

displayed by many cultivated garden flowers are no doubt due to the horticultural selection of alterations in the underlying ABC program.

There are many further variations to the basic ABC model. In many lineages, gene duplications have led to multiple copies of the ABC genes. In turn, these gene duplicates can evolve so as to parse the original function or to acquire new roles. There also are instances in which the original gene copy has been lost and a derived duplicate version has taken on the role of specifying organ identity. An additional consequence of ABC gene evolution is that the changes in the resulting ABC proteins can diversify their interaction partners, resulting in new or modified protein complexes with altered affinities for target gene binding sites.

In some cases, the evolution of new functional roles for ABC gene duplicates may well explain morphological novelties observed in some species. For instance, a duplicated B gene is responsible for the development of a novel floral organ type, the stamenodium, in columbines (Figure 3). ABC gene functions can even be heterotopic; expression of B class genes imparts petaloid characteristics to the petal-like bracts of dogwoods (Figure 3). What is remarkable about the ABC model, though, is its robustness; although the ABC gene network is constantly evolving, the overall logic of the network has been retained across the vast majority of flowering plants.

What about pine trees and other non-flowering plants?

The angiosperms and the gymnosperms together comprise the seed plants. Gymnosperms, including evergreens, cycads, and ginkgos, produce cones, not flowers (Figure 3). While flowers generally produce stamens and carpels on the same axis, cones are either male and produce pollen, or female and contain ovules. Gymnosperms ('naked seed') are so named because they lack the carpels typical of flowering plants. Other land plant lineages include the non-vascular plants, such as mosses, and the seedless vascular plants, such as ferns and lycophytes. To what extent does the ABC model apply to these non-flowering plant lineages?

Gymnosperms possess copies of B and C class genes. The gymnosperm C genes are expressed in male and female cones, while B gene expression is limited to male cones. Thus, specification of male and female identity appears to be conserved across angiosperms and gymnosperms. By contrast, analyses of the genomes of the moss *Physcomyrella patens*, or the lycophyte *Selaginella moellendorffii*, indicated that these species lack orthologs of any of the ABC genes. It thus appears that the ABC gene network arose coincident with the angiosperms. The angiosperms are easily the most speciose group within the plant kingdom; the foundations for their considerable success could well be due to the evolution of this robust gene network.

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Primer

Succulent plants

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The peculiar morphologies of succulent plants have been variously considered as grotesque monstrosities and exotic curiosities, but succulents have always been perceived as unique. The succulent syndrome is considered to be one of the most remarkable examples of convergent evolution across the plant kingdom. Common to all succulents is the presence of large cells for water storage. However, cellular succulence can occur in any vegetative plant organ, with the level of succulence in roots, stems, and leaves being subject to a certain degree of evolutionary coordination. Furthermore, cellular succulence scales up to morphological succulence according to various anatomical schemes that confer contrasting functional characteristics. This means that succulence is associated with a broad range of ecophysiological strategies and occurs in plants that have evolved in many different environments.

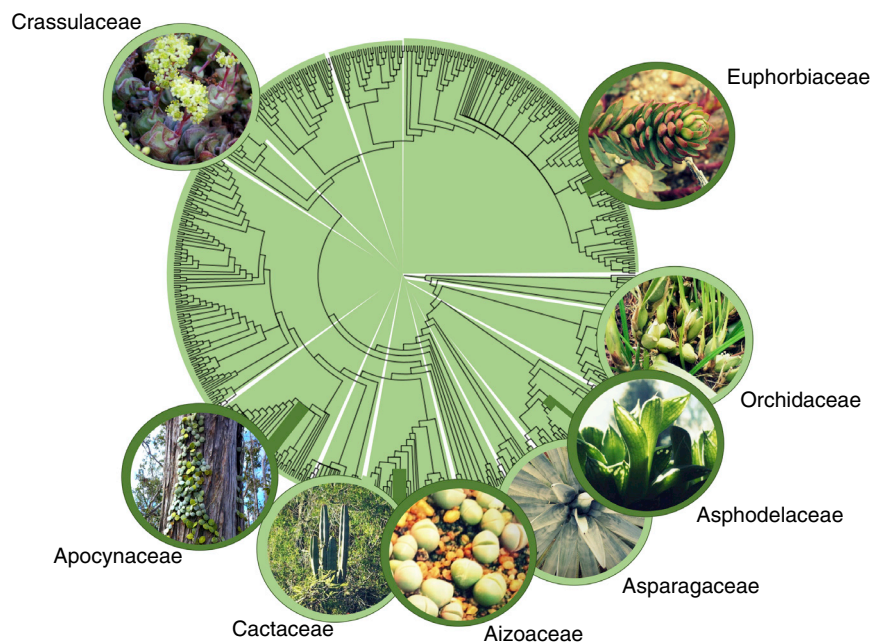
The term 'succulence' itself is generally agreed to refer to the storage of a significant amount of withdrawable water in living cells. Since it is dependent on variation in quantitative parameters, such as cell volume, cell packing, and tissue thicknesses, succulence is better considered as a continuous rather than a binary trait. Running parallel to this spectrum of succulence is a corresponding and underappreciated spectrum of ecological strategies based on contrasting water-use characteristics. Nevertheless, categorisation is sometimes necessary, and approximately 3–5% of all flowering plants are commonly described as succulents — a small but important proportion. Although some succulent lineages have undergone much greater net species diversification than others, there is no strong bias in the phylogenetic distribution of origins of succulence, suggesting that it is a relatively 'evolutionarily accessible' syndrome.

The phylogenetic placement of some of the major radiations of succulents in the angiosperms is shown in Figure 1.

We will first consider how the structural and functional properties of succulent plants influence their ecology, beginning with a survey of the core commonalities of the succulent syndrome. We will then go on to consider how these relationships have shaped the diversity of different succulent subtypes, and further define these categories in terms of habitat preferences and global distributions.

Key attributes of the succulent syndrome

The primary role of succulence is the storage of water in living cells for later remobilisation, and the water content of succulent organs may reach 90–95%. This hydraulic capacitance is fundamental to the ecophysiological strategies of succulent plants, but is underpinned by a range of structural varieties. Plants with specialised achlorophyllous water-storage tissue (hydrenchyma) are known as ‘storage succulents’, in contrast with those which simply store water in expanded chlorenchyma cells and are called ‘all-cell succulents’. Many all-cell succulents are annual plants, and utilise their leaves as single-use stores to extend the effective growing season. Transpiration can be maintained while the stored water is gradually spent, allowing maximal carbon gain before seed-set and senescence. Storage succulents are generally perennial, using stored water to buffer transpiration and chlorenchyma water potential during drought, and refilling their hydrenchyma during periods of water availability. The remobilisation of water to the chlorenchyma is facilitated by elastic cell walls in the hydrenchyma, which make this tissue highly collapsible. In both storage and all-cell succulents, symplastic water storage may be augmented by the secretion of polysaccharides into extracellular spaces, increasing the water-retentive capacity of the apoplast and forming a gelatinous substance known as mucilage. The importance of mucilage as a water store varies widely between succulent species.



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Figure 1. Phylogenetic distribution of some major succulent plant groups across the angiosperms.

Phylogeny based on data from Smith *et al.* (2011).

A low surface area to volume ratio (SA:V) is characteristic of most succulent plant organs, providing maximal volume for water storage and minimal surface area for transpirational water loss. In some leaf-succulents, the optimal solution for water conservation in terms of SA:V has evolved — entirely spherical leaves. In keeping with their conservative water-use strategies, succulents tend to display thick cuticles, low stomatal density, high stomatal sensitivity to environmental stimuli, and low hydraulic conductances (sometimes associated with anatomically-reduced vasculature). Recent developments in plant hydraulic research are opening up many new opportunities for characterising the pathways of water transport in plant tissues, which could be of special relevance to processes of water remobilisation and recharge in succulents (see below).

The high cell volumes found in succulent plants are also important for the operation of crassulacean acid metabolism (CAM), the photosynthetic pathway which is an integral component of the ecophysiology of the vast majority of succulents.

This is because CAM requires large vacuoles for the storage of organic acids produced during nocturnal primary CO_2 fixation. Since stomatal opening occurs principally at night in canonical CAM, gas exchange occurs under higher ambient humidity, meaning that CAM confers enhanced water-use efficiency relative to C_3 photosynthesis. Moreover, CAM is also a highly plastic photosynthetic syndrome, which in many species can be expressed at varying intensities or as a facultative response to drought or other environmental stressors.

Drought avoidance in succulents

Contrary to a common misconception, succulents are not abundant in the most arid desert environments. Instead, they tend to occur in semi-arid zones where there is regular and predictable, though not necessarily frequent, rainfall. The seasonal water deficit of these environments may be strong, but rains do return after a relatively fixed period of time. Moisture input from fog or dew may supplement direct precipitation in some cases, and occasionally accounts for a large proportion of the plant's total water

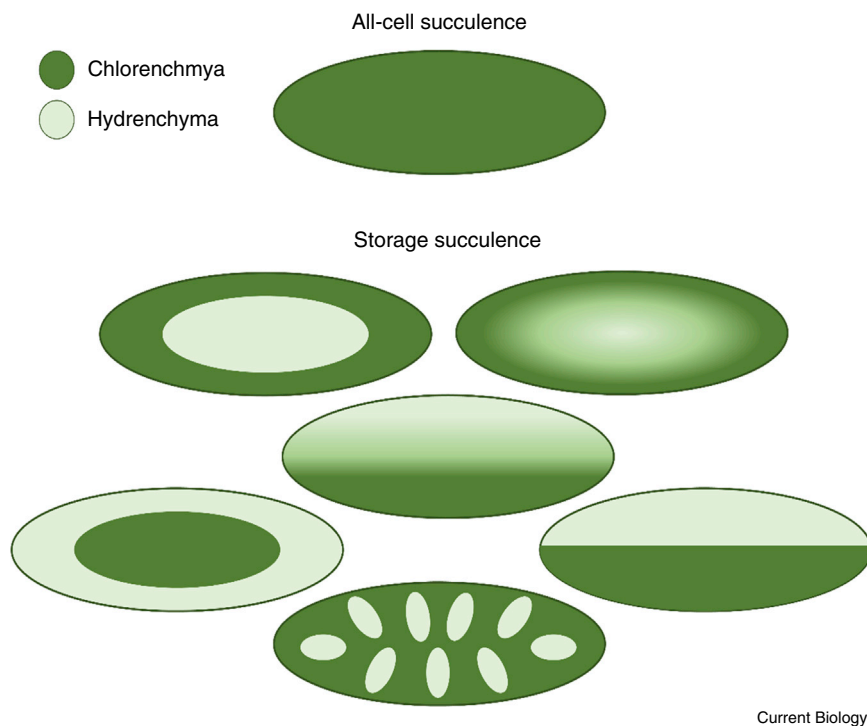


Figure 2. The anatomical diversity of succulence.

Examples of possible distributions of chlorenchyma and hydrenchyma in all-cell and storage-leaf succulents, including abrupt and gradual transitions between tissue types.

uptake. The ‘atmospheric’ bromeliads of some South American coastal deserts use absorptive leaf hairs to move condensate directly into the leaf. However, water uptake is more usually mediated by wide, shallow root systems, sometimes with a central taproot.

The array of anatomical and biochemical adaptations they display allow succulents of all kinds to maintain high water potentials during drought. There is often dramatic contrast between the dry-season water potentials developed by sympatric C_3 shrubs and succulent plants — the water status of the woody perennial shrubs will usually track soil water/matric potentials, down to -3.0 or -5.0 MPa, while the water potentials for succulents very rarely fall below -1.2 MPa. Quantification of the water potential at turgor loss point in succulents shows that these plants are in fact highly sensitive to cellular drought, and often have a relatively limited capacity for cellular mechanisms of drought acclimation, such as osmotic adjustment.

Adaptation for hydraulic recharge in storage succulents

There is increasing interest in the evolutionary trade-offs associated with regulating water transport within plant systems, between roots, stems and aerial photosynthetic organs, and the partitioning of limitations between vascular and extra-vascular pathways. These characteristics are only now being explored for succulent plants, where the process of hydraulic recharge in storage succulents offers an exciting study system. The diffuse, shallow roots of storage succulents are extremely well adapted for rapid rehydration when water becomes available during short, intense rainfall events. These roots absorb a high proportion (up to 50%) of such rain events, while the taproot usually does not make contact with the water table, but provides firm anchorage. Roots tend to be very sensitive to soil water potential, and may mechanically contract or undergo biochemically mediated or cavitation-effected loss of hydraulic conductance during drought, which has the advantage of hydraulically

isolating the shoot from the drying soil.

Evolutionary gains of ‘three-dimensional’ venation in leaves, where the vasculature is no longer restricted to a single horizontal plane, have been associated with increased levels of succulence, which highlights the importance of hydraulic connectivity. It is possible that the three-dimensional proliferation of veins in tissues with inherently low vein and mesophyll hydraulic conductances has not been driven by the need for slow and steady metering of water for transpiration between rain events, which often occurs through low stomatal conductances and nocturnal gas exchange in CAM plants. However, if three-dimensional venation allows the rapid recharge of succulent water storage tissues *during* rain events, this would be consistent with the high proportional use of each rain event. In the extra-xylary compartment, there is a need for functional characterisation of aquaporins in succulent tissues, which may help establish the importance of these channels for dynamic changes in radial hydraulic conductances relevant to the process of redistribution and recharge.

Variation in the spatial configuration of the chlorenchyma and hydrenchyma in storage succulents could also be of considerable functional significance (Figure 2). In some cases, there is a central core of hydrenchyma surrounded by a chlorenchymatous rind, or the reverse can occur, with water being stored in a specialised epidermis or hypodermis. Alternatively, the hydrenchyma can be limited to sheet-like structures above, below, or sandwiching the chlorenchyma. In some cases, the transition from chlorenchyma to hydrenchyma is very abrupt, while in other cases it is more gradual. Our understanding of the physiological consequences of this anatomical variation is still in its infancy, but it is likely to involve divergences in tissue hydraulic conductances and the kinetics of recharge and water remobilisation during drought. It may additionally be of special significance for leaf–light relations, given the differing optical

properties of the chlorenchyma and hydrenchyma.

Interactions with other environmental factors

Apart from their role in water storage, succulent organs interact with the environment in a number of other ways. Firstly, their size, density and water content confer high thermal capacity. Since evaporative cooling through transpiration is usually precluded by succulent morphology and physiology, succulents must be particularly tolerant of high tissue temperatures. Having a high thermal capacity can also be beneficial — slow radiative heat loss during the night can decouple plant temperature from air temperature, and protect core tissues and nocturnal metabolism from low temperatures (Figure 3). However, most succulents are susceptible to freezing damage at very low temperatures, and this is an important factor in defining range edges for some temperate zone and subalpine species.

Secondly, the light relations of succulent tissues differ substantially from those of equivalent non-succulent tissues. Proportionally less light arrives at the centre of a more succulent leaf, although this is to some extent compensated for by the high light levels characteristic of many environments inhabited by succulents. Meanwhile, exposure of superficial tissues to excess light can be damaging, and many succulents from high light intensity desert and semi-desert environments have evolved adaptations to reduce epidermal light transmission, including glaucous epicuticular waxes, powders, spines and leaf hairs. Furthermore, the orientation of *Opuntia* cladodes can be seen to minimise light interceptions at low latitudes, and optimise light absorption on a single planar surface at higher latitudes.

Thirdly, the tight cell packing in photosynthetic succulent organs reduces the mesophyll conductance to CO_2 (g_m), with air spaces often only comprising 5–10% of tissue volume as compared with 30–40% in typical mesophytic leaves. This can strongly restrict the maximal rate of photosynthesis, and constrain

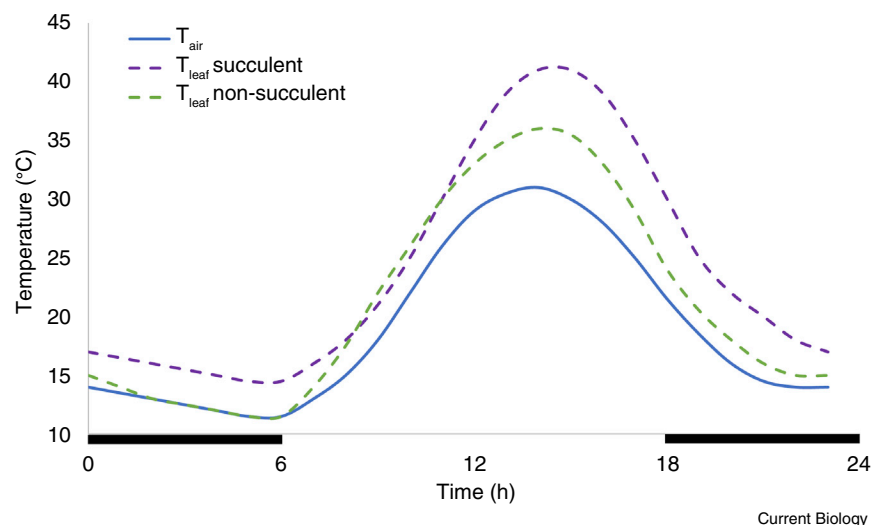


Figure 3. Effect of succulence on diurnal fluctuations in leaf temperature (T_{leaf}).

In massive leaf-storage succulents, high thermal capacity and limited evaporative cooling cause T_{leaf} to reach high levels relative to ambient air temperature (T_{air}) during the day, but T_{leaf} remains relatively high at night. In non-succulent species, T_{leaf} tracks T_{air} more closely, reaching a nocturnal equilibrium.

overall leaf thickness and hydraulic capacitance in all-cell succulents. In storage succulents, where there is a division of labour between photosynthetic and water storage capacity, chlorenchyma cells are not necessarily as densely packed as in all-cell succulents. Thus, g_m may remain relatively high in storage succulents. Furthermore, density-related constraints on g_m can be offset somewhat by the presence of stomata on both sides of the leaf. In species with CAM, denser tissues will have lower g_m during nocturnal CO_2 fixation but greater capacity for organic acid storage and reduced leakiness to CO_2 during the daytime portion of the CAM cycle.

Finally, succulence also has important implications for plant mechanical properties. Heavily succulent aerial organs are often mechanically supported either by woodiness in dicots or by high levels of fibre in monocots lacking secondary growth. This trade-off with investment in mechanical support could have important consequences for the level of succulence that can be achieved in challenging, resource-limited environments. In areas where strong winds are frequent, robust architecture is of special importance to prevent damage from shear. However, fragments of succulents

detached by wind or other means can often take root and grow, particularly in species with modular architecture.

Succulent growth forms and their environments

Succulent growth forms are highly diverse, ranging from small herbaceous rosettes and cushion plants to woody shrubs and trees. Some examples of different succulent growth forms are illustrated in Figure 4. Some of the major groupings, including columnar and opuntoid stem succulents and massive-leaf succulents, are distributed in similar climatic zones characterised by low water availability and high evaporative potential. Evolutionary analyses have shown that many lineages representative of these functional groups underwent contemporaneous diversification in response to palaeoclimatic and palaeoatmospheric change. However, other succulent growth forms show rather different ecological specialisation, in association with strongly contrasting structural and functional properties. We briefly outline some of the key succulent growth forms to emphasise how the environments in which they have evolved have shaped their structural and functional characteristics.

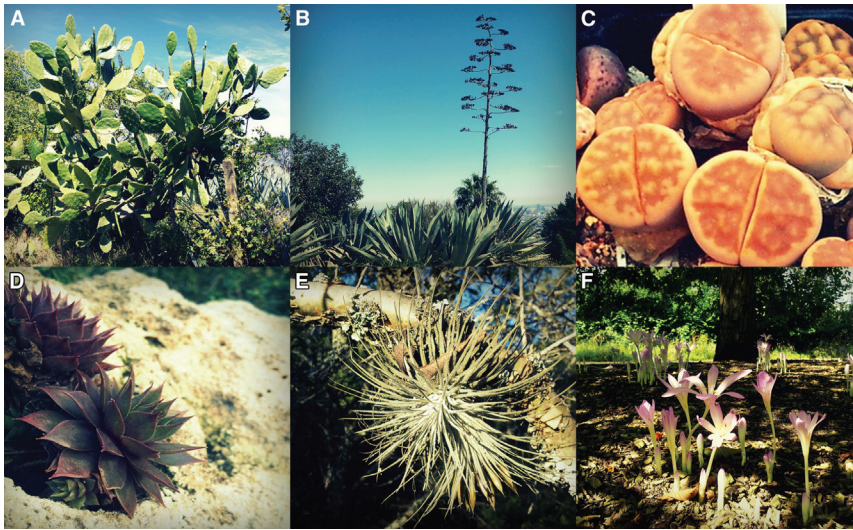


Figure 4. Examples of some of the major succulent growth forms.

(A) *Opuntia ficus-indica* (Cactaceae), an opuntoid stem succulent; (B) *Agave americana* (Asparagaceae), a massive-leaf succulent; (C) *Lithops aucampiae* (Aizoaceae), a miniature desert succulent; (D) *Sempervivum tectorum* (Crassulaceae), an arctic-alpine succulent; (E) *Tillandsia magnusiana* (Bromeliaceae), a succulent epiphyte; and (F) *Colchicum laetum* (Colchicaceae), a succulent geophyte. Images: Jamie Males.

Columnar and opuntoid stem succulents

Columnar stem succulents are the stereotypical semi-desert succulents of the popular imagination, best exemplified by the Old World euphorbias and New World cacti. Cylindrical stems comprise a photosynthetic rind and central core of hydrenchyma, which provides the high hydraulic capacitance these plants need to survive extended seasonal periods of intense drought. Stems are also often ribbed, allowing accordion-like swelling and shrinking depending on water content, and improving mechanical support. Another common feature of this group is the reduction of leaves to spines, providing a defence against thirsty herbivores and demonstrably reducing the heat and light load on the stem. In the cacti of the Opuntieae tribe, stems are laterally compressed in disc-shaped segments known as cladodes.

Massive-leaf succulents

Epitomised by the aloes and agaves (the latter also displaying stem succulence), massive-leaf succulence involves a very high degree of succulence in a rosette of large leaves. Hydraulic capacitance is therefore high, but the semi-

desert environments in which these plants usually occur have shaped their morphology in other ways too. Adaptive differences in phyllotactic fraction and leaf inclination angle regulate the degree of self-shading to optimise light interception. Plant size and compactness are also important traits that have been subject to environmental filtering in this group, with high-altitude species that are tolerant of cooler conditions, such as *Agave montana*, tending to be of smaller and more compact stature. This reduced night-time heat loss and improves insulation of meristematic tissue.

Miniature desert and semi-desert succulents

In deserts such as the Namib in southern Africa, many herbaceous perennial succulents are miniaturised. These small plants are often dependent on fog and dew formation for their water balance. In the case of storage succulent *Lithops* spp. (Aizoaceae), which grow half-buried in the stony substrate, translucent ‘windows’ of hydrenchyma on the surface of the leaf allow light to penetrate to the chlorenchyma in the subterranean part of the plant. The growth habit of *Lithops* spp. allows them to

remain coupled to more stable soil temperature rather than air temperature, which may be of particular importance in preventing low temperature stress during cool desert nights.

Of similar size but ecologically distinct are the annual all-cell succulents of families such as the Aizoaceae. These plants show a bewildering range of leaf morphologies, which have been able to evolve due to the duplication of a master regulator gene involved in leaf development. The ecophysiological significance of leaf morphology variation among these plants is not clear, since many co-occur in the same environments. The different morphologies may therefore be associated with as yet undetected micro-environmental adaptation and environmental niche partitioning. Clonal propagation is common in succulents inhabiting stressful environments, but it is especially strongly expressed in this group, many of which are rapidly spreading invasives where they have been introduced outside of their native ranges.

Pachycauls

Among plants with the capacity for secondary growth, stem succulence is sometimes associated with a highly convergent morphological syndrome known as pachycauly. Pachycauls display a strongly swollen woody stem with often highly reduced branches. Well known examples include the Gondwanan baobab trees (*Adansonia* spp.), the Sahelian desert rose (*Adenium obesum*), and the Socotran cucumber tree (*Dendrosicyos socotranus*). Water storage in wood parenchyma is by no means exclusive to pachycauls, but attains its greatest expression among these plants. Green photosynthetic tissue is frequently present on the surface of the stem, particularly among those pachycauls exhibiting strong foliar reduction, and predominantly fixes respiratory, rather than atmospheric, CO₂. Pachycauls are usually also drought deciduous, dropping their leaves at the beginning of the dry season and using stored water to initiate a flush of new growth just prior to the start of the rainy season.

Arctic–alpine succulents

Some succulent plants have evolved tolerance of very cold conditions as well as very hot. Alpine succulents, including roseroots (*Rhodiola* spp.), stonecrops (*Sedum* spp.) and houseleeks (*Sempervivum* spp.), occur well above alpine snow lines and into the Arctic tundra zone. The high thermal capacity associated with succulence and the compact rosette habit typically displayed by arctic–alpine succulents can make a contribution to the avoidance of damage caused by very low air temperatures and freezing, but it is also important to note that some succulents are also freeze tolerant. Some of the biochemical mechanisms involved in freeze tolerance have probably evolved from drought-resistance mechanisms.

Epiphytes

Succulence is very common among epiphytes — plants that grow in the canopies of other plants. The combination of epiphytism and succulence occurs in groups such as the orchids (often in the form of strongly succulent pseudobulbs), bromeliads, gesneriads and some ferns, making a particularly important contribution to the floristic and functional diversity of forests throughout the tropics. Nearly one-third of the total leaf biomass of some wet tropical forests is contributed by succulent epiphytes. Some morphologically reduced epiphytes (e.g., Spanish moss, a bromeliad) are strongly succulent at the anatomical level, despite their non-succulent appearance. Among some groups of epiphytes, there are correlations between succulence and the degree of exposure in species-specific microhabitats. Phenotypic plasticity is also observed in the degree of succulence expressed among conspecific individuals growing in canopy sites of differing levels of exposure.

Geophytes

Since the most important role of subterranean storage organs (e.g., bulbs, corms, tubers) in geophytes appears to be water storage, these plants are sometimes considered borderline succulents. Geophytism

is especially common in regions with a Mediterranean climate, and has evolved in a wide range of plant families, including the amaryllidaceae (e.g., onions, daffodils, snowdrops), iridaceae (irises), and zingiberaceae (gingers) in the monocots, and the asteraceae (dahlias), primulaceae (cyclamen), and solanaceae (potatoes) in the dicots. The storage organs of geophytes have evolved from several different plant parts. For example, bulbs are modified leaves and corms are formed from stem tissue, while tubers may be derived from either stem or root tissue. The environmental factors that have selected for the geophytic habit are equally diverse, and include seasonal drought, extreme temperatures, fire, and herbivory. What degree of physiological diversity exists between succulents growing in different environments and using different storage organs is currently an open question.

Halophytes

Water storage in water-limited environments is not always the primary function of succulence. Halophytes (plants which thrive under saline conditions) are often markedly succulent, often in combination with C_4 photosynthesis. This pairing of traits enables halophytes to achieve high water-use efficiencies while accumulating high levels of salt to help extract water from substrates with very negative water potentials. This may come at the cost of a rapid rate of leaf turnover, as endogenous salt levels quickly become toxic, although some species have either specialised epidermal bladder cells for compartmented salt storage or mechanisms for efficient foliar secretion of salt crystals. The unique environment in which halophytes have evolved has therefore selected for a special kind of succulence integrated in an ecophysiological syndrome that is rather different from that of other succulents groups.

The future of succulents: challenges and opportunities

At a fundamental level, there is still much to learn about the nuts and bolts of succulence. Ongoing

physiological research, making use of improved modelling methodologies and empirical tools including transcriptomics and gene-editing techniques, will provide greater clarity on key aspects of the functional biology of succulent plants. At the same time, efforts to generate more robust phylogenies for key succulent radiations will be crucial to elucidating how succulence has influenced evolutionary dynamics and ecological trajectories.

Filling in knowledge gaps about succulence will also be pivotal to advancing important projects in applied plant biology. There is currently intense interest in the potential of succulent plants and the succulent syndrome to provision bioenergy production on marginal land. In conjunction with CAM, succulence can confer high and climate-resilient productivity under semi-arid conditions. The possibility of engineering succulence into non-succulent agricultural and biomass crops to improve their environmental tolerances is also being explored. These efforts will have to take into account how complex structural–functional coordination mediates the efficiency of physiological processes in, and the environmental tolerances of, succulent plants.

In the development of production systems on marginal land, care must also be taken not to exacerbate pressures on populations of wild-growing succulents. Many groups of succulents, including cacti, are threatened by ongoing habitat destruction, unsustainable harvesting for the horticultural trade, and climate change. Efforts to raise international awareness of tropical conservation have hitherto tended to show disproportionate bias towards rain forests, to the exclusion of other vulnerable tropical biomes including dry forests, xeric shrublands, savannas, deserts and semi-deserts, where a great deal of succulent diversity is concentrated. Effective conservation measures are sorely needed to protect imperilled regions with diverse succulent flora. These initiatives could benefit from process-based models of species' bioclimatic relations. The elaboration of such models will be

contingent on a clear, quantitative understanding of the integration of organism–environment relations by structural–functional trait complexes, and may help safeguard the future of this fascinating and diverse group of plants.

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Primer

How to make a domesticate

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The Neolithic Revolution brought about the transition from hunting and gathering to sedentary societies, laying the foundation for the development of modern civilizations. The primary innovation that facilitated these changes was the domestication of plants and animals. In the case of plants, this involved the cultivation and selection of individuals with larger edible parts, easier harvesting, and decreased defenses, traits that allowed for the production of a food surplus and occupational specialization. Plant domestication is a process which started approximately 10,000 years ago and has thereafter been repeated independently in many locales around the world. Here, we offer a perspective that seeks to predict what factors influence the success of domestication, how many genes contributed to the process, where these genes originated and the implications for *de novo* domestication.

What is a domesticate?

Defining domestication is not straightforward, and it is likely that no one concept fits all species. Here, we define domestication as the process of adaptation to agro-ecological environments and human preferences by anthropogenic selection. The advantage of this definition is that it views the domestication status of a crop as a continuum rather than a binary trait, allowing for a spectrum of domestication from the simple tolerance or cultivation of wild plants (e.g., hops and many herbs) to semi-domesticated crops showing a number of agronomic adaptations (e.g., amaranth, flax and olive) and fully domesticated crops such as maize, barley and soybean. These and other crop species demonstrate that domestication is often gradual, ongoing and without easily defined start and end points. While much of the initial selection by humans was likely unintentional, fully domesticated

species have also adapted to intentional selection as well. Part of the reason why domestication may be difficult to define is that it generally does not act upon a single trait but instead leads to a suite of morphological and physiological modifications that may differ among taxa. These changes typically affect traits related to production and human preferences (e.g., taste, seed and fruit size), and together are referred to as the domestication syndrome (Figure 1). The domestication syndrome frequently overlaps between crops with similar purposes, but may differ dramatically between those with distinct purposes. In cereals, for example, the domestication syndrome includes larger seeds as well as reduced seed shattering and dormancy, but these traits were likely of lesser importance for plants domesticated for leaves or fiber. In addition to traits common to the domestication syndrome, many domesticates may also exhibit unique phenotypic changes as well as adaptations that have allowed them to spread outside of their initial geographic region of origin.

Which plants were domesticated?

Successful and widespread crops comprise only a tiny fraction of angiosperm species. From the over 250,000 described angiosperms only about 2,500 crops have been partially or fully domesticated, and of these only a dozen provide more than 90% of human staple food. In the following we discuss potential explanations for the selection of a species to be domesticated, including geography, life history, and genetics.

The domestication and adoption of crops was likely influenced by a number of regional and cultural factors. At least 15 centers of plant domestication have been robustly identified by archaeological and other work, each giving rise to a different assemblage of domesticates. Often, several complementary crops were domesticated alongside in a single center of domestication. For instance, energy rich cereals such as wheat and barley were domesticated together with the protein rich legumes lentil and chickpea in the Fertile Crescent, a pattern mirrored by rice and soybean in Southeast Asia or maize and common bean in the Americas. This suggests