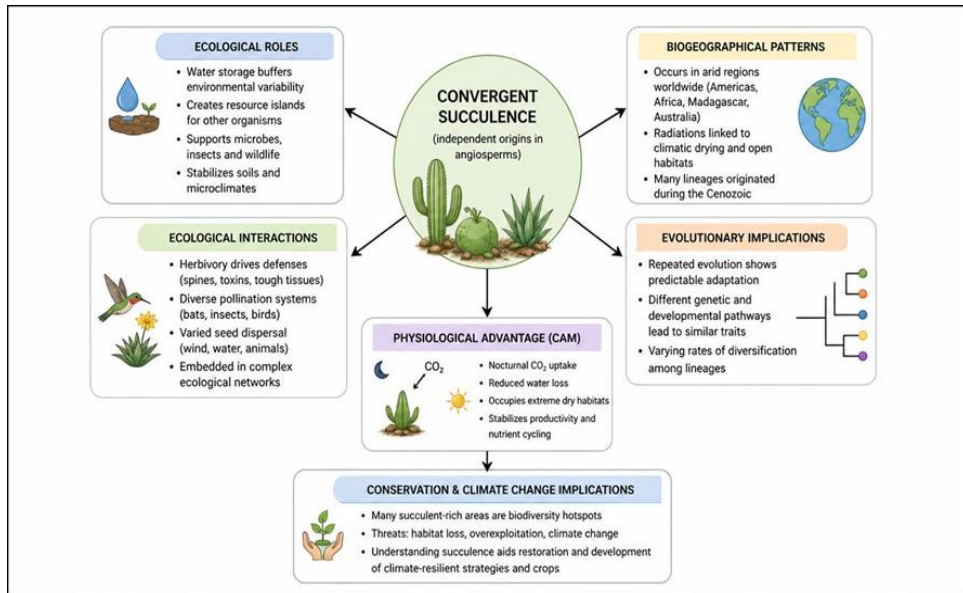


Figure 2. Schematic overview of the ecological, biogeographical, and evolutionary implications of convergent succulence in angiosperms. Original illustration by the authors

Functional dimension: physiological convergence in succulent angiosperms

Physiological convergence represents a central component of the adaptive success of succulence, enabling distantly related angiosperms to maintain metabolic activity under severe water limitations. Succulents exhibit remarkably similar functional strategies that optimise water-use efficiency, carbon

assimilation, and stress tolerance across diverse lineages. These shared physiological traits arise in response to comparable environmental pressures, particularly aridity, high irradiance, and episodic water availability, demonstrating how natural selection repeatedly shapes analogous solutions at the functional level (Folk *et al.*, 2020; Hočevár *et al.*, 2025). A hallmark of physiological convergence in succulents is the widespread evolution of crassulacean acid metabolism, a specialised mode of carbon fixation that reduces transpirational water loss. In CAM plants, stomata open predominantly at night, allowing CO₂ uptake under cooler and more humid conditions, and close during the day to minimize water loss (Lüttge, 2010). The absorbed CO₂ is stored as malic acid in vacuoles and is subsequently released during daylight for photosynthesis. This temporal separation between gas exchange and carbon assimilation significantly enhances water-use efficiency compared to C₃ and C₄ photosynthesis. The repeated independent evolution of CAM in angiosperms underscores its adaptive value and exemplifies a clear case of functional convergence (Onstein, 2020; Qadir *et al.*, 2026). In addition to CAM, succulents have additional physiological mechanisms that contribute to drought tolerance. One key feature is the ability to store large quantities of water within specialised tissues, which act as a buffer against prolonged periods without rainfall. This internal reservoir supports continued metabolic activity and prevents cellular dehydration of the cells. The regulation of water movement within these tissues is mediated by aquaporins and osmotic adjustments, which maintain cell turgor and facilitate efficient water redistribution (Yaaran and Moshelion, 2016). These processes are often finely tuned to environmental conditions, allowing succulents to respond dynamically to water availability fluctuations. Another important aspect of physiological convergence is the regulation of stomatal behaviour. Succulents typically exhibit reduced stomatal density and enhanced control over stomatal opening and closing, which minimizes water loss while maintaining sufficient CO₂ uptake (Males and Griffiths, 2017). In CAM species, stomatal rhythms are closely linked to circadian regulation, ensuring synchronization between environmental cues and metabolic processes (de Barros Dantas *et al.*, 2023). This coordination highlights the integration of physiological and molecular mechanisms to achieve efficient water use. Photoprotection and thermal regulation also play crucial roles in succulent physiology. High light intensity and temperature extremes in arid environments can lead to photoinhibition and increased oxidative stress. Succulent plants mitigate these risks through mechanisms such as increased antioxidant production, non-photochemical quenching, and reflective properties of their surfaces (Michalak *et al.*, 2026). In addition, the high water content of succulent tissues provides thermal buffering, thereby reducing the impact of temperature fluctuations on cellular processes (Nievola *et al.*, 2017). These adaptations enable succulents to maintain photosynthetic efficiency under conditions that are detrimental to less specialised plants. Metabolic flexibility is another defining feature of the physiological convergence of succulents. Some species exhibit facultative CAM,

allowing them to switch between C_3 photosynthesis and CAM, depending on environmental conditions (Holtum *et al.*, 2017). This plasticity provides a competitive advantage in variable environments, as plants can optimise carbon gain when water is abundant and conserve water during periods of drought. The ability to modulate metabolic pathways in response to environmental cues reflects a high degree of physiological adaptability and underscores the importance of regulatory mechanisms in convergence (Nautiyal and Nautiyal, 2026). Water-use efficiency in succulents is further enhanced by the integration of carbon metabolism and hydraulic processes. The accumulation of organic acids during CAM not only facilitates carbon storage but also influences cellular osmotic potential, contributing to the water retention (Bronson *et al.*, 2011). This dual function illustrates how metabolic pathways can serve multiple roles in adaptation to water limitation. Moreover, the coordination between carbon assimilation and water storage ensures that succulents maintain a positive carbon balance, even under prolonged stress conditions (Rhodes *et al.*, 1986). Despite these shared features, variations exist in the degree and expression of physiological convergence among succulent lineages. Differences in habitat, evolutionary history, and life history strategies can lead to diverse combinations of traits, even among species that occupy similar environments (Alvarado-Cárdenas *et al.*, 2013). For example, some succulents rely heavily on CAM, whereas others depend more on water storage or drought avoidance strategies. This diversity highlights that convergence operates along a continuum, producing a range of functional solutions, rather than a single optimal strategy. Physiological convergence in succulent angiosperms reflects a coordinated suite of adaptations that enhance survival in water-limited environments. Succulents achieve high levels of water-use efficiency and stress tolerance through mechanisms such as CAM photosynthesis, efficient water storage, stomatal regulation, and metabolic flexibility. These traits demonstrate how similar environmental challenges can repeatedly shape functional strategies across diverse plant lineages, providing a powerful example of convergent evolution at the physiological scale.

Critical synthesis: evidence strength, uncertainties and alternative evolutionary interpretations

Taken together, the available literature strongly supports succulence as a recurrent functional response to water limitation, but the strength of evidence differs considerably among the structural, physiological, and genomic mechanisms proposed to explain its convergent evolution. A critical distinction is therefore required between traits whose adaptive functions have been demonstrated experimentally and molecular mechanisms whose evolutionary roles remain largely inferred from comparative patterns.

Among the most firmly supported components of the succulent syndrome is the functional importance of water-storage tissues. Enlarged, highly hydrated tissues provide an internal reservoir capable of buffering short- to long-term

fluctuations in external water availability, while specialized anatomical configurations influence hydraulic functioning and tissue water relations (Griffiths and Males, 2017; Mauseth, 2006; Fradera-Soler *et al.*, 2022). However, even this apparently straightforward relationship should not be interpreted as evidence for a single anatomical solution. Stem succulence, leaf succulence, differences in mesophyll organization, mucilaginous tissues, and variation in vascular architecture demonstrate that comparable water-storage functions can emerge through substantially different developmental routes. Thus, convergence is considerably stronger at the level of functional outcome than at the level of anatomical construction.

The relationship between succulence and crassulacean acid metabolism provides an especially important example of the need to distinguish association from evolutionary dependence. CAM is one of the best-characterized physiological mechanisms for increasing water-use efficiency because nocturnal CO₂ uptake reduces transpirational water loss under conditions of high daytime evaporative demand (Lüttge, 2010; Males and Griffiths, 2017). Its physiological operation is therefore supported by strong experimental evidence. Nevertheless, the evolutionary relationship between CAM and succulence is less straightforward. CAM occurs along a continuum from weak or facultative expression to strong constitutive CAM, and not all succulent plants rely on CAM (Winter *et al.*, 2008; Holtum *et al.*, 2017; Messerschmid *et al.*, 2026). Moreover, anatomical characteristics frequently associated with CAM are not necessarily sufficient predictors of photosynthetic function (Heyduk *et al.*, 2021). Consequently, the repeated co-occurrence of CAM and succulence should not be interpreted as evidence that one invariably causes or precedes the other. An alternative interpretation is that tissue water storage and CAM represent partially independent innovations that can become functionally integrated when ecological conditions favour both water buffering and conservative carbon acquisition.

This distinction also affects interpretations of morphological convergence. Reduced leaves, compact growth forms, modified stomatal behaviour, thickened tissues, and extensive water-storage parenchyma are recurrent among succulent lineages, but their relative importance differs among taxa and environments. Similar selective pressures therefore do not necessarily generate an identical adaptive syndrome. Some lineages may rely predominantly on internal water storage, whereas others combine storage with CAM, drought avoidance, enhanced stomatal regulation, or other stress-tolerance mechanisms. The available evidence consequently favours a model of many-to-one functional convergence, in which different combinations of traits generate broadly similar ecological performance, rather than a model in which succulent lineages repeatedly evolve an invariant set of characteristics.

At the genomic level, conclusions require still greater caution. Comparative genomic and transcriptomic studies increasingly support the recurrent recruitment of genes involved in circadian regulation, carbon metabolism, water transport, osmotic adjustment, and stress signalling during

adaptation to dry environments (Artur and Kajala, 2021; Chomthong and Griffiths, 2023; Li *et al.*, 2024). Regulatory reprogramming is therefore a plausible general mechanism because evolutionary changes in the timing and magnitude of expression of existing genes can alter physiological function without requiring the independent origin of entirely new genes. The diel regulation of CAM-related genes provides particularly convincing evidence that changes in temporal gene expression are central to CAM function (Yang *et al.*, 2017). However, recurrent differential expression or enrichment of similar functional gene categories across lineages does not by itself demonstrate that the same regulatory changes caused the independent evolution of succulence. Much of the evidence remains comparative, and functional validation is available for a considerably smaller number of genes and taxa. Regulatory convergence should therefore be regarded as strongly supported for particular components of CAM and stress response, but less conclusively demonstrated as a universal explanation for the evolution of the complete succulent phenotype.

Gene duplication presents a similar interpretative challenge. Whole-genome, segmental, and local duplication can provide genetic redundancy from which subfunctionalization and neofunctionalization emerge, and expansions of gene families associated with CAM and environmental responses have been documented in some plant lineages (Kaltenegger *et al.*, 2018; Groot Crego *et al.*, 2024). Nevertheless, duplication cannot currently be considered a necessary prerequisite for succulent evolution. Different succulent groups possess different histories of genome and gene-family duplication, and similar phenotypes can apparently be achieved without identical duplication events. Gene duplication is therefore better interpreted as one of several mechanisms capable of increasing evolutionary potential rather than as a universal causal driver of convergence. Distinguishing duplication events that directly contributed to adaptive innovation from those that merely preceded diversification remains an important challenge.

Evidence for epigenetic regulation is even more preliminary in an explicitly evolutionary context. DNA methylation, histone modification, and chromatin remodelling provide biologically plausible mechanisms for environmentally responsive regulation, and the reversible induction of CAM demonstrates that substantial transcriptional plasticity can occur without changes in protein-coding sequences (Brilhaus *et al.*, 2016; Miryeganeh, 2025). However, evidence that particular epigenetic modifications repeatedly caused the independent evolutionary origin of succulence remains limited. Epigenetic mechanisms may contribute more directly to short-term phenotypic plasticity and environmentally induced physiological switching than to the long-term fixation of succulent phenotypes. Demonstrating an evolutionary role will require evidence that environmentally responsive epigenetic states are stable, functionally relevant, and connected to heritable differences among populations or lineages.

Aquaporins, osmolyte metabolism, and stress-response pathways illustrate another difficulty in assigning causality. Their involvement in cellular water relations and drought responses is well established (Chaumont and Tyerman,

2014; Ghosh *et al.*, 2021), but these mechanisms are widespread among non-succulent plants as well. Their presence or increased expression in succulent tissues cannot therefore be considered specific evidence for the evolution of succulence. A central unresolved question is whether succulent evolution required qualitatively novel molecular mechanisms or, more plausibly, quantitative and spatiotemporal reorganization of stress-response systems already present in ancestral angiosperms. Current evidence more strongly supports the latter interpretation, but broader comparative analyses between succulent and closely related non-succulent species are needed to test it.

A further limitation concerns the distinction between adaptation and historical contingency. Similar environmental conditions can favour similar functional traits, but the phenotype that ultimately evolves is constrained by the developmental architecture and genetic background inherited from each lineage. Stem succulence in Cactaceae and leaf succulence in Crassulaceae illustrate how different developmental starting points can produce analogous water-storage strategies. Thus, the repeated evolution of succulence reflects both deterministic environmental filtering and lineage-specific evolutionary opportunity. The relative contribution of these two processes remains difficult to quantify, particularly because many comparisons involve distantly related groups that differ in numerous traits beyond succulence.

The available literature is also uneven in taxonomic and methodological coverage. Detailed physiological and molecular information is concentrated in a limited number of model or economically important taxa, whereas many independent origins of succulence remain poorly characterized. This creates a risk of interpreting mechanisms identified in well-studied lineages as universal characteristics of succulent angiosperms. Similarly, genomic and transcriptomic correlations are increasingly abundant, but direct functional tests remain comparatively scarce. Genome editing, reciprocal comparisons between succulent and non-succulent relatives, common-garden experiments, and phylogenetically explicit analyses will be particularly important for separating causal mechanisms from lineage-specific associations.

Overall, the strongest conclusion emerging from the available evidence is therefore not that succulent angiosperms repeatedly evolved through an identical structural, physiological, or genomic pathway. Rather, convergence is most evident at the functional level: independent lineages repeatedly evolved mechanisms that improve water storage, reduce water loss, and maintain carbon assimilation under water limitation. The anatomical routes producing these functions are more heterogeneous, while genomic convergence appears to involve recurrent recruitment of similar functional networks without necessarily involving identical genes, mutations, or duplication events. This hierarchy of evidence from strong functional convergence to more variable structural convergence and comparatively less resolved molecular convergence provides a more cautious framework for interpreting succulence as an evolutionary

phenomenon and identifies the distinction between correlation and causation as a central priority for future research.

Future Directions and Research Priorities

The repeated emergence of succulence across diverse angiosperm lineages provides an important framework for investigating how similar adaptive outcomes evolve under comparable environmental constraints. However, future research should clearly distinguish between mechanisms that are already supported by anatomical, physiological, or molecular evidence and evolutionary hypotheses that remain to be directly tested. Considerable progress has been made in characterizing the morphology and physiology of succulent plants, but the causal mechanisms underlying the repeated evolutionary origin of these traits remain less completely resolved (Onstein, 2020). Addressing these uncertainties will require an integrative framework combining evolutionary biology, genomics, ecology, developmental genetics, and systems biology (Loewe, 2009; Calderon Moreno *et al.*, 2025; Walia *et al.*, 2025).

Expanding genomic comparisons: from associations to causal mechanisms

Established evidence indicates that succulent lineages exhibit modifications in genes and regulatory pathways associated with carbon metabolism, stress responses, water relations, and environmental adaptation. However, available genomic resources remain concentrated in a relatively limited number of taxa, restricting the extent to which these observations can be generalized across the multiple independent origins of succulence (Alharbi, 2026). Consequently, the hypothesis that convergent succulent phenotypes repeatedly arise through modification of the same genetic networks remains incompletely tested.

A major research priority is therefore to obtain high-quality genomic resources from phylogenetically independent succulent lineages and, critically, from closely related non-succulent taxa. Such comparisons could determine whether similar phenotypes result from repeated modification of homologous pathways or from distinct molecular routes producing equivalent functional outcomes (Osmanski *et al.*, 2023). Gene-family evolution, regulatory elements, structural genomic variation, and epigenetic modifications represent candidate mechanisms that warrant investigation (Bonnin *et al.*, 2025), but their recurrent association with succulence should not be considered evidence of causality without functional and phylogenetically controlled validation.

Developmental genetics of water-storage tissues: an unresolved mechanism

The occurrence of enlarged water-storage tissues composed predominantly of highly vacuolated parenchymatous cells is a well-established anatomical characteristic of succulence. Their contribution to internal water storage and

drought buffering is also supported by physiological and anatomical evidence. What remains substantially less understood is how developmental genetic programs have been independently modified to generate these tissues across different angiosperm lineages (Deng *et al.*, 2025).

At present, it should therefore not be assumed that independent origins of stem, leaf, or root succulence involve the same developmental genes or regulatory pathways. Similar anatomical outcomes could result from modifications of homologous developmental programs, but they could equally arise through distinct lineage-specific developmental mechanisms. This represents a testable evolutionary hypothesis rather than an established mechanism. Transcriptomics, single-cell approaches, and functional genetics could help identify the regulatory processes controlling cell expansion, tissue differentiation, vacuolar development, and organ architecture in succulent tissues (Nakayama *et al.*, 2026). Comparisons between independent succulent lineages and their non-succulent relatives will be particularly important for determining whether developmental convergence occurs at the molecular level or primarily at the phenotypic level (DiFrisco and Jaeger, 2021).

Water-storage tissues and CAM: association does not establish evolutionary sequence

The relationship between anatomical succulence and crassulacean acid metabolism represents another area in which established functional evidence must be distinguished from evolutionary inference. It is well established that CAM can substantially increase water-use efficiency and that water-storage tissues can provide the internal water reserves and cellular architecture compatible with CAM function. CAM and succulence are therefore functionally complementary in many species.

However, their frequent association does not establish a universal evolutionary sequence. It remains unresolved whether increased tissue succulence generally preceded CAM, whether CAM facilitated subsequent increases in succulence, whether the two traits evolved together under common selective pressures, or whether different sequences occurred independently among lineages. The existence of variation in CAM expression and the diversity of succulent anatomies argue against assuming a single universal trajectory.

The proposition that anatomical succulence may facilitate the evolution of stronger CAM expression should therefore be regarded as an evolutionary hypothesis requiring further testing, rather than as an established sequence of events. Studies of transitional species exhibiting intermediate anatomical and physiological characteristics could help reconstruct the order in which these traits evolved (Heyduk, 2022). Phylogenetically explicit comparisons and analyses across environmental gradients will also be necessary to determine whether particular ecological conditions repeatedly favour the joint evolution of water-storage tissues and CAM (Wadgyman *et al.*, 2017).

Epigenetic regulation: established regulatory capacity, uncertain evolutionary role

Epigenetic mechanisms can modify gene activity and contribute to environmentally responsive phenotypic plasticity without altering the underlying DNA sequence (Chalopin *et al.*, 2026). This general regulatory capacity is well established. However, its significance for the origin and convergent evolution of succulence remains considerably less certain (Zhang *et al.*, 2025).

Current observations provide a basis for hypothesizing that epigenetic regulation may contribute to environmentally responsive changes in physiological traits associated with drought adaptation (Zimmer *et al.*, 2013). Nevertheless, demonstrating environmentally responsive epigenetic variation is not equivalent to demonstrating that such variation caused the evolutionary origin of a succulent phenotype. The possibility that epigenetic mechanisms facilitated repeated transitions toward succulence or contributed to the evolutionary stabilization of CAM-related traits should therefore be considered a working hypothesis.

Future research should determine whether candidate epigenetic modifications are reproducible across independent succulent lineages, whether they directly alter traits related to water storage or CAM, and whether such modifications are sufficiently stable to contribute to evolutionary change. Comparative and functional approaches will be necessary to distinguish transient environmentally induced epigenetic responses from modifications that have evolutionary significance (Bonnin *et al.*, 2025).

Microbiomes: a promising hypothesis rather than an established driver of succulent evolution

Plant-associated microbial communities can influence nutrient acquisition, plant growth, and responses to abiotic stress, providing a strong general basis for investigating plant–microbiome interactions under water limitation (Singh *et al.*, 2023). However, direct evidence demonstrating that microbiomes represent a causal mechanism underlying the convergent evolution of succulence is currently limited. The contribution of microbial communities to succulent evolution should therefore not be presented as an established mechanism.

Instead, the possibility that recurrent associations with drought-adapted microorganisms improve the performance of succulent plants represents a promising research hypothesis. Such microorganisms could potentially influence nutrient acquisition, root function, water relations, or stress tolerance, but whether these interactions contributed historically to the evolution or diversification of succulent lineages remains unknown.

Future studies should characterize microbial communities associated with independent succulent lineages and compare them with those of closely related non-succulent plants growing under comparable environmental conditions. Experimental manipulation of microbial communities will be particularly important for separating simple ecological association from functional effects on host drought tolerance. Only through such approaches will it be possible to

determine whether microbiomes primarily influence the contemporary ecological performance of succulents or have also contributed to their long-term evolutionary trajectories.

Climate change and adaptive capacity

A further priority concerns the response of succulent plants to ongoing climate change. Current ecological knowledge establishes that temperature and water availability strongly influence plant distribution and performance, but predictions regarding the responses of individual succulent lineages to future climates remain inherently uncertain. Increasing temperatures, altered precipitation regimes, and changes in the distribution of arid environments may modify the geographical ranges and selective environments experienced by succulent species (Al-Bakre, 2025).

Long-term field experiments, ecological modelling, and studies of population-level genetic variation will therefore be required to evaluate resilience, migration potential, and adaptive capacity under future environmental conditions (Sgrò *et al.*, 2011). These approaches should avoid assuming that traits advantageous under present-day aridity will necessarily confer equivalent advantages under future combinations of temperature, drought intensity, rainfall variability, and other environmental stresses.

From evolutionary hypotheses to practical applications

Succulent plants provide valuable biological models for understanding efficient water use, tissue water storage, and carbon assimilation under water limitation. These established physiological characteristics create opportunities for research aimed at improving crop resilience and developing more water-efficient agricultural systems. However, transferring these traits to conventional crops remains a research objective rather than an established technological outcome.

Future studies should therefore determine which components of succulent physiology can realistically be transferred or manipulated without compromising plant productivity. Insights into drought adaptation, carbon assimilation, and tissue water storage may ultimately contribute to breeding and biotechnology strategies (Wang *et al.*, 2025), but their agricultural application will require direct experimental validation. Integrating evolutionary research with applied plant science may consequently provide new approaches to climate-resilient agriculture while simultaneously improving our understanding of the fundamental mechanisms underlying plant adaptation (Currie *et al.*, 2024).

Overall, future research should move from identifying correlations toward experimentally testing causality. Developmental genetic control of water-storage tissues, the evolutionary coupling between succulence and CAM, epigenetic contributions to long-term adaptation, and microbiome-mediated effects should presently be treated as testable hypotheses of different levels of plausibility rather than universally established mechanisms. Combining phylogenetically controlled comparisons with functional genomics, physiological experiments,

developmental analyses, and ecological studies will be essential for determining which mechanisms repeatedly contributed to the independent evolution of succulence and which instead represent lineage-specific or environmentally induced responses.

CONCLUSIONS

Succulence is among the most remarkable examples of convergent evolution in angiosperms, having arisen independently in numerous lineages exposed to recurrent water limitation and environmental stress. The repeated evolution of this trait across phylogenetically distant groups demonstrates how similar selective pressures can promote comparable adaptive solutions despite distinct evolutionary histories. As a result, succulent plants provide an exceptional framework for exploring the interplay between form, function, and genome evolution. The success of succulent species is based on a suite of integrated adaptations that improve survival under drought-prone conditions. Water-storage tissues, modifications in leaf and stem architecture, specialized hydraulic properties, and efficient water-use strategies collectively enhance plant performance in arid and semi-arid habitats. In many cases, these structural adaptations are associated with physiological innovations such as crassulacean acid metabolism (CAM), which further reduces water loss while maintaining carbon assimilation. Together, these features illustrate how complex adaptive syndromes can evolve in response to environmental constraints.

Advances in genomics, transcriptomics, and comparative biology have significantly improved our understanding of the mechanisms underlying succulent evolution. Evidence increasingly suggests that convergent phenotypes may emerge through both shared and lineage-specific genetic pathways. Consequently, succulence should not be viewed as a single evolutionary outcome but rather as a collection of alternative solutions that converge on similar functional objectives. This perspective highlights the importance of integrating molecular, developmental, physiological, and ecological approaches when studying plant adaptation. Despite substantial progress, many aspects of succulent evolution remain poorly understood. Key questions concern the developmental origins of water-storage tissues, the evolutionary relationships between succulence and CAM photosynthesis, and the genetic factors that repeatedly facilitate adaptation to arid environments. Addressing these challenges will require broader taxonomic sampling and increased availability of genomic resources across diverse succulent groups. Beyond its evolutionary significance, succulence has growing relevance in the context of global climate change. As drought events become more frequent and severe, understanding the mechanisms that enable succulent plants to thrive under water scarcity may provide valuable insights for crop improvement, conservation planning, and ecosystem resilience. Overall, the study of succulent angiosperms continues to reveal fundamental principles of adaptation and convergence, emphasizing the extraordinary capacity of plants to evolve innovative solutions to environmental challenges.

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