REVIEW PAPER

Undervalued potential of crassulacean acid metabolism for current and future agricultural production

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Abstract

The potential for crassulacean acid metabolism (CAM) to support resilient crops that meet demands for food, fiber, fuel, and pharmaceutical products far exceeds current production levels. This review provides background on five families of plants that express CAM, including examples of many species within these families that have potential agricultural uses. We summarize traditional uses, current developments, management practices, environmental tolerance ranges, and economic values of CAM species with potential commercial applications. The primary benefit of CAM in agriculture is high water use efficiency that allows for reliable crop yields even in drought conditions. Agave species, for example, grow in arid conditions and have been exploited for agricultural products in North and South America for centuries. Yet, there has been very little investment in agricultural improvement for most useful Agave varieties. Other CAM species that are already traded globally include Ananas comosus (pineapple), Aloe spp., Vanilla spp., and Opuntia spp., but there are far more with agronomic uses that are less well known and not yet developed commercially. Recent advances in technology and genomic resources provide tools to understand and realize the tremendous potential for using CAM crops to produce climate-resilient agricultural commodities in the future.

Keywords: Agave, agroecosystems, aloe, cacti, crops, drought, Opuntia, orchid, pineapple, vanilla, water use efficiency.

Introduction

Crassulacean acid metabolism (CAM) is a photosynthetic pathway observed in plant families all around the world in many climates (Winter and Smith, 1996; Silvera et al., 2010; Edwards and Ogburn, 2012), but it is not widely recognized as a characteristic that is favorable for agricultural plants. The wide temperature and moisture tolerance ranges exhibited in many CAM plants would, however, be advantageous for crops grown in locations with extreme weather events, especially where drought occurs. The increasing frequency of droughts, floods, and extreme temperatures occurring as a result of climate change (Kirtman et al., 2013; Naumann et al., 2018) are already motivating breeders and biotechnologists to develop...
more resilient varieties of common commodity crops. While most crop improvement strategies emphasize increased production of crops already in production, an alternative strategy could involve diversifying investments to develop more resilient crop species (Davis et al., 2018). This article reviews the potential of CAM crops to support more sustainable and resilient agricultural markets.

The expression of CAM in plants ranges from weak to strong, with some plants reverting to CAM only when under stress (facultative) and other plants operating with CAM constitutively through the entire life cycle (e.g. Agave spp.). Some plant families, like Portulacaceae and Bromeliaceae, include species with a wide range of CAM expression from constitutive CAM to no CAM at all. Species within the Portulacaceae family range from C4 to CAM (e.g. Koch and Kennedy, 1980; Holtum et al., 2017) and species within the Bromeliaceae range from C3 to CAM (e.g. Crayn et al., 2015). The plasticity of CAM and the wide-ranging expression of CAM have led to some debate about the evolutionary rise and permanence of this condition in plants. While a comprehensive phylogenetic count of CAM plants has not been completed, CAM has been discovered in over 34 families (Winter and Smith, 1996) and frequently occurs in succulent plants, which in total are represented in 70 flowering plant families (Nytßler et al., 2008). Increasing recognition of CAM in many plant taxa underscores the potential for CAM to be exploited for agricultural production (Borland et al., 2009; Davis et al., 2014; Yang et al., 2015b).

Of the 168 crop product categories that are inventoried by the Food and Agriculture Organization of the United Nations, only four are sourced from CAM plants (agave fibers, pineapples, sisal, and vanilla) (FAO, 2018). In the last agricultural census of United States cropland, only 1 of 26 specified crops of importance was a CAM crop (pineapple), with 42 farms reporting production of pineapple and no acreage specified (USDA NASS, 2018). With over 2 million farms reporting data from the census (USDA NASS, 2018), the portion dedicated to CAM crops is insignificant (0.002%). Given this perspective, it is perhaps not surprising that plant physiological research, agricultural management, and crop production models have thus far focused primarily on C3 and C4 plants while CAM has received far less attention. As a result, the potential for CAM to improve sustainable agricultural production is under-realized, particularly considering that about 6% of all vascular plants use CAM (Winter and Smith, 1996).

The potential production of high-yielding CAM plants has been described for over four decades (e.g. Kluge and Ting, 1978), but there is a resurgent interest in the potential of CAM species for agriculture with recent studies of crops such as Agave spp. (e.g. Davis et al., 2010, 2016; Holtum et al., 2011) and Opuntia spp. (e.g. Owen and Griffiths, 2014; Cushman et al., 2015). Here, we review these well-known and high yielding species along with less recognized CAM species that have potential for supplying commercial agricultural products even under conditions with rapidly progressing climate change. We first review current geographic ranges of production, uses, management strategies, environmental tolerance ranges, and other characteristics of CAM species that have market value. We then review technological developments that can support agricultural improvements in CAM crops.

**CAM species with agricultural value**

*Agavoideae (Asparagaceae)*

Agave species are currently cultivated for multiple agricultural markets that include fiber, sweeteners, beverages, food, and ornamentals. Traits of some of the more widely recognized species are summarized in Table 1. The Agave genus is endemic to the Americas. Of the 200 described species, 150 are found in Mexico plus a further 36 subspecies, bringing the number of taxa reported in Mexico to 186 (García-Mendoza, 2007). Natural populations of Agave species are found in around 75% of Mexican territory and are most abundant in arid and semiarid regions of the central and northern states. The flowers of most species (*cactayas*) are edible. The warm, humid states of Tabasco, Campeche, and Quintana Roo lack natural populations although many species have been introduced as ornamentals, and for cultivation in some cases. Agave spp. are now dispersed throughout the world.

The Agave genus is divided into two subgenera: *Agave* and *Littaea*, mainly distinguished by their paniculate or spicate inflorescences, respectively. While the subgenus *Littaea* contains only 47 species, the subgenus *Agave* is the largest with 103 species that are further divided into specific groups, and the group Rigidae contains most of the commercially exploited species (Gentry, 1982). García-Mendoza (2007) reports that many Agave species show local endemism with up to 69% of the described taxa growing only within very specific regions bounded by 1–3° latitude and longitude. Specific habitats are diverse, ranging from sea-level to 3400 m above sea-level, and include both arid and semi-arid zones, exposed areas within forests, and river banks; but the plants are most abundant in xerophilous regions. *Agaves* can grow on both igneous and sedimentary type soils but are found principally on limestone.

In Mexico, Agave species have been exploited for food, fiber, construction materials and fermented beverages since the pre-hispanic era and were of such importance to the ancient cultures that they were represented by their own deity: the goddess Mayahuel. Today Agave species remain as icons of Mexican culture and are prominent in art and cinematography. Although currently the best-known Agave products are undoubtedly tequila and mezcal, the fiber industry was even more commercially important in the 19th and early 20th century. Many other applications have been identified for potential exploitation, including the extraction of antimicrobial compounds such as sapogenins, precursors for steroid hormone synthesis (Sidda et al., 2016) and extraction of fructan polymers (inulins/agavins) for use as dietary supplements (Huazano and López, 2015).

*Agaves* are exploited at three different levels in Mexico: harvested from the wild, semi-domesticated, or grown industrially. Subsistence farmers exploit wild agaves of many species for different purposes, with population densities ranging from 20–1500 plants per hectare in forested land and reaching up to 3000 plants per hectare in grassland. Local residents are encouraged not to overexploit resources by replacing harvested plants, harvesting only mature plants, and protecting plants and their pollinators from animals and fire. In some cases, such as *A. victoria-reginae* (Martínez-Palacios et al., 1999), species are in
| Species | Number of variants | Uses/products | Optimal Temp (°C) | Temperature tolerance range (°C) | Optimal annual rainfall (mm) | Average annual rainfall in growing region (mm) | Fertilizer required | Center of diversity | Mechanized harvest | Land area currently dedicated (ha) | Current economic value (million US$ year\(^{-1}\)) |
|---------|-------------------|---------------|-------------------|-------------------------------|-----------------------------|-----------------------------------------------|-------------------|-----------------|-----------------|-------------------------------|-----------------------------------------------|
| Agave americana L.\(^a\) | 10 | Ornamental, pulque, fiber, anti-inflammatory, anti-carcinogenic, antioxidant, steroidal, bioethanol | 25 day/15 night | −9−>50 | 530 | 600−800 | Unknown, broad tolerance | Northern Mexico and Southwestern USA | No | None commercial | Unknown |
| Agave angustifolia Haw.\(^b\) | >20 | Mescal, brooms, fiber or textiles, pulque, rope | 22-38 | 5−60 | 125−1680 | Unknown, not usually applied | Oaxaca | No | −249 | 206 |
| Agave fourcroydes Lem.\(^c\) | 3 | Fiber for textiles, rope, fuel, sandals, construction | 18-36 | −2−40 | 500−1000 | Unknown, leaves and bagasse | Yucatan | No | −15 000 | 12.6 |
| Agave mapisaga Trev.\(^d\) | 1 | Pulque, fiber, cattle feed, food, construction | 12−16 | 700 | Unknown, manure | Central Mexico | No | None commercial | Unknown |
| Agave salmiana Otto ex Salm-Dyck\(^e\) | 4 | Pulque, mescal, food, jewellery, toys, decoration, ornamentals, fuel, pulque | 12−16 | 125−800 | Unknown | San Luis Potosi and Hidalgo | No | None commercial | Unknown |
| Agave sisalana Perrine\(^f\) | 2 | Fiber for textiles, ornamental, medicine | 35−40 | 5−40 | 1200 | 500−800 | Variable | Unknown, introduced from Mexico | No | 331 330 | 111 |
| Agave tequilana Weber var. azul\(^g\) | 7 | Tequila, fuel, sweeteners | 30 day/15 night | −3−>50 | 700 | 40−60 kg N ha\(^{-1}\) year\(^{-1}\), other nutrients depend on soils | Jalisco | No | 330 000 | 314 |
| Aloe spp.\(^h\) | 360 species | Burns, digestion, inflammation, wounds, diabetes, immunity, antitumorogenic, cosmetics, ornamental, phytoremediation | Variable | Variable | 150 ml kg\(^{-1}\) plant | >100 | Manure used at 5−10 Mg ha\(^{-1}\) | Southern Africa, Arabian peninsula | Partially | 100 (raw) | 125 000 (in products) |
| Aloe barbadensis\(^i\) | | | 19−27 | 10−30 | 1900−3000 | 80−40−80 or NPK | Partially | \* | 1 122 520 | 3351 |
| Ananas comosus (L.) Merrill \(^j\) | 5 varieties, 13 cultivars | Fruit, beverages, fiber or textiles, medicine, poison, fishing line, nets, hammocks | 30 day/20 night | 0−>35 | 600 | 25−100 kg N ha\(^{-1}\) to soil, 200−600 kg N ha\(^{-1}\) year\(^{-1}\) to leaves; 25−100 kg P ha\(^{-1}\) | Guyana Shield in South America | Partially | 1 122 520 | 3351 |
| Cactaceae family (except Opuntia)\(^k\) | >>100 wild species, 12 domesticated, many managed | Ornamental (both potted and landscape plants), fruit, medicinal use, ceremonial use | Variable, but mainly dry-tropical 15−35 | Variable, 0−>50 | ca 500 | 50−500 | Broad tolerance, well-drained soils | Mexico, South America | No | Unknown acreage under cultivation. Millions of ha in wild populations | Unknown, but likely in the range of 20−200. Rapidly increasing |
| Species                  | Number of variants | Uses/products                                                                 | Optimal Temp (°C) | Temperature tolerance range (°C) | Optimal annual rainfall (mm) | Average annual rainfall in growing region (mm) | Fertilizer required                      | Center of diversity | Mechanized harvest | Land area currently dedicated (ha) | Current economic value (million US$ year⁻¹) |
|-------------------------|--------------------|-------------------------------------------------------------------------------|-------------------|---------------------------------|-----------------------------|---------------------------------------------|------------------------------------------|-------------------|------------------|----------------------------------|--------------------------------------------|
| Opuntia ficus-indica    | 81                 | Food, beverages, cosmetics, forage, pharmaceuticals                            | 25 day/15 night   | −7–65                           | 500                         | −50–100 kg N ha⁻¹ year⁻¹, 10–30 kg P ha⁻¹ year⁻¹, 20–50 kg K ha⁻¹ year⁻¹, 10–50 kg ha⁻¹ year⁻¹, Ca at planting | Central Mexico                          | No               | >600 000                     | 2520                           |
| Orchidaceae family      | >29 000 species    | Ornamental (both cut flowers and potted plants), food, medicinal use, ceremonial use | Variable          | Variable                        | Variable                    | Variable                                    | Variable Ca at planting Tropical humid climates | Only for ornamental                                    |
| Vanilla Mill           | 107 species       | Food, spices, medicine, woven figures and baskets                            | 21–32             | 10–33                           | >1500                       | >1500                                       | Unknown, mulch and compost Central Mexico                          | No               | 93 119                        | 762                             |

References:

a Gentry, 1982; Ocaña-Nava et al., 2007; Escamilla-Treviño, 2012; Hamissa et al., 2012.
b Gentry, 1982; Colunga-GarcíaMarín et al., 1999; Aguirre et al., 2001; Bautista-Cruz et al., 2007; Eguiarte and Souza, 2007; Palomino et al., 2007; Zrumbo-Villarreal and Colunga-GarcíaMarín, 2007; Rivera-Lugo et al., 2018.
c Colunga-GarcíaMarín et al., 1993; Colunga-GarcíaMarín and May-Pat, 1993; Irish and Irish, 2000.
d Cruz-Ramírez et al., 2006; Aguilar-Júarez et al., 2014.
e Gentry, 1982; Ocaña-Nava et al., 2007; Aguilar-Juárez et al., 2014; Espanza-Ibarra, 2015.
f Gentry, 1982; Debnath et al., 2010.
g Valenzuela-Zapata, 1994; Valenzuela-Zapata, 1997; Mancilla-Margall and López, 2006; Bautista-Cruz et al., 2007; Pimenta-Barios et al., 2007; Holtum et al., 2011; Núñez et al., 2011.
h Valenzuela-Zapata, 1994; Valenzuela-Zapata, 1997; Mancilla-Margall and López, 2006; Bautista-Cruz et al., 2007; Pimenta-Barios et al., 2007; Holtum et al., 2011; Núñez et al., 2011.
i James and Reynolds, 1986; Ahlawat and Khatkar, 2011; Liontakis et al., 2016; Katerere, 2018.
j Saha et al., 2006; Ahlawat and Khatkar, 2011.
k Bartholomew et al., 2002; Ming et al., 2015; FAOSTAT, 2018.
l Casas and Barbera, 2002; Nerd et al., 2002.
m Nobel and Israel, 1994; Nobel, 2002; Nobel and De La Barrera, 2003; Griffith, 2004; Stintzing and Carle, 2005; Feugang et al., 2006; Aguilar-Barreiro et al., 2013; Yang et al., 2015a; Arba et al., 2017; Inglese et al., 2017.

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a Gentry, 1982; Ocaña-Nava et al., 2007; Escamilla-Treviño, 2012; Hamissa et al., 2012.
b Gentry, 1982; Colunga-GarcíaMarín et al., 1999; Aguirre et al., 2001; Bautista-Cruz et al., 2007; Eguiarte and Souza, 2007; Palomino et al., 2007; Zrumbo-Villarreal and Colunga-GarcíaMarín, 2007; Rivera-Lugo et al., 2018.
c Colunga-GarcíaMarín et al., 1993; Colunga-GarcíaMarín and May-Pat, 1993; Irish and Irish, 2000.
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danger of extinction due to overexploitation, but in other cases local inhabitants are the stewards of traditional customs that sustainably exploit Agave spp.

Semi-domesticated plants are sexually or asexually propagated and usually managed by subsistence farmers with small plots of land. Agave species are actively planted and often serve as fences to protect property. They can be grown in combination with other crops or natural vegetation and are of different ages allowing farmers to harvest each year without the need to wait 8–10 years until all plants reach maturity. Farmers harvest and replace only mature plants and some organic fertilizer may be added, but input and labor costs are low allowing the farmers to obtain acceptable income. This low intensity management (with few inputs required) is common for production of pulque in Mexico State, Hidalgo, and Puebla from fermented Agave sap using essentially the same methods as were used in pre-hispanic times. Large species with long life cycles, such as A. americana, A. mappisaga, A. atrovirens, and A. asperima, are harvested just before flowering; the apical meristem is removed and part of the stem hollowed out. The sap is extracted and left to ferment and on average 300 liters of sap can be obtained from a plant over a 3-month period. Pulque is a relatively cheap beverage consumed as an alternative to beer and has seen a revival as young Mexicans begin consciously upholding traditional customs (Escalante et al., 2016).

Plants cultivated on an industrial scale are exclusively asexually propagated and planted in monoculture with intensive management (fertilization, weed and pathogen control). Until recently, most plantations were initiated using offsets, but currently some large-scale producers are turning to in vitro propagated germplasm in order to ensure homogeneity and eliminate rental germplasm in order to ensure homogeneity and eliminate diseases. Large-scale production of mezcal is associated with different Agave species in different regions of Mexico. The most important of these are A. pacifica (now synonymous with A. viripana L.) in Sonora, A. salmiana in Zacatecas, San Luis Potosi, and Guanajuato (Aguirre et al., 2001; Aguilarr-Juárez et al., 2014), and members of the ‘A. angustifolia complex’ in Oaxaca (Bautista-Cruz et al., 2007; Cruz-García et al., 2013). The renewed interest in mezcal has led to registration of each region and species with a controlled denomination under the auspices of the Mezcal Regulatory Council.

Tequila, undoubtedly the best known ‘mezcal’, is produced under a separate, strictly controlled denomination of origin overseen by the tequila regulatory council (CRT, 2018) that states that tequila can only be produced using the cultivar A. tequilana Weber var. azul in designated counties of five Mexican states: Jalisco, Guanajuato, Nayarit, Michoacán and Tamaulipas. Crop yields from plantations in the tequila producing region are estimated to be around 22 Mg ha$^{-1}$ year$^{-1}$ (Davis et al., 2014). Agave tequilana is by far the most efficient species in terms of production of alcohol given the higher levels of fructan accumulation and shorter life cycle in comparison with species used for mezcal.

Fertilization requirements for Agave grown commercially in Mexico depend on soil composition, plant age, and growth rate. Often urea is applied to provide nitrogen, but phosphorus and potassium are also required in some regions (Holtum et al., 2011). Some studies show that A. tequilana productivity is limited by low nitrogen, phosphorus, potassium, and boron in soil, and that disk ploughing decreases the levels of organic carbon, nitrogen, and phosphorus in A. tequilana plantations in Western Central Mexico (Bautista-Cruz et al., 2007). Soil nutrient levels can affect both plant growth and the flavor of tequila (Núñez et al., 2011).

Harvesting of Agaves on an industrial scale is still labor intensive. Agave tequilana plants flower between 5–8 years after planting whereas mezcal species will usually take at least 7 years. Flowering, from February to May, signals the end of the Agave life cycle and inflorescences are removed manually soon after emergence to preserve accumulated carbohydrates. Flowering is not homogeneous and farmers can choose to harvest over several years to maximize the sugar content of plants or harvest the whole plantation including plants not ready to flower and with lower sugar content. Plants are harvested manually removing the leaves and transporting the stem or head for sugar extraction and fermentation. Agave tequilana stems usually weigh around 40–90 kg with a sugar content of 30° brix (Zúñiga-Estrada et al., 2018) whereas mezcal species can reach over 200 kg but have a sugar content of between 6 and 21° brix depending on the species.

Asexual reproduction of A. tequilana and mezcal species has led to a narrow germplasm base that makes Agave plantations extremely vulnerable to pests and pathogens, the most common of which are Phytophthora spp., Pseudococcus spp., Acataspis agavis, Agathymus rethon, Strategus oleus, and Scyphophorus acupunctatus. Pest management strategies include weed control, soil handling, nutrition, and black light traps. Biological control involving Beauveria bassiana, Metarhyzium anisoplae, and Chiloborus cacti has also been used in addition to the application of chemical insecticides. Common pathogens include wilt (Fusarium spp.), grey spot (Cercospora spp.), stem rot (Envinia spp.), leaf spot (Botryodiplodia spp., Phytophthora spp., and Alternaria spp.), and fungicides or chemical treatments are applied for control (Bernal et al., 2006; Rulfo et al., 2007).

In addition to Agave species exploited specifically for spirits and pulque, other species are notable for their current and potential exploitation for production of bioenergy, pharmaceuticals, and fibers. For example Agave americana L. is most commonly used as an ornamental and to a lesser extent for pulque and fiber production, but has recently been introduced as a biofuel crop for semi-arid conditions (Davis et al., 2016). Because of its high antioxidant activity, extracts from A. americana leaves are used in traditional medicine as an anti-inflammatory agent and studies have shown anti-carcinogenic and antioxidant properties (Hamissa et al., 2012). Saponins, tigogenin, and hecogenin are also extracted from the waste residues of A. americana fibers for synthetic steroid hormones (Escamilla-Treviño, 2012). This species could potentially be more widely exploited by pharmaceutical and cosmetic industries.

Hard fibers produced from Agave are often indistinctly referred to as henequen or sial, but several different Agave species are associated with fiber production. In Mexico A. fourcroydes has been used since pre-hispanic times in the Mayan culture of the Yucatan peninsula for production of henequen (Colunga-GarcíaMarín and May-Pat, 1993; Colunga-GarcíaMarín et al., 1999; Colunga-GarcíaMarín, 2003). Spanish colonists largely
ignored fiber production from *Agave* until the invention of the automatic harvesting/binding machine (1845) for hay and wheat in the USA led to huge demand for twine that was safe for animals. From 1850 onwards, plantations in Mexico were the source of \( >85\% \) of henequen fiber and machines for de-cortication were introduced. At the height of production in 1910–1915, \( >150 \) 800 tons of fiber were produced annually and \( >659 \) million plants were grown. With the introduction of synthetic fibers after World War II, the industry declined and the technology was sold to Brazil (Evans, 2007). Most of the henequen ‘haciendas’ and plantations are currently abandoned or being developed as hotels and restaurants to cater to the tourist industry (Evans, 2007). Current interest in natural fibers and products could represent an opportunity to reinvigorate the industry in Mexico in order to become competitive with China and Brazil, where production of *Agave* for fiber has recently increased (FAO, 2018).

*Agave sisalana* Perrine, which probably originated in Chiapas by hybridization between *A. angustifolia* and *A. keuvenis* (Gentry, 1982), is named for the port of Sisal in Yucatán, Mexico from where it was originally exported during the 19th century for development of fiber production in India, Africa, and Brazil. The *A. sisalana* cultivar Hildana was widely used in East Africa, but a high yielding hybrid, H11648 ((*A. amaniensis* \( \times A. \) angustifolia) \( \times \) *A. amaniensis*), has replaced *A. sisalana* in Tanzania and other regions of Africa and is now the genotype cultivated in China (Bos and Lensing, 1973).

Tanzania, the most important producer of sisal until the 1960s, has now been overtaken by Brazil (Brink and Achigan-Dako, 2012). For fiber production, plantations are initiated from either offsets or bulbils, but in *vitro* propagation is also possible. Seed plants are usually around 30–40 cm tall and have around 15 leaves. Planting can be carried out both in the dry season (March to May) and in the rainy season (June to September). Density of planting is between 3000 and 4000 plants per hectare, and in some cases double rows are planted and/or legumes are intercropped. Plants begin to be harvested between 3 and 7 years after planting and between 9 and 12 leaves are harvested at 6-month intervals. Annual crop yields of sisal are estimated to be 13 Mg ha\(^{-1}\) year\(^{-1}\) in commercial production (Davis et al., 2014).

**Aloaceae**

*Aloe* species are widely used CAM plants, with records dating back to Sumerian clay tablets from 2100 BC, and extensive use by ancient Egyptian, Arab, Greek, Roman, and Indian cultures (Sánchez-Machado et al., 2017). Today, the extracted tissues are processed for treatment of radiation (burn) injuries (Rao et al., 2017; Silva et al., 2014), gastrointestinal issues (Xu et al., 2016; Boudreau et al., 2017), inflammation (Vázquez et al., 1996), wounds (Choi et al., 2001), diabetes (Bunyahraphatsara et al., 1996; Tabatabaei et al., 2017), and mitigation of immune system weakening associated with HIV–AIDs (Olatunya et al., 2012), and it even has antitumorigenic properties (Hussain et al., 2015; Shalabi et al., 2015). *Aloe* spp. are also consumed as a health food and beverage, commonly appear as an ingredient in cosmetics (Javed and Atta-ur-Rahman, 2014), and can be used as a bioabsorbant of pollutants in ecosystems (Giannakoudakis et al., 2018). The long list of commonly known, novel, and sometimes exaggerated uses of *Aloe* fuels demand on a global scale (Liotakis et al., 2016; Katerere, 2018). The global industry for *Aloe* spp. in raw form has been estimated to be about 125 million US dollars, the volume of industry for finished products is alleged to be around 110 billion US dollars, and Americans alone spent almost 40 billion US dollars on related products in 2008 (Ahlawat and Khatkar, 2011).

While still closely related to plants found in the Liliaceae family, plants within the *Aloe* genus are now assigned to the family Aloaceae, which contains over 360 species all interchangeably referred to by the common name aloe vera (Eshun and He, 2004; Sánchez-Machado et al., 2017). The plants within the *Aloe* genus originate from southern Africa, but many of the medicinal varieties have diversity centered in the Arabian peninsula (Grace et al., 2015). *Aloaceae* species typically have succulent, tapered leaves attached directly to a central stem forming simple rosettes. The leaves often have spines along margins and on both abaxial and adaxial surfaces and have a thick rind that surrounds a clear gel-like mesophyll. These morphological traits allow for *Aloe* to survive in arid habitats, and \( \delta^{13} \)C values reveal that *Aloe* performs CAM constitutively (Winter et al., 2005), which is likely an adaptation to use water with extreme efficiency under drought conditions.

Though many plants found within the Aloaceae family can be considered economically important, many of these species are wild-cultivated (Nejatzadeh-Barandozi et al., 2012). Of these species, *Aloe perryi* Baker, *Aloe ferox*, *Aloe arborescens*, and *Aloe barbadensis* Miller are all medicinal. The latter is also commonly found in commercial production, and has a variant, *A. arborescens* Mil. var. *natalensis* Berger (Eshun and He, 2004; Nejatzadeh-Barandozi et al., 2012; Sánchez-Machado et al., 2017), that is poorly understood.

**Aloe barbadensis**

*Aloe barbadensis* Mil. has so far been demonstrated to have the greatest medicinal value within the Aloaceae family (Eshun and He, 2004). It is cultivated on a large scale in South Africa, Madagascar, Arabia, and India in well-draining soils (Nejatzadeh-Barandozi et al., 2012), and is a perennial crop that requires two years to reach maturity with a lifespan of 12 years (Ahlawat and Khatkar, 2011). It reproduces mostly by clonal pups but may also produce a single inflorescence seasonally with long yellow to orange flowers that are pollinated by the long beak of a sunbird (Rathod et al., 2014). Once matured, leaves can be harvested four to six times per year with planting density of 10 000–20 000 plants per hectare (Yepes et al., 1993; Áñez and Vásquez, 2005). Silva et al. (2010) performed a study in which irrigation treatments were applied in 20, 15, 10, and 5% of the mean evaporative demand measured in a field site (Chile) that receives an annual precipitation rate of about 100 mm per year\(^{-1}\). At the optimal treatment of 15% evaporative demand added, 17.1 g of *A. barbadensis* gel could be produced per liter of water and 76.2 tons of gel could be harvested per hectare of 4-year-old plants (Silva et al., 2010).

*Aloe barbadensis* grows well in saline conditions and can even be irrigated with seawater (Jin et al., 2007). Nitrogen and
phosphorous additions have been shown to increase growth and gel content (Pareek et al., 1999), and an N–P–K of 80–40–80 is sufficient for growth (Saha et al., 2005). The addition of mycorrhizal fungal symbionts has been shown to increase nitrogen and phosphorus uptake in this species (Tawaraya et al., 2007). Aloe barbadensis is highly productive with low water input, but like other CAM crops, also suffers from a lack of cold tolerance. Even brief frost events are enough to kill most accessions of A. barbadensis (Grindlay and Reynolds, 1986). However, A. barbadensis has relatively few pests and pathologically only suffers from surface fungal infections and bacterially caused soft rotting (Ahlawat and Khatkar, 2011).

The worldwide cultivation and radiation of A. barbadensis has given rise to an unknown amount of accessions, many of which have adapted unique traits within their new environments that may prove to be beneficial crop traits for future breeding programs (Nayananantha et al., 2010; Tripathi et al., 2011; Nejatzadeh-Barandozi et al., 2012; Chandra and Choudhary, 2014). Furthermore, the diversity of species within the Aloaceae family gives rise to the possibility of breeding new varieties with desired traits, as in the case of A. barbadensis, a diploid, rarely tetraploid, species (Nejatzadeh-Barandozi and Akbari, 2013), amenable to genomic editing techniques (Nadakuduti et al., 2018). Efforts to enhance the efficiency in extracting over 200 different chemicals (Ahlawat and Khatkar, 2011) would lead to an increase in economic return from A. barbadensis (Rana et al., 2018) because of the many medicinal applications. Further research is needed for a better understanding of the environmental limitations to productivity of Aloe.

Cactaceae

Cacti are not only showy, strange, and uniquely modified plants, they are also important agricultural and wild harvested species. A large proportion of the flora traditionally used in the dry-tropical and subtropical Americas are cacti. For example, of the 762 edible fruit species reported for Mexico, the largest share, almost 12% (88 species), are cacti (Segura et al., 2018). The inventory reported is far from complete and does not mention many of the species regularly used by many indigenous groups (see for example Felger and Moser, 1985; Luque et al., 2017). These additional species might easily duplicate the number of useful cacti species in Mexico. All the harvested species described by Segura et al. (2018) are reported as wild, but many have suffered some form of manipulation (Casas and Barbera, 2002). Opuntia is by far the most important agricultural cactus crop. The young developing pads of many Opuntioid species, as well as Nopalea are prepared as greens, and their fruits are relished throughout the world. Many Opuntia species are also used as animal fodder and to produce cochineal, the source of the natural dye carmine.

Almost all cactus fruits are edible, from the small, red or greenish fruits of Mammillaria species (named ‘chilitos’ in Mexico for their resemblance to miniature long and slender chilies) to the rich, sweet fruits of the pitahaya or dragon fruit (Hylocereus undatus and other Hylocereaceae) now grown throughout the tropical world. Other edible parts of the plant include flower buds and flowers cooked to produce pickles (mainly from Ferocactus and columnar cacti); seeds that are eaten raw or toasted (for most cactus species); and the inner flesh, which is processed and candied (for Ferocactus and Echinocactus species) (Casas and Barbera, 2002). In addition, the woody ‘skeletons’ of opuntioid species and the ‘ribs’ of columnar cactus species, as well as the wood of the larger species are used as substitutes for more traditional lumber products, both for purely utilitarian construction material and for furniture and decorative purposes (Yetman, 2007). Recently, even saguaro-rib walking sticks have been marketed online.

Aside from species of Opuntia and Hylocereus, other species of cacti are rarely recognized as agriculturally important despite their widespread use. Among those harvested or domesticated for agricultural purposes, columnar cacti provide a significant resource, particularly for indigenous groups throughout the American continents (Yetman and Búrquez, 1996; Casas and Barbera, 2002). As happens with most CAM plants, cacti are superbly adapted to dry conditions, with high water use efficiency (WUE), and columnar cacti represent the pinnacle of evolution in terms of size and performance under harsh conditions (Gibson and Nobel, 1986; Nobel and Bobich, 2002; Mauseth, 2017). As a consequence, many columnar cactus species are locally used as wild or semi-domesticated crops. Both in North and South America, columnar cacti represent important material and spiritual elements of many native cultures (Yetman, 2007). In both continents, columnar cactus species growing in natural communities have a variety of uses, from providing highly nutritious and energetic fruits to construction materials and shamanistic and medicinal uses. However, few columnar species have been domesticated and even fewer have attained a major role as agricultural produce because most harvesting happens in the wild with little or no management.

Most documented uses of columnar cacti published since the 1800s are purely ethnographic, describing the use of columnar cacti resources by native cultures of the drylands of the Americas. For example, in the northwest of Mexico and southwest of the United States, the saguaro (Carnegiea gigantea) is a major cultural and food element for the O’odham (Thackery and Leding, 1929; Greene, 1936; Bruhn, 1971). Slightly further south into Mexico, the sahuiseo, also known with the generic name of cardón (Pachycereus pringlei) and the pitaya agria (Stenocereus gummosus) have been harvested for millennia by the Comcaac (seri) people (Felger and Moser, 1985; Hodgson, 2001). Inland, the organ pipe cactus (Stenocereus thurberi) is a major staple of Lower Pima, Yaqui and Mayo native Americans. Also, for the Mayo and the Guarigio, the etcho (Pachycereus pecten-aboriginum) is of paramount importance, and the sahuina (Stenocereus montanus) is a major staple and a primary construction material for southern Sonora and northern Sinaloa native people (Yetman, 2007). Further south into Mexico, dozens of species of columnar cacti are used in the same fashion by native indigenous people and by the Mexican mestizo population (Pérez–Negrón et al., 2014).

In South America, the use of columnar cactus resources is less widespread, but still very relevant to some indigenous groups. From disperse information, many South American columnar cactus fruits are markedly less tasty and bland (although
not distasteful) when compared with the scrumptious, sweet, and juicy fruits of most North American columnar cactus species. South American columnars usually have lower sugar content than North American species (less than 10% compared with 10–25% sugar). For example, the fruits of copaú (Eulychnia acida) from northern Chile have less than 1% sugar content (Salvaterra et al., 2010) and the fruit of Jasminocereus thouarsii, endemic to the Galápagos Islands, is less than 3% sugar (AB, pers. obs.). The pusakanas and cardón fruits of Echinopsis spp., Corryocactus spp., and Browningia candelaís among other South American species are eaten with sugar added, and the acidity of the fruit of pichiá (Orocereus leucotrichus) is cut with salt (Villagrán and Castro, 2003).

Despite the widespread use of columnar cacti, mainly for their delicious fruits, only a few species are described by Casas and Barbera (2002) as subject to domestication or incipient husbandry. The use of most cactus species can be classified as ‘gathering of natural resources’. For context, the other categories of management include (i) tolerance actions directed to maintain useful plants, (ii) enhancement directed to further the presence of useful plants, and (iii) protection from competitors and predators, fertilizing, and pruning among other actions. In North America, about 12 cactus species are cultivated, all of them in central Mexico (Casas and Barbera, 2002). In South America there is no record of widespread cultivation of any species, but Echinopsis peruvianus is known to be closely associated to archaeological and present domestic environments (Albesiano and Kiesling, 2012).

The process of domestication and agricultural potential of columnar cactus species has been addressed by many authors. The agricultural potential of cactus species has been shown to be highly promising as new fruit crops for drylands as well as for animal feed and biomass production (Nerd et al., 1993, 2002; Mason et al., 2015). However, despite their importance, there are very few statistics of production of cactus agricultural products, and the production from columnar cacti is still largely unknown. Aside from major species related to internal or export markets, there is a paucity of studies estimating the volumes harvested for local, domestic consumption. Orozco (2007) presented compelling information on the economic impact of organ pipe cactus from recollection in indigenous and mestizo localities in Sonora, Mexico, reporting that the income from harvesting the fruits of this wild species could add up to 10 times the minimum wage at the time of the study. For the region of Quiotepec, at the lowest part of the valley of Cuicatlán in Oaxaca, Mexico, Pérez-Negrón et al. (2014) showed that harvesting wild species of columnar cacti could complement up to one-third of the income from drylands agriculture with the harvest from the three most common columnar cactus species.

A search at the Mexican Agrifood and Fisheries Information Service (Servicio de Información Agroalimentaria y Pesquera: https://www.gob.mx/siap) revealed that columnar cacti during 2017 made up a dismally small proportion of the formal agricultural economy. For example, the pitahaya fruits, mainly from Stenocereus pruinosos, S. quetlanensis, and allied species in the states of Oaxaca, Jalisco, and Puebla are worth 3.5 million US dollars. For Hylocereus, during 2016, the states of Quintana Roo, Yucatán, and Puebla produced about 4200 metric tons with a mean value of 700 US dollars per ton. In comparison, during 2016, the production of Opuntia pads (nopalitos) for the internal market was close to 811 000 metric tons (70% produced in Mexico City and the state of Morelos), and exports of 45 000 metric tons were valued at 14 million US dollars (https://www.gob.mx/siap/articulos/nopalitos-en-2016-se-vendieron-al-exterior-44-8-mil-toneladas). A better comparison is with tunas and xoconostles, the fruits of Opuntia species, where annual production in 2017 was 470 000 metric tons, with the export market comprising 17 000 metric tons worth 8.9 million US dollars (https://www.gob.mx/siap). These figures, however, are probably gross underestimations of real harvesting rates because they do not include the much larger volume traded in informal markets, nor the harvest of wild and cultivated cacti products for domestic consumption.

**Opuntia**

Among the Cactaceae family, the genus *Opuntia* is the most abundant and widespread worldwide. *Opuntia* originated from Mesoamerica and comprises around 78 wild species, located mainly in the Meridional Highland Plateau of Mexico (Reyes-Aguero and Aguirre-Rivera, 2011). There are an estimated 181 cultivated species, distributed mainly in Mexico, North and South America, and introduced to the Mediterranean zone of Europe and Africa, as well as Australia (Majure et al., 2012). Approximately 67% of the species of *Opuntia* have been domesticated and are cultivated worldwide for human consumption of their fruits (known as prickly pears in North America and *tunas* in South America).

Different wild and cultivated *Opuntia* species produce edible fruits such as *O. megacantha* Salín-Dyck, *O. amylena* Tenore, *O. streptocantha* Lemaire, *O. stricta* Haw, *O. dilemni* (Ker Gawl.) Haw, *O. schumannii* Weber, and *O. robusta* Wendel (Arba et al., 2017). However, *O. ficus-indica* (L.) Mill is the cactus species with the highest degree of domestication and the greatest importance for agriculture in arid and semiarid regions of the world (Peña-Valdivia et al., 2012). It has been cultivated since prehistoric times and its domestication began around 14 000 years ago by the Mesoamerican civilizations in the south of the meridional Mexican highlands (Kiesling and Metzing, 2017). The determination of its taxonomic relationships within the genus are scarcely known due to centuries of artificial selection with different purposes, favoring their hybridization and polyploidy, leading to an enhancement of both fruit and cladode characteristics such as flavor, shape, color, size, and texture (Santos Díaz et al., 2017).

The flat stems or cladodes (also called nopalitos) of *Opuntia* spp. are an important food source for both humans and animals, with cultivation for this purpose in Mexico on 12 000 ha and an annual production of 600 000 metric tons (Yahia, 2012). The commercial species are *O. ficus-indica* and *O. inermis*. Production for livestock forage improves the availability of fodder in dry areas, and the plants can supply the main source of water for the animals with approximately 180 tonnes ha−1 year−1 of water (Dubeux et al., 2017).

The commercial varieties produced in Mexico for human consumption include Milpa Alta, COPENA V-1, COPENA
The cladoxes are harvested between 1 and 3 years after planting, their weight ranges from 40 to 100 g, and they measure 11–20 cm in length. Due to CAM activity, the cladodes accumulate high amounts of acid during the night, so the best time of the day to harvest them is at dusk when the acidity is lower and the sugar content and pro-vitamins (A and C) are higher. In addition, the cladodes provide a source of minerals (calcium, sodium, potassium, iron) and fiber, making the nutritional value high (Guzmán Loayza and Chávez, 2007).

In different regions of North America, Opuntia is produced as an emergency crop during drought seasons where grasses and cereals are senescent and cannot supply the cattle food needs. As a consequence of the variable rainfall, some maize producers adopted Opuntia cultivation, obtaining a consistent production that assures the stock of cattle feed on marginal lands, converting these locations into productive zones (Russell and Felker, 1987). The low protein and fiber content of cladodes requires other food sources as supplements (such as alfalfa, sorghum, cornmeal, maize, dry bean, and wheat, among others). According to López-García et al. (2001), the daily consumption of cladodes for cattle and sheep is 15–95 kg day^{-1} per animal, which can be double under drier conditions and decreases in rainy periods due to the availability of other plants (grasses or grains).

Of the 200–300 species within the Opuntia genus (Arba et al., 2017), field studies involving Opuntia ficus-indica have demonstrated some of the highest productivity values of any CAM species, with above-ground biomass values between 2.4 and 47.3 Mg ha^{-1} year^{-1} (Dubeux et al., 2006; Nobel et al., 1992; Sánchez et al., 2012). As an energy crop, O. ficus-indica has a lower potential for ethanol production compared with traditional energy crops, but a higher than average potential for methane production (Yang et al., 2015a; Santos et al., 2016). CAM-idling (Brulbert et al., 1987), root shrinkage (Nobel and Cui, 1992; Snyman, 2006), and stem succulence are all traits that provide O. ficus-indica with extraordinarily high drought resistance (Snyman, 2013).

The world-wide cultivation of O. ficus-indica in a variety of soil types for a variety of products has complicated efforts to assess the exact fertilizer application that is optimal thus far. However, in O. ficus-indica, higher growth and fruit yield has been associated with higher calcium-to-nitrogen and potassium-to-nitrogen ratios, respectively, than that of common crop species (Galizzi et al., 2004), and growth is halted under saline conditions (Nerd et al., 1991; Murillo-Amador et al., 2001). Opuntia ficus-indica is typically propagated clonally, a feature that contributes both to commercial production and to extreme invasiveness (Shackleton et al., 2011). Several insect pests of O. ficus-indica exist including Cactoblastis cactorum and Dactylopius coccus (Annecke and Moran, 1978), the first serving as a biological control (Schartel and Brooks, 2018) and the second harvested from pads to produce carmine dye (Mazzeo et al., 2018), which was considered a luxury prior to the advent of synthetic dyes. Opuntia ficus-indica is primarily limited in range by cold tolerance, but other low yielding cold-tolerant relatives such as O. ellisiana (Guevara et al., 2003) may contribute to an understanding of cold tolerance mechanisms in the Opuntia genus that may increase the productive range.

Opuntia ficus-indica is a xerophytic plant growing predominately in arid and semi-arid zones tolerating temperatures up to 65 °C, but it can also be found in extremely different environmental conditions such as high altitudes in the Peruvian Andes, tropical regions of Mexico, and as far north as Canada. It is also adapted to poor and sandy soils with a pH of 6–7.5 and an adequate drainage (Duarte and Paull, 2015). WUE is very high, ranging from 4 to 100 mmol CO_{2} mol^{-1} H_{2}O, compared with C_{3} and C_{4} plants (1–1.5 and 2–3 mmol CO_{2} mol^{-1} H_{2}O, respectively), allowing growth in zones with a mean annual precipitation of 250–700 mm (Yahia and Säenz, 2011; Duarte and Paull, 2015).

The production of Opuntia has been extended around the world and it has become an alternative crop in areas with deficient soil quality and with water deficit. In Mexico, the largest producer and consumer, Opuntia cultivation is concentrated mainly in three regions: Puebla, Valley of Mexico, and the Potosino-Zacatecano high plateau. The latter contributes about 50% of the total volume of national production (Méndez Gallegos and García-Herrera, 2006). The production of O. ficus-indica for human consumption and forage also occurs in Brazil (40 000 ha), Tunisia (16 000 ha), Italy (2500 ha), and Chile (1100 ha), and in smaller areas in Morocco, Egypt, Algeria, Libya, South Africa, Bolivia, Argentina, Peru, Ecuador, the United States, Israel, Jordan, and Venezuela (Piumienta-Barrios, 1994; Yahia and Säenz, 2011).

The average yield of the commercially produced fruit (prickly pear) in Mexico is around 7 tons ha^{-1} with a range across different producing regions of 5–20 tons ha^{-1} (Méndez Gallegos and García-Herrera, 2006). The genotype–environment interaction in the regions where Opuntia is produced provides a higher diversity of cultivars with different characteristics, such as shape, taste (acids and sweets), size, seed content, and presence of antioxidants (Russell and Felker, 1987; Inglese et al., 1995; Mondragon-Jacobo and Bordelon, 1996; Mejia and Cantwell, 2003). On the contrary, in most countries other than Mexico, the fruit production depends on one or two cultivars (Méndez Gallegos and García-Herrera, 2006).

Orchidaceae

Considered one of the largest families of angiosperms, the Orchidaceae comprises over 29 000 species and can be found in all inhabited continents (Swarts and Dixon, 2009; Hinsley et al., 2017), although they are most common in the tropics. Only a small number of genera are commercially cultivated, all of which belong to subtribes and genera that show CAM in their lineage. However, CAM cannot generally be assigned to the whole genus, since CAM may occur in some species but not in others (Arditti, 1992; Silvera et al., 2009). Vanilla (Table 1) is the only genus that is commercially grown for its
edible fruit with relevant flavor and aroma compounds (De La Cruz Medina et al., 2009). There are several other uses such as production of flour made from orchid tubers called salep in the eastern Mediterranean and Middle east, and chikanda cake in south-eastern Africa, and various orchids are used in traditional Chinese medicine and health supplements (Fay, 2018). The orchids used for these purposes are harvested only from the wild. Although their use might be minor and limited to specific regions, there are growing concerns that collection and trade of these wild orchids will result in scarcity or even extinction (Liu et al., 2014; Fay, 2018).

The most common use of orchids is as ornamentals, and tackling the potential risk of extinction for certain species cannot be done without raising awareness in the horticultural community, including hobbyists, that actively search for rare species (Hinsley et al., 2015), and amongst international traders. The most important genera for cut orchids are Cymbidium, Oncidium, and Phalaenopsis, although the latter is mostly sold as a potted plant. Interestingly, orchids were considered a minor crop by the USDA until 1997, and no product information was collected (Lopez and Runkle, 2005). Phalaenopsis in particular is now considered an important commodity in the horticultural sector. In the USA, 21 million potted Phalaenopsis plants were sold in 2012 (USDA, 2015), representing a wholesale value of 177 million US dollars, and accounting for 19% of the potted plant market. In Europe, 2017 figures from the Dutch flower auction (Royal Flora Holland, 2018) indicate that 135 million Phalaenopsis plants were sold (53% of all house plants), representing a turnover of 494 million euros (32%).

Orchids clearly have important economic value, but orchid growers have only recently recognized the specialized management requirements of orchids that exhibit CAM. Studies on orchid production requirements (e.g. Cameron, 2011; De et al., 2014; Lopez and Runkle, 2005) indicate that physiology and growth under controlled conditions are limited. Detailed cultivation guides developed by breeders exist for only a few varieties, e.g. for Phalaenopsis (van der Knaap, 2005). The commercial value of orchids offers the opportunity to combine the economic interest of companies with the need to further understand CAM expression.

Vanilla Mill.

Vanilla was originally domesticated in Mexico, where it played an important role as currency for trade within the Aztec empire. After the Spanish and Portuguese colonization of Central and South America, the French in the 18th century started to export cuttings of Vanilla to their own colonies, such as Madagascar and Réunion. Because the natural pollinator, the Melipona bee, was not exported along with the plants, hand-pollination became necessary to successfully produce vanilla beans (Fouché and Jouve, 1999; Cameron, 2011).

In commercial practice today, pollination is still done by hand, which is a delicate and time-consuming task. With only one flower per plant opening per day, this is a costly process. If successful, the bean needs to ripen for 9 months on the plant, and to be cured for another 3–6 months to reach the marketable stage. Harvesting beans is also a labor-intensive task. The vines need to be checked daily to find mature beans that are ready for harvest. The harvested green vanilla beans undergo a curing process that consists of several steps and varies throughout different producer countries (e.g. Ramachandra Rao and Ravishankar, 2000; De La Cruz Medina et al., 2009; Wongshere et al., 2013).

Considerable research has been done on curing to improve vanillin production and relevant biochemical pathways are well defined (Dignium et al., 2001; Walton et al., 2003; Yang et al., 2017), but the pre-harvest aspect is seriously neglected. Current descriptive information suggests that vanilla should not be cultivated in the same way as the most popular orchids; it should instead be grown in humid conditions with shade and constant high temperatures (e.g. Fouché and Jouve, 1999; Cameron, 2011; Havkin-Frenkel and Belanger, 2011). Very recently, additional studies have described optimal growth conditions (e.g. Diez et al., 2017; Ramirez-Mosqueda et al., 2017) and the possibility of production in greenhouses to ensure reliable quality of vanilla (Havkin-Frenkel and Belanger, 2011).

Climate conditions favorable for vanilla also stimulate growth of pathogens, fungi in particular, and present a challenge for production. Advances in phytopathology are needed to prevent serious plant damage from pathogens that can cause crop losses of up to 80%. The most common pathogen is root and stem rot, often caused by Fusarium oxysporum, which has resulted in plantation abandonment in some cases (Pinaria et al., 2010; Cameron, 2011). Development of integrated disease management strategies is urgently needed in vanilla production. Although certain wild types (e.g. V. pompona) and hybrids seem to be resistant to Fusarium, they fail to meet desired bean quality standards (Koyyappurath et al., 2016).

There is strong competition from artificially produced vanillin for flavoring foodstuffs, although natural vanilla is still superior and has many more flavor components than just vanillin. The increased demand of consumers for organic and fair trade products might have a positive effect on maintaining production of natural vanilla (Cameron, 2011; Havkin-Frenkel and Belanger, 2011). This demand, combined with developing research on ecophysiology, phytopathology, and hybridization of vanilla, has the potential to improve vanilla agriculture in the future.

Bromeliaceae – Ananas comosus (L.) Merrill (pineapple)

While there are many plants in the Bromeliaceae family that are used ornamentally, Ananas comosus (L.) Merrill (pineapple) is the most important agricultural crop. Pineapples are probably the most well-known among CAM crops that are commercially produced because they are traded globally as common produce and have substantial economic value (Table 1). While most pineapples are consumed as fresh fruit, canning facilitates transport across long distances and has been used since the early 1900s (Rohrbach et al., 2002). Pineapples have been cultivated as intensively managed monocultures in Indonesia, The Phillipines, Thailand, and Hawaii for a century (Malezieux et al., 2002), but 88 countries currently produce pineapples, with Costa Rica and Brazil leading production in 2016 (FAO, 2018).
The center of diversity for pineapple and most plants in Bromeliaceae is most likely the Guiana Shield in South America, which includes northern Brazil (Coppen d’Eckenbrugge and Leal, 2002). In fact, pineapples are still harvested in the wild and intercropped with other plants in Brazil (Malleux et al., 2002). There are five varieties of the species *Ananas comosus* currently recognized (Coppen d’Eckenbrugge and Leal, 2002), although at least 10 varieties were described by Griffin in 1806 (Rohrbach et al., 2002). The most widespread varieties in cultivation are commonly known as ‘Smooth Cayenne’ and ‘Queen’, both of which are native to the Americas but were then dispersed for agricultural markets throughout Europe (Rohrbach et al., 2002). Most cultivated pineapple is self-incompatible (Brewbaker and Gorez, 1967) and clonally reproduced.

The genome of pineapple was recently sequenced and provides insight into the evolutionary history of CAM (Ming et al., 2015). With the first genome-wide probe of an obligate CAM plant, pineapple emerged as a model for CAM expression and gene regulation patterns (Ming et al., 2015).

Of 1893 species (a little more than half of the total) in Bromeliaceae that were evaluated by Crayn et al. (2015), 20% had plant tissue δ¹³C values that were consistent with CAM activity. There are a wide range of CAM plants in this family that might be useful for fiber or other products, and some are cultivated from wild forests (e.g. Ticktin et al., 2003). While there is potential for developing agricultural crops, non-timber forest products also have advantages for habitat conservation in many areas of the world where species of Bromeliaceae are found. Traditional uses of the many CAM varieties in this family are not consistently documented across the wide geographic range of distribution.

**Technological advances that can facilitate agricultural production in the future**

In response to increasing arid landscapes and the challenges of climate change, there is growing interest in the potential of CAM crops to be cultivated with reduced irrigation for food, fuel, and forage (Borland et al., 2015; Mason et al., 2015). Two strategies are suggested to meet the growing demand for food, bioenergy, and crops for other bioresources in a future climate: the improvement of current CAM crops, and the engineering of CAM into C₃ or C₄ crops as a means of improving their WUE (Borland et al., 2014; Yang et al., 2015b). Recent advances in the understanding of CAM gene expression lay the groundwork for potential genetic engineering of CAM to improve crop tolerance (e.g. Amin et al., 2019; Lim et al., 2019).

To date, CAM crops have undergone the least amount of study (relative to C₃ and C₄ crops) to accomplish genetic improvements, develop models of crop efficiency, maximize yield, and improve commercial viability (Yan et al., 2011; Davis et al., 2015). The potential of CAM to improve WUE in agriculture has only recently been addressed using a systems-based approach. The relatively recent publication of CAM genomes (Ming et al., 2015) and CAM physiological models (e.g. Owen and Griffiths, 2013) is providing a platform to directly engineering towards optimization of current CAM crops through identification and selection of genes controlling traits of interest (Heyduk et al., 2018; Lim et al., 2019).

Previous CAM models described metabolic level (Owen and Griffiths, 2013) and plant level (e.g. Nobel, 1984; Niechayev et al., 2019) processes, but Hartzell et al. (2018) recently developed the open source Photo3 model, which is the first model of productivity and WUE that uses a parallel structure for C₃, C₄, CAM, and C₃/CAM intermediates that takes into account a wide range of environmental conditions, stomatal functioning, and a resistor–capacitor model of the soil–plant–atmosphere continuum (https://samhartz.github.io/Photo3/). Such holistic models allow better understanding of crop productivity across varying climate and ecological conditions and provide insights to direct further research and crop improvement approaches.

The emerging area of genomics-assisted breeding also offers many tools for crop improvement, including the use of DNA markers for marker assisted breeding via single nucleotide polymorphisms and insertion deletions (InDels). High throughput DNA fingerprinting techniques, such as genotyping by sequencing, provide increased marker density, thus facilitating the identification of novel allelic variants for particular traits through linkage analysis or genome-wide association studies (Kole et al., 2015). The resolution provided enables better estimates of phylogenetic relationships and kinship, which in turn contribute to a better understanding of the relationships between CAM and WUE over different eco-geographical locations.

**Current genomic resources available for CAM crops improvement**

Several possible models for the CAM genome have emerged in recent years. Pineapple is one of the most economically important CAM crops, and has whole genome sequencing available (Ming et al., 2015). Pineapple grows across a diverse range of climates with a broad range of genotypes and WUE, and as such contains a wealth of information that could be explored for investigating drought tolerance (Davis et al., 2015). Tsai et al. (2017) highlight the progress in orchid genomics research, with interesting developments that include transcriptome data investigating pod development in the prized vanilla orchid, *Vanilla planifolia* (Rao et al., 2014), and whole genome sequencing for the moth orchid *Phalaenopsis equestris* (Cai et al., 2015; Albert and Carretero-Paulet, 2015). Heyduk et al. (2018) used comparative transcriptomics to determine gene expression difference between CAM and C₃ species of orchids in the *Erycina* genus that are closely related.

Along with the pineapple and orchid genomes, the saguaro cactus has been sequenced, opening an avenue to exploring the genomic background of cacti and the chance for comparative genomic research among different CAM groups. In the case of the long-lived saguaro, researchers have found a genetic pattern that could explain why long-lived columnar cactus classification using simple sets of markers is so intractable (Copetti et al., 2017). Other CAM varieties have proved more difficult to sequence. The ploidy level across *Agave* species ranges from diploid to octoploid and even aneuploid, making complete genome sequencing challenging (Simpson et al., 2011). Transcriptomic
comparisons of A. tequilana, adapted to semi-arid conditions, and A. deserti, adapted to xeric conditions, have been used to model the molecular and physiological adaptations to their environment for the development of bioenergy crops (Gross et al., 2013). The comparison of diel transcriptome, proteome, and metabolome of A. americana with C3 Arabidopsis (Abraham et al., 2016) provides valuable insights for the engineering of CAM into C3 plants for enhanced WUE. Further genomic and transcriptomic resources for A. tequilana and A. sisalana are discussed in Simpson et al. (2011) and Zhou et al. (2012). Kalanchoë fedtschenkoi has been suggested as a model species to study functional genomics of CAM because of the relatively small genome and amenability to stable transformation. It displays developmental CAM, where its youngest leaves are C3-like and transition to become increasingly CAM as they age, with older leaves expressing full CAM. Genomic resources for Kalanchoë have facilitated the functional genomics of many CAM genes (Hartwell et al., 2016). The first transgenic CAM plants with down-regulated CAM-associated genes were made in K. fedtschenkoi using a hairpin RNA transgene RNAi approach for NAD malic-enzyme and pyruvate orthophosphate dikinase (Dever et al., 2015) and phosphoenol pyruvate kinase (Boxall et al., 2017). Genome editing through CRISPR-Cas9 systems have recently been established for K. fedtschenkoi (Liu et al., 2018). High throughput phenotyping and functional characterization of such lines is important for the genetic improvement of CAM plants and for the engineering of CAM into C3 plants.

Following whole genome sequencing of K. fedtschenkoi, Yang et al. (2017) analysed the genomic signatures of convergence shared between eudicot (Kalanchoë) and monocot (pineapple and orchid) CAM species. This comparative analysis provided evolutionary insights into molecular convergence and building blocks of CAM. Yang et al. (2017) identified genes predicted to have undergone convergent evolution during the emergence of CAM from C3 systems, representing crucial candidates for engineering CAM into plants with C3 photosynthesis. The results suggest that rewiring of the diel transcript abundance patterns for most of the candidate genes would be required, while amino acid mutations occurred in some other candidate genes (Yang et al., 2017). The transcriptional and metabolite changes that occur during a drought-induced transition from C3 to CAM in the weak CAM plant Tálium triangular are also demonstrated in Brillhaus et al. (2016). Cascading transcriptional changes are further described as fundamental for the expression of CAM in Erycina spp. (Heydük et al., 2018). Experimental approaches are now required to investigate the effects of the C3-to-CAM transition and to determine the potential for accelerating crop improvement.

Across the agricultural sector, the microbiome and rhizosphere are areas of intensive study to increase nutrient availability and improve plant health and yield. Although key C3 and C4 crops have undergone intense study, less work has been done on CAM to date. Genomic studies of symbiotic relationships between soil bacteria and fungi in Agave and cacti have been suggested as factors that could influence species adaptation to arid environments (Citlali et al., 2018). The main focus to date has been on the biogeography and local biodiversity of these microbial and fungal communities, and studies are now required to determine the benefits of a healthy root zone, rhizosphere, and phyllosphere microbiota to CAM crops.

**Conclusion**

The potential for CAM to support resilient agricultural production far exceeds currently realized levels of production. Agave spp., cacti, orchids, and pineapples provide examples of CAM crops that have high yields, environmental benefits, substantial market value, and international trade networks (respectively). Many CAM crops can thrive even with climate conditions that are intolerable for most C3 and C4 crop species, making these attractive agricultural commodities that can be expanded as climate change continues to progress.

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