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Forum

Potential expansion of plants with crassulacean acid metabolism in the Anthropocene

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Abstract

An overlooked phenomenon is a potential increase in the distribution and abundance of plants with the highly water-usage-efficient crassulacean acid metabolism (CAM). In the present article, we critically analyze recent research to investigate to what extent and why CAM plants may have recently expanded their range and abundance under global change. We discuss the ecophysiological and evolutionary mechanisms linked with CAM succulence and the drivers underlying potential CAM expansion, including drought, warming, and atmospheric carbon dioxide enrichment. We further map the biogeographic pattern of CAM expansion and show that some CAM plants (e.g., Cylindropuntia, Opuntia, and Agave) are expanding and encroaching within dryland landscapes worldwide. Our results collectively highlight the recent expansion of CAM plants, a trend that could be sustained under increasing aridity with climate change. We recommend that CAM expansion be evaluated in a data-model integrated framework to better understand and predict the ecological and socioeconomic consequences of CAM expansion during the Anthropocene.

Keywords: crassulacean acid metabolism (CAM), succulence, ecophysiology, evolution, biogeography

Increased biophysical and environmental constraints (e.g., resource scarcity and climate extremes) combined with altered disturbance regimes (e.g., fire and grazing) affect community structure and ecosystem processes under global environmental change (Anderegg et al. 2020). So far, studies have widely documented land degradation with significant shifts in vegetation cover or biomass (e.g., tree mortality; Anderegg et al. 2013) and plant community composition (e.g., shrub encroachment; D'Odorico et al. 2012). On the other hand, studies have also documented vegetation greening trends largely associated with resource (e.g., carbon dioxide) enrichment or land-use change (Piao et al. 2020). However, these studies have mostly focused on C_3- and C_4-dominated plant communities. Unlike C_3 and C_4 plants, crassulacean acid metabolism (CAM) confers much higher water-use efficiency because of nocturnal stomata opening. CAM photosynthesis is found in nearly 7% of vascular plant species across drylands and tropical epiphyte habitats (Gilman et al. 2023). Recent years have seen a growing interest in this photosynthetic pathway, especially in terms of the driving factors responsible for CAM plant ecophysiology, biogeography, and evolutionary history (Yu et al. 2017, Edwards 2019, Heyduk et al. 2019, 2019), which together infer the potential for CAM plant expansion under global change (e.g., drought, warming and carbon dioxide enrichment) in the Anthropocene (figure 1; Drennan and Nobel 2000, Borland et al. 2009, Reyes-García and Andrade 2009). This physiological advantage may be further increased by biotic factors, such as increased competitive advantage (Yu and D'Odorico 2015, Yu et al. 2019), as well as human introduction of alien CAM species (Davis et al. 2011, Novoa et al. 2015, Holtum et al. 2016), both of which could directly and indirectly favor CAM expansion. However, a synthesis of how ecophysiological and evolutionary mechanisms, biogeography, and global change drivers increase the potential for CAM plant expansion is still missing.

The carbon-limitation hypothesis states that CAM evolution and adaptive radiation were likely favored by periods of low atmospheric carbon dioxide concentrations in Earth history (Arakaki et al. 2011, Edwards 2019, Sage et al. 2023). However, surprisingly, CAM plants currently appear to be favored by ongoing carbon dioxide enrichment combined with increased drought frequency and intensity, warming temperatures, and higher vapor pressure deficit (VPD; Drennan and Nobel 2000, Osmond et al. 2008, Yu et al. 2019, Hogewoning et al. 2021). Indeed, it is unclear why atmospheric carbon dioxide enrichment, in which the C_4 component of CAM photosynthesis using phosphoenolpyruvate

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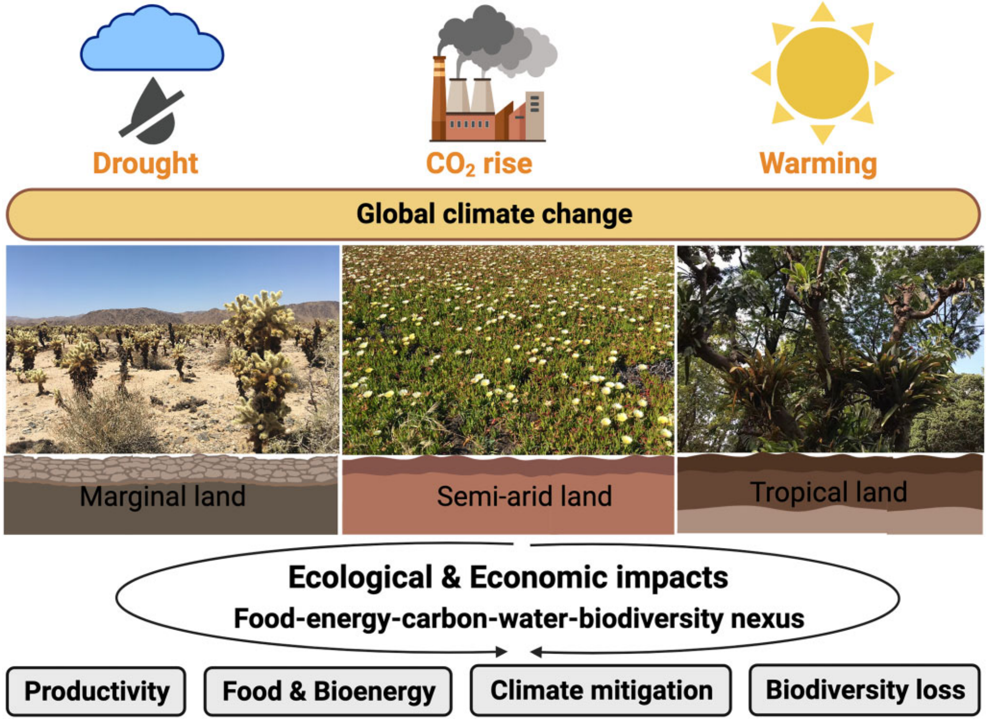

Figure 1. CAM plant expansion under drivers of global change and its ecological and socioeconomic consequences. Global change drivers such as drought, carbon dioxide enrichment and warming promote expansion of CAM plants. The representative (expanding) CAM species are Cylindropuntia spp., Carpobrotus spp. (e.g., Carpobrotus edulis), Billbergia spp. in marginal, semiarid, and tropical lands, respectively. Expansion of CAM is expected to have both positive and negative ecological and socioeconomic impacts which could be assessed by the lens of food–energy–carbon–water–biodiversity nexus. It can promote food and bioenergy production, carbon sequestration (climate mitigation), and soil stability across marginal, semiarid, and tropical lands. Alternatively, it could also negatively influence native plant communities with potential biodiversity loss.

carboxylase (PEPC) is thought to be saturated, has been found to increase the rates of CAM photosynthesis and productivity comparable in magnitude with that of C_3 plants (Drennan and Nobel 2000, Osmond et al. 2008, Yu et al. 2019, Hogewoning et al. 2021).

The expansion of CAM plants is expected to have both positive and negative ecological and socioeconomic impacts that could be assessed by the lens of food–energy–carbon–water–biodiversity nexus (see figure 1). Theoretical (Owen et al. 2016, Shameer et al. 2018, Hartzell et al. 2021) and empirical studies (Lewis et al. 2015), as well as reviews (Borland et al. 2009, Davis et al. 2011, Yang et al. 2015) discuss the potential of using CAM plants such as *Agave* and *Opuntia* as a climate change mitigation strategy by promoting food and bioenergy production, carbon sequestration, and soil stability in marginal or degraded lands, especially within their native ranges. In some cases, CAM plant production on marginal and degraded lands would not compete for land with important C_3 or C_4 crops, avoiding a carbon debt in the sense that bioenergy production from CAM plants would not come at the expense of increased emissions from land-use change or loss of ecosystem productivity (Gelfand et al. 2013). Specifically, it has been estimated that substantial (e.g., 6.1 billion liters) ethanol could be provided by *Agave* reestablishment as a bioenergy feedstock without significant land-use change (Davis et al. 2011, Owen et al. 2016). Optimistically, the high water-use efficiency of CAM plants could help overcome constraints on water availability (Gilman et al. 2023) and could offer the potential to expand or intensify (bioenergy) CAM crop cultivation in drylands (Lewis et al. 2015, Hartzell et al. 2021), increasing food supply, bioenergy and carbon sequestration. These benefits would be augmented by considering additional ecosystem services such as wildlife habitat and cultural services (Grodsky and Hernandez 2020) and colocation with solar infrastructure in drylands (Ravi et al. 2016). As such, technological advances and policy changes together with high solar radiation supply could lead to increased large scale solar infrastructure installations and CAM crop cultivation in drylands, safeguarding both food and energy supplies. Furthermore, through genetic engineering, the efficient water usage and competitive advantage of CAM plants in water stressed environments could be leveraged to increase water-use efficiency and drought tolerance of C_3 or C_4 crops and trees (Borland et al. 2014, Yang et al. 2015, Abraham et al. 2016). This has the potential to facilitate climate-resilient agroforestry (Borland et al. 2015) with impacts on global carbon and water cycling and their feedback to climate. A climate feedback could also be expected because of changes in the distribution of CAM epiphytes and their expansion in tropical regions (Einzmann et al. 2021), which could influence energy and biogeochemical cycling and, potentially, climate because of nocturnal carbon dioxide uptake (Miller et al. 2021).

CAM expansion may also affect species interactions and cause shifts in plant community composition (Yu and D'Odorico 2015, Rondeau et al. 2018, Huang et al. 2020) with potential negative consequences on native plant communities. Acting as keystone species, some CAM species such as *Carnegiea gigantea* provide food, shelter, and habitat to a variety of birds, mammals, and insects (Drezner 2014). Alternatively, caution would be needed in terms of the impacts of CAM expansion on native species composition and biodiversity while introducing, cultivating, or naturally expanding CAM plants (crops) in locations with competing native grasses (figure 1). In such scenarios, the encroachment of potentially invasive CAM plants (e.g., *Opuntia* spp. in eastern Africa or Western United States) displaces native grasses and can limit the use of arid and semiarid grasslands for livestock (Witt et al.

2018). Programs and techniques aimed at controlling *Opuntia* spp. encroachment are often labor and resource intensive (Hernandez et al. 2003). Similarly, several alien CAM plant species (e.g., lineages of Cactaceae, *Agave*, and Aizoaceae) have rapidly spread over broad areas across Africa, Australia, and the United States (Adams et al. 1998, Osmond et al. 2008, Novoa et al. 2015), causing a wide variety of negative ecological and socioeconomic impacts (Novoa et al. 2016).

Despite its importance, research on the expansion of CAM plants and their potential impacts is limited, especially regarding efforts to integrate long term and large-scale field and remote sensing observations with models. Addressing these knowledge gaps requires leveraging a variety of methods, including advances in field and remote sensing observations and integrating them with process-based modeling and a systematic framework to bridge these approaches. Doing so could provide insights or tools to evaluate to what extent and at what locations CAM plant expansion could be useful as natural climate solutions and mitigation strategies.

In the present article, we review recent advances in the study of the ecophysiology, evolution, and biogeography of CAM plants to infer the increased distribution and abundance of CAM species, mainly facilitated by human introduction and global change. We focus on the constitutive (strong) CAM plants, such as species that perform CAM photosynthesis independently of environmental stresses (Gilman et al. 2023) while placing less emphasis on facultative (weak) CAM species such as *Mesembryanthemum crystallinum*, which have the capacity to switch from C_3 to CAM photosynthesis to adapt to environmental or competitive stress (e.g., increased salinity or drought; Yu et al. 2017). We further evaluate the empirical evidence of potential expansion of constitutive CAM species, their underlying dynamics, and related ecological impacts. We critically appraise recent results in the study of ecophysiological mechanisms and global change drivers underlying the potential expansion of CAM plants. We also identify novel insights into CAM plant expansion by evaluating their evolutionary history and environmental drivers. Our synthesis of CAM plant research calls for a data-model-integrated framework suitable for the evaluation of the trends, patterns, and impacts of CAM plant expansion under global change and highlights open questions for future research on CAM-dominated vegetation.

Ecophysiological mechanisms and drivers of CAM expansion

Most CAM plants are succulents or plants that can store water in their tissues (Griffiths and Males 2017). Therefore, they are well adapted to long and intense drought through two important traits: the ability to store water and use it during dry spells and their high water-use efficiency resulting from the nocturnal carbon dioxide uptake characteristic of the CAM photosynthetic pathway. Because of these traits, CAM plants have an advantage in situations of extreme drought compared with C_3 or C_4 plants, as was demonstrated by their widespread distribution in deserts, marginal, and degraded lands (Borland et al. 2009, Arakaki et al. 2011), as well as a number of drought experiments (Yu et al. 2019, Huang et al. 2020). Succulence in CAM plants is supplemented by root plasticity to quickly take up water in response to precipitation events or restrict water loss under conditions of water deficit through rectifier-like roots (figure 2a; North and Nobel 2006). The potential advantage of CAM plants over other functional groups, particularly C_3 plants, is also expected to be enhanced by warmer climates as CAM plants typically exhibit a higher optimal temperature for photosynthesis, lower photorespiration rates, and avoidance of high daytime atmospheric water stress (Drennan and Nobel 2000, Reyes-García and Andrade 2009).

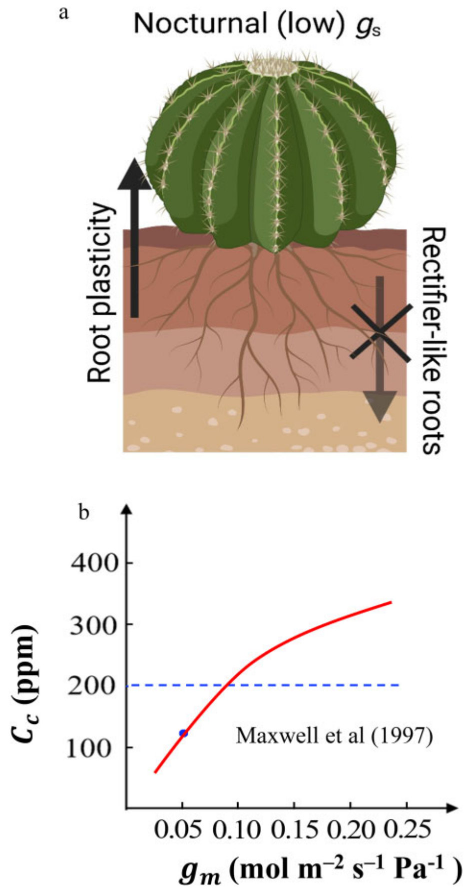

Figure 2. Ecophysiology of CAM plants conferring competitive advantage in a carbon dioxide–enriched, drier and warmer climate. (a) CAM succulence is supplemented by root plasticity to quickly take up water in response to precipitation events and the rectifier-like roots to restrict water loss under conditions of water deficit, as well as nocturnal (low) stomatal conductance and high water usage efficiency. Succulence provides drought and heat tolerance, conferring the competitive advantage of CAM in a drier and warmer climate with high VPD. (b) Unsaturated CAM photosynthesis in phase 1 via PEPC to carbon dioxide enrichment, which is hypothesized to be linked with CAM succulence and mesophyll conductance (Maxwell et al. 1997, Yu et al. 2019, Hogewoning et al. 2021). The increased carbon dioxide uptake in phase 1 is expected to favor phase 3—decarboxylation of malic acid for the Calvin cycle via Rubisco during the day. Conceptually, there is an increased relationship between availability of carbon dioxide at the carboxylation site ($\mathbf{C_c}$) and mesophyll conductance associated with CAM succulence. As was demonstrated in previous studies (e.g., Maxwell et al. 1997), high CAM succulence can reduce mesophyll conductance ($\boldsymbol{g_m}$, 0.05 mols of carbon dioxide per square meter per second per Pascal) and $\mathbf{C_c}$ (109 ppm) to a level lower than the saturation point (approximately 200 ppm) of nocturnal carbon dioxide uptake by PEPC, leading to the unsaturated response of CAM photosynthesis and productivity to carbon dioxide enrichment.

CAM photosynthesis is often associated with four temporal phases. Increasing succulence is expected to favor phase 1 of carbon capture via PEPC (C_4 photosynthesis) due to the increased vacuole and cell size available for malic acid synthesis and storage during night followed by phase 3 decarboxylation of malic acid for the Calvin cycle (C_3 photosynthesis) via Rubisco during the day (Nelson and Sage 2008, Winter 2019). The photosynthetic plasticity achieved by shifting the temporal phases of C_4 (phase 1) versus C_3 (phase 3) photosynthesis versus transitional stages (phase 2 and 4) to adapt to drought stress and optimize resource usage (e.g., in response to varying rainfall pulses) has been found to increase total daily photosynthesis and productivity of CAM plants (Borland et al. 2011). Moreover, CAM cell succulence is typically associated with reduced intercellular air space (IAS) and reduced mesophyll surface exposed to IAS (Maxwell et al. 1997, Ripley et al. 2013). This creates physical barriers for carbon dioxide diffusion (Flexas et al. 2008) and lowers the availability of carbon dioxide (e.g., as low as 110 parts per million [ppm]) at the carboxylation site (Maxwell et al. 1997, Hogewoning et al. 2021), where carbon dioxide concentration is below the saturation point (approximately 200 ppm) of nocturnal carbon dioxide uptake during phase 1 of CAM photosynthesis. Therefore, cell succulence and the relatively low mesophyll conductance (g_m) could be the likely ecophysiological traits underlying the positive response of CAM photosynthesis and productivity to a carbon dioxide enriched environment (figure 2b). Indeed, carbon dioxide fertilization has been identified as another important environmental driver favoring CAM plant expansion (Drennan and Nobel 2000, Reyes-García and Andrade 2009, Yu et al. 2019). The effects of low mesophyll conductance (g_m) on plant response to carbon dioxide enrichment has been also found in non-CAM leaves. For instance, evergreen trees with thicker leaf and low g_m show a higher response of photosynthesis and intrinsic water usage efficiency in a carbon dioxide enriched atmosphere (Niinemets et al. 2011). Dynamic vegetation models can underestimate the effects of carbon dioxide fertilization on ecosystem productivity if they fail to account for mesophyll conductance limitations on plant photosynthesis (Sun et al. 2014). It is worth clarifying, however, that the comprehensive four phase response by CAM plants to carbon dioxide enrichment varies depending on succulence and duration of each phase (Drennan and Nobel 2000, Osmond et al. 2008). Indeed, weak or facultative CAM species with lower cell succulence and longer phase 4 would be expected to benefit from carbon dioxide fertilization mainly through increased daytime carbon dioxide uptake by the (C_3) Calvin cycle via Rubisco. As such, theoretical and empirical estimates of increased CAM production under carbon dioxide enrichment would need to compare and integrate the four phases of CAM photosynthesis across a variety of weak and strong CAM species.

Evolution of CAM plants and insights for CAM expansion

The carbon-limitation hypothesis suggests that low atmospheric carbon dioxide concentrations in Earth history could have been the selection force for promoting CAM evolution and radiation (Arakaki et al. 2011, Edwards 2019). A recent study which used phylogenetic chronologies of 72 CAM clades demonstrated earlier CAM origins (approximately 30 million years ago) at low atmospheric carbon dioxide concentrations (Sage et al. 2023). However, it remains unclear how CAM evolutionary history across lineages and the evolutionary origins of CAM versus succulence can shed insight on the radiation and expansion of CAM plants at evolutionary and ecological timescales. In the present article, we synthesize a data set (supplementary table S1) of 3691 species from 395 genera on the basis of a literature survey across C_3 succulents, weak (C_3-CAM) and strong CAM succulents to examine CAM evolution and its evolutionary radiation. The results showed that the evolutionary origin or history of the earliest C_3 succulents dates back to approximately 130 million years ago, whereas the early CAM plants such as Bromeliaceae and Orchidaceae originated around 30 million years ago, corresponding to a time period of carbon dioxide drawdown (the dramatic carbon dioxide decrease during early Oligocene). Since then, most of the CAM or C_3-CAM evolutionary radiation events also corresponded to temperature or carbon dioxide drawdown periods—for example, approximately 18 million years ago for weak CAM lineages in Montiaceae and Orchidaceae, as well as approximately 10 million years ago for the radiation of strong CAM lineages in Cactaceae, Aizoaceae, Asparagaceae, Orchidaceae, and some Bromeliaceae (figure 3), further supporting the carbon limitation hypothesis. Collectively, our results suggest that the evolutionary origin of succulence dated much earlier than the emergence of CAM photosynthesis, highlighting the likely divergence of their evolutionary selection forces—drought (succulence) versus carbon dioxide (CAM), although some caution is needed before drawing generalized conclusions because of the lack of data on historical drought. Indeed, a more comprehensive data set than that currently compiled in figure 3 is needed to further advance the understanding of these evolutionary selection forces.

Because a low atmospheric carbon dioxide concentration seems to be the driving force of CAM evolution or radiation, an interesting question arises as to why the opposite trends—carbon dioxide enrichment in the Anthropocene—have led to increased CAM photosynthesis and productivity at rates comparable in magnitude with C_3 plants (Drennan and Nobel 2000, Osmond et al. 2008, Yu et al. 2019, Hogewoning et al. 2021)? The adaptive trait evolution by CAM succulence may shed insights on this question. CAM succulence, a relatively accessible evolutionary trait (Griffiths and Males 2017, Edwards 2019, Winter and Smith 2022), could have evolved under evolutionary selection by drought. This could have led to low mesophyll conductance and nonsaturated nocturnal carbon dioxide uptake by PEPC (figure 2b) favoring high CAM growth without a trade-off with mortality in a carbon dioxide enriched atmosphere (Males and Griffiths 2018). As such, carbon dioxide enrichment in the Anthropocene could favor the competitive advantage of CAM plants and could, therefore, increase their distribution and abundance, a trend that could increase in a future drier and warmer climate. These insights suggest the potential divergence of environmental drivers in the origin or radiation of CAM species at evolutionary time scales, and in expansion of CAM abundance at ecological time scales. Although the evolutionary history of some CAM species (e.g., *Euphorbia* spp. and others) is currently clear (Horn et al. 2014), a comprehensive physiological and phylogenetic sampling across C_3, weak CAM, and strong CAM species (Edwards 2019, Heyduk et al. 2019) with intercomparison along the gradients of environmental evolutionary drivers (e.g., increasing carbon dioxide, drought, and VPD) or by manipulative experiments with carbon dioxide starvation or enrichment and drought (Suissa and Green 2021) could shed more light on CAM evolutionary history and its relations with succulence and climate change across a broad plant phylogeny. Alternatively, a modeling approach that is based on optimal trait adaptation and evolution and that has been used for C_4 plants (Zhou et al. 2018) may be adopted to reconstruct the past history of CAM plants and project future CAM adaptation and evolution trends.

Evidence of CAM competitive advantage and biogeography of CAM expansion

Evidence supporting a competitive advantage for CAM plants in a drier, warmer, and carbon dioxide–enriched atmosphere has been previously reported (Drennan and Nobel 2000,

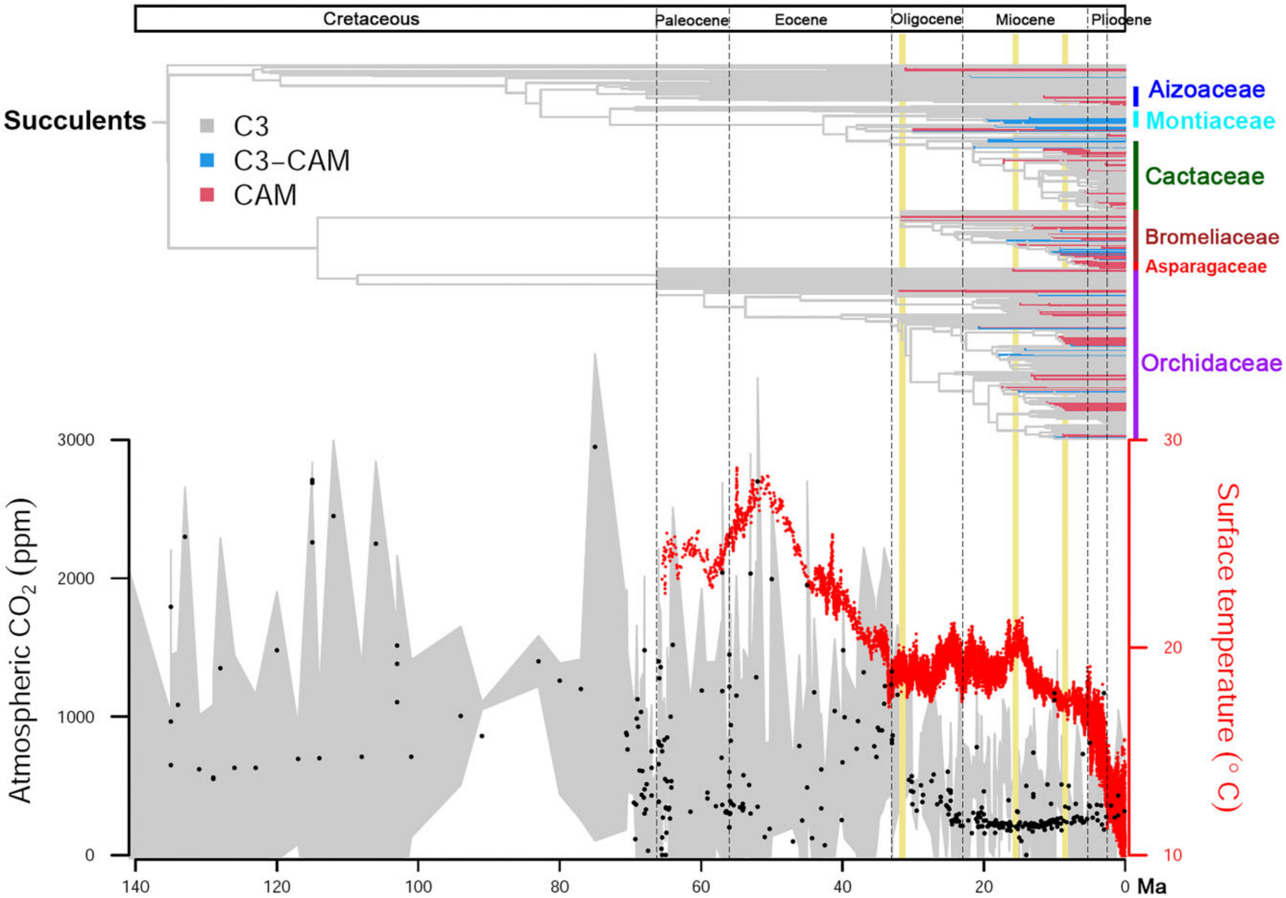

Figure 3. Data synthesis across C_3 succulents, weak (C_3-CAM) and strong CAM succulents to show carbon dioxide drawdown as the driver of CAM evolution and its evolutionary radiation. All succulent plants from 395 genera (the entire phylogenetic tree branches and tips), weak (the blue branches and tips), or strong (the red branches and tips) CAM species are shown in the phylogenetic tree, with geological epoch names, the Cretaceous, and five main CAM families (Aizoaceae, Montiaceae, Cactaceae, Bromeliaceae, Orchidaceae) labeled on the side of the phylogenetic tree. The corresponding available historical surface temperature from (Hansen et al. 2013) and reconstructed atmospheric carbon dioxide levels from Royer (2006) and their uncertainty (the grey area) through time are also plotted. Strong CAM succulents are associated with longer phase 1, whereas weak CAM succulents have longer phase 4. The phylogenetic tree was built at a genus level to reduce the uncertainty of unbalanced species numbers within each genus because of the lack of information of photosynthetic types of many species. It was built using the R package V.PhyloMaker2 on the basis of mega-tree GBOTB.extended.tre in this package including 74,531 species of 479 families, the largest dated plant phylogeny derived from two mega-trees, based on molecular data from NCBI GenBank, phylogenetic data from the Open Tree of Life, and fossil records (Zanne et al. 2014, Smith and Brown 2018).

Osmond et al. 2008, Borland et al. 2009). Recent research used indoor manipulative experiments to show the direct or indirect effects of these global change drivers on competition between CAM plants (*Cylindropuntia imbricata* and *Opuntia phaeacantha*) and grasses (*Bouteloua eriopoda* and *Bouteloua curtipendula*; Yu et al. 2019, Huang et al. 2020), as well as tropical CAM epiphytes (*Phalaenopsis*; Hogewoning et al. 2021). These studies provide evidence of relatively high CAM productivity comparable with that of C_3 plants, which was also recently demonstrated theoretically (Shameer et al. 2018). On the other hand, although most CAM species could propagate and expand vegetatively across landscapes, the competitive advantage and expansion of CAM plants could have been restricted by their shallow roots, pollination, and dispersal limitations, as well as disturbances such as fires (Reyes-García and Andrade 2009, Hultine et al. 2023). For instance, the treelike cactus species such as *Carnegiea* spp. could suffer from extreme droughts and recruitment or growth limitations because their shallow roots cannot support large aboveground biomass under extended drought, and they lack vegetative propagation (Pierson and Turner 1998).

Although studies of CAM plant expansion in a changing climate remain limited to a few taxa relative to non-CAM plants, some field observations and model predictions exist for natural biogeographic expansion for some CAM genera or species. For instance, field observations in native and protected desert grasslands in the western United States indicate that CAM plants such as *Cylindropuntia imbricata* have been increasing in abundance in desert grasslands (Rondeau et al. 2018). Moreover, long-term vegetation surveys over 21 years have documented the increase in abundance and diversity of CAM epiphytes growing on tree stands in Barro Colorado Island, Panama (Einzmann et al. 2021). However, most observations of CAM expansions are those involving the invasion of alien CAM plants. For example, *Mesembryanthemum crystallinum* (Aizoaceae; ice plant) is native to southern and eastern Africa, and it was introduced to and then spread throughout western Australia, the Mediterranean basin, and along coasts of the western United States, Mexico, and the Caribbean (Adams et al. 1998). *Opuntia* spp. (Cactaceae; crop) a genus native to the Americas, has been introduced to and is currently expanding through regions of Australia, Europe, and South Africa (Novoa et al. 2015). *Opuntia* species are also increasing in abundance in their own native habitat, such as the southwestern United States (Hernandez et al. 2003). A model simulation suggested that the expansion of CAM plants could have been favored by the direct and indirect

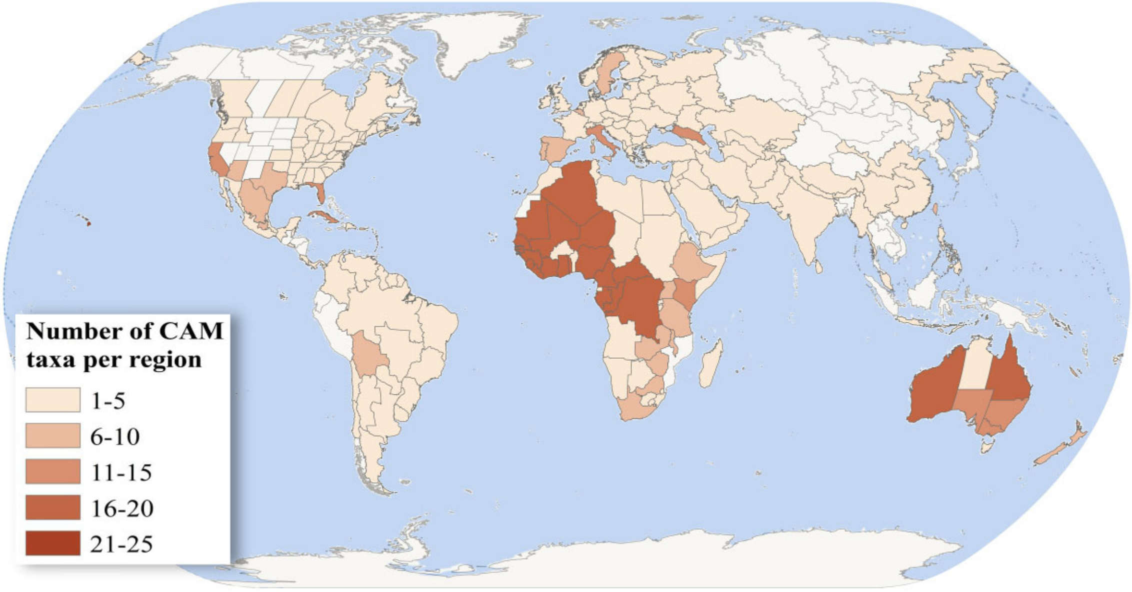

Figure 4. Biogeographic evidence of naturalization by number of alien CAM taxa per region. The data were derived from the Global Inventory of Floras and Traits (GIFT) and the Global Naturalized Alien Flora databases. The map shows the number of naturalized CAM taxa (e.g., CAM species that sustain populations over many life cycles without direct human intervention) per region of the world (e.g., islands, archipelagos, political or biogeographical units, or protected areas). Moreover, seed mass and clonal growth of the 392 CAM plant taxa recorded in GIFT were used to examine whether CAM naturalization is promoted by clonal growth or large seed size using a Wilcoxon rank sum test with continuity correction using R version 4.1.3.

facilitation from nurse plants (Yu and D'Odorico 2015). Indeed, this indirect facilitation effect under carbon dioxide enrichment could have been strengthened by the increased dominance of dryland woody (C_3) plants (shrub encroachment; Wang et al. 2022). Shrub encroachment could facilitate CAM recruitment and growth as nurse plants and decrease disturbance such as fires that cause high CAM mortality (Yu and D'Odorico 2015).

To explore the expansion of invasive CAM plants, we used the Global Inventory of Floras and Traits (GIFT) database, a global archive of regional plant checklists and floras and plant functional traits which contains information on the floristic status and functional trait information of 281,836 species across 3485 geographic regions worldwide (Weigelt et al. 2020). We used the GIFT R package to obtain a list of 392 CAM taxa. Then, we used the Global Naturalized Alien Flora database (van Kleunen et al. 2019), which contains information on the identity and occurrence of 13,930 naturalized plant taxa in 1029 regions (e.g., countries, provinces, islands) around the globe, to identify which of these CAM taxa have been reported as naturalized outside their native ranges. Overall, 112 CAM taxa from 30 genera and nine families (i.e., Aizoaceae, Asparagaceae, Bromeliaceae, Cactaceae, Crassulaceae, Didiereaceae, Euphorbiaceae, Hydrocharitaceae, and Xanthorrhoeaceae) were reported as naturalized. That is, their populations were sustained over many life cycles without direct human intervention (Richardson et al. 2000) in 627 regions (e.g., islands, archipelagos, political or biogeographical units, or protected areas). We then mapped the regions where these taxa were found to be naturalized. Some of these taxa have been recorded as naturalized in many regions. For example, *Opuntia ficus-indica*, *Kalanchoe pinnata*, *Agave americana*, *Agave silane*, and *Aloe vera* are recorded as naturalized in 193, 174, 161, 127, and 104 regions (e.g., islands, archipelagos, political or biogeographical units, or protected areas), respectively (figure 4). A further analysis using a Wilcoxon rank sum test with continuity (see the legend in figure 4) showed that naturalized CAM taxa are significantly ($p = .0015$) more likely to present clonal growth than CAM taxa that have not been recorded as naturalized outside their native range. However, it is currently unclear whether CAM naturalization is further promoted by climate change and the naturalization rate of CAM species is higher than in C_3 taxa. Collectively, these patterns suggest that CAM plants, or at least some lineages, have expanded and encroached across drylands likely as a result of climate change adaptation or human activities (Borland et al. 2009, Reyes-García and Andrade 2009).

Needs for future CAM research

The advances in future CAM research would need to focus on long term CAM field studies, digital CAM research and a hybrid model for CAM research as described in details below.

Long term CAM field studies

A better understanding of CAM plant ecophysiology, evolution, and biogeography would require extensive long-term ecological field surveys. These field based surveys would need to focus on continuously surveying CAM plant distribution and abundance with time and providing more evidence of CAM expansion, especially for native CAM species; scaling up from traits to populations, communities, or ecosystems; linking traits with demography and ecosystem function; and linking traits with evolutionary history.

Plant functional traits have been instrumental in linking plant ecophysiology and plant demography in non-CAM species (Adier et al. 2014). Some long-term field studies have investigated CAM demography and life history strategies (Drezner 2014, Ohm and Miller 2014), but the links with anatomic and morphological traits are poorly understood. Plant functional traits have been found to have globally consistent effects on competition and community assembly in non-CAM species (Kunstler et al. 2016). These engines of plant functions can be more easily measured than demographic patterns and therefore they can be effectively used to scale up ecological processes and functions from individuals to communities and ecosystems (Niechayev et al. 2019). In the case of CAM plants, the role of critical functional traits such as, succulence, mesophyll conductance, CAM expression (e.g., nocturnal carbon dioxide uptake and photosynthesis), and CAM productivity in determining CAM evolutionary and ecological responses to global change at evolutionary and ecological time scales remains poorly understood (Reyes-García and Andrade 2009, Yu et al. 2019). There is a crucial need for research linking or integrating plant traits, CAM ecophysiology and evolution, species interactions, and community assembly with ecosystem functions.

Digital CAM research

Remote sensing is a promising approach to study the biogeography of CAM plants, especially for lineages with large plant sizes (e.g., *Opuntia*, *Agave*, *Clusia*, and *Yucca*), although studies in this field are scarce. The dearth of remote-sensing-based research on CAM plant biogeography is presumably not due to technical obstacles in the ability of remote sensing to detect or observe CAM plants. Indeed, remote sensing has been used to study grass invasion (Weisberg et al. 2021), and there have been studies using hyperspectral imagery to map nonnative plants including CAM plants such as the facultative *Carpobrotus* spp. in California (Underwood et al. 2003) and thermography to monitor CAM plants (Barkla and Rhodes 2017). Rather, the main reason seems to be related to the limited value societies have historically given to CAM research and the limited appreciation for the ecological and societal role of CAM plants except for some charismatic species (e.g., large cacti and *Yucca* spp.; Grodsky and Hernandez 2020). Besides hyperspectral imagery, there are also new remote sensing technologies, such as the passive solar-induced chlorophyll fluorescence (SIF), that can be used to map CAM plant distribution and productivity (Porcar-Castell et al. 2014). This may be theoretically feasible because of the existing link between phase 3 light reaction and phase 1 nocturnal carbon dioxide uptake through metabolic products such as PEPC (Cushman et al. 2008, Borland et al. 2009, Shameer et al. 2018). Recent experimental evidence directly demonstrated the control of diel carbon gain by the light integral during phase 3 (Hogewoning et al. 2021), which could be sensed by SIF. Previous studies in this field concentrated on lab measurements of fluorescence (Kuźniak et al. 2016), whereas field-scale applications to CAM plant mapping are still in an early stage of conceptualization. Technically, SIF measures can be combined with flux measurements from eddy covariance towers to potentially partition the ecosystem productivity contributions by CAM versus non-CAM species. More field scale studies (e.g., using pulse amplitude-modulated methods) are needed to use SIF measurements from remote sensing and other recent advances in remote sensing technology on CAM plants (Stavros et al. 2017). It remains to be examined whether the active and passive microwave remote sensing (e.g., through vegetation optical depth), which has been largely leveraged to infer vegetation water content and biomass in C_3 or C_4 plant communities (Konings et al. 2021), could be used to investigate CAM biogeography.

A hybrid model for CAM research

Data from field and remote sensing observations could be fused into models to project the distribution, dynamics, and productivity of CAM plants in a future climate. Modeling the distribution and productivity of CAM plants has been attempted by using empirical indices to link CAM species to environmental factors defining their habitat (Nobel 1984), a dynamic system approach to describe metabolite concentration (Nungesser et al. 1984) circadian rhythm (Owen and Griffiths 2013, Bartlett et al. 2014), and the coupling of soil–plant–atmosphere continuum models with a unified representation of the C_3, C_4, and CAM photosynthetic pathways (e.g., the Photo3 model; Bartlett et al. 2014, Hartzell et al. 2021). Recently, a systematic modeling approach has been used to examine CAM metabolism and its associated energetics and productivity (Shameer et al. 2018). Recent reviews of CAM modeling have highlighted the importance of and challenge in scaling up from anatomic trait to canopy scales (Davis et al. 2015) and proposed a bottom-up, mechanistic modeling approach toward capturing the physiological controls for phylogenetically diverse CAM systems (Chomthong and Griffiths 2020). Challenges and large uncertainty, however, still exist in being capable of projecting CAM plant distribution, dynamics, and productivity in a future climate by accounting for the combined (synergistic or antagonistic) effects of carbon dioxide enrichment, rainfall (drought), and temperature (warming), which could act as drivers of widespread CAM plant expansion or increase in CAM productivity (Drennan and Nobel 2000, Osmond et al. 2008, Yu et al. 2019, Hogewoning et al. 2021).

A hybrid modeling framework could be used to combine mechanistic simulations of CAM plant dynamics and productivity with data-driven formulations or parameterizations from machine or deep learning in a future drier, warmer, and carbon dioxide enriched atmosphere. This hybrid modeling approach would be motivated by recent advances to integrate physical or ecological processes that are mechanistically interpretable with data-driven machine or deep learning, which is highly flexible in adapting to empirical data (Reichstein et al. 2019). This approach is used in various disciplines (Reichstein et al. 2019) but is new to research on CAM plants. Advances in CAM modeling would need to be focused on the soil–plant–atmosphere continuum to scale up across individuals, canopies or communities, and landscapes. It would need to link key CAM anatomical traits—succulence, mesophyll conductance—with CAM demography (growth and mortality) and interactions with society. The physical laws of conservation of mass and energy and the biological constraints (e.g., C_4 and C_3 photosynthesis, competition for resources) could be merged with a data-driven approach by machine or deep learning to improve parameter estimation and evaluate the model–data mismatch (Reichstein et al. 2019). Recent pioneering advances in 3D image-processing techniques to estimate IAS potentially allow for the mechanistic estimation of mesophyll conductance (g_m) and carbon dioxide at the carboxylation site by linking with CAM anatomy—succulence with simple equations (Earles et al. 2018). The physical approaches with focus on allometry proposed by previous studies (Davis et al. 2015) and recently advanced by machine learning (Gilman et al. 2024) allow for scaling up from anatomical traits and CAM ecophysiology to the canopy scale. At the community scale, competition could be mechanistically simulated (e.g., by a niche model; Godoy et al. 2018). In contrast, the biological regulations (e.g., root water and nutrient uptake and its plastic and rectifier-like root behaviors; see figure 2a; Reichstein et al. 2019), CAM mortality or respiration and the effects of human activities or other natural disturbances across landscapes would be challenging to mechanistically simulate and could, therefore, be learned from data.

While scaling up, the typical CAM trait—succulence—could be the potential nexus to bridge CAM ecophysiology, evolution, and biogeography underlying the probable expansion of CAM plants under global change. At the individual scale, CAM succulence is a relatively accessible and adaptive trait (Griffiths and Males 2017, Edwards 2019, Winter and Smith 2022) to drought at evolutionary time scales. High drought and heat tolerance (Borland et al. 2009, Arakaki et al. 2011) and unsaturated photosynthetic response to carbon dioxide enrichment (Maxwell et al. 1997, Drennan and Nobel 2000, Yu et al. 2019, Hogewoning et al. 2021) offer CAM plants a competitive advantage in a drier, warmer, and carbon dioxide–enriched atmosphere expected in drylands, which themselves are predicted to expand during the Anthropocene (Wang et al. 2022). At canopy and community scales, CAM succulence influences CAM allometry or morphology, which determines how CAM plants occupy and compete for resources (Davis et al. 2015), influencing community assembly, growth and mortality, and carbon sequestration. At the landscape scale, succulence could interact with disturbances, including human activities (Griffiths and Males 2017), further influencing demographical and carbon dynamics.

Significant ecological and socioeconomic consequences of CAM plant expansion have been summarized in this study through the lens of the food–energy–carbon–water–biodiversity nexus (figure 1). We have advocated for advances in hybrid model observation efforts, which would facilitate a quantitative estimate of the potential extent and impacts of CAM expansion. Future studies would also need to develop multidimensional optimization frameworks to assess food- and climate-smart strategies that can leverage the potential expansion of CAM plants to enhance societal resilience in the Anthropocene.

Conclusions

In this study, we synthesized research on CAM ecophysiology, evolution, and biogeography and sheds light into potential CAM plant expansion under global change. Our results present empirical evidence and collectively highlight the potential expansion of CAM plants in the Anthropocene. A reconstruction of succulent–CAM evolutionary history points to carbon limitation as the underlying evolutionary driving force in CAM evolution and radiation in terms of CAM diversity. Succulence, nocturnal opening of stomates, and the unsaturated productivity response to carbon dioxide enrichment would favor the expansion of CAM distribution and abundance at ecological time scales under contemporary global change. Some lineages of CAM plants (e.g., *Cylindropuntia*, *Opuntia*, and *Agave*) have expanded and encroached into drylands worldwide in the past decades. We suggest that this trend of CAM expansion, inferred from its ecophysiology, evolutionary history and biogeographic pattern, is expected to accelerate in the twenty-first century in a drier, carbon dioxide enriched, and warming atmosphere with higher VPD. Future CAM research would benefit from a data-model-integrated framework with CAM succulence as a potential lens to evaluate its distribution and dynamics under future climate scenarios as well as potential benefits and problems of CAM plant expansion in the Anthropocene.

Supplemental material

Supplemental data are available at *BIOSCI* online.

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