



## REVIEW PAPER

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

Sarah C. Davis<sup>1,2,\*</sup>, June Simpson<sup>3</sup>, Katia del Carmen Gil-Vega<sup>3</sup>, Nicholas A. Niechayev<sup>4</sup>, Evelien van Tongerlo<sup>5</sup>, Natalia Hurtado Castano<sup>6</sup>, Louisa V. Dever<sup>7</sup> and Alberto Búrquez<sup>8</sup>

<sup>1</sup> Voinovich School of Leadership and Public Affairs, Ohio University, Athens, OH, USA

<sup>2</sup> Department of Environmental and Plant Biology, Ohio University, Athens, OH, USA

<sup>3</sup> Department of Genetic Engineering, Cinvestav Unidad Irapuato, Irapuato, Guanajuato, México

<sup>4</sup> Department of Biochemistry and Molecular Biology, University of Nevada, Reno, NV, USA

<sup>5</sup> Horticulture and Product Physiology, Wageningen University, Wageningen, The Netherlands

<sup>6</sup> School of Natural and Environmental Sciences, Newcastle University, Newcastle upon Tyne, UK

<sup>7</sup> Department of Functional and Comparative Genomics, Institute of Integrative Biology, University of Liverpool, Liverpool, UK

<sup>8</sup> Instituto de Ecología, Universidad Nacional Autónoma de México, Unidad Hermosillo, Sonora, México

\* Correspondence: [daviss6@ohio.edu](mailto:daviss6@ohio.edu)

Received 5 December 2018; Editorial decision 2 May 2019; Accepted 3 May 2019

Editor: Kevin Hultine, Desert Botanical Garden, USA

## 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 C<sub>4</sub> to CAM (e.g. Koch and Kennedy, 1980; Holtum *et al.*, 2017) and species within the Bromeliaceae range from C<sub>3</sub> 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 (Nyffeler *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 C<sub>3</sub> and C<sub>4</sub> 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 (*cacayas*) 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 (Sidana *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

Table 1. Summary of varieties, uses, environmental tolerance ranges, management requirements, devoted land area, and economic value of CAM species with potential agricultural importance

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 <sup>-1</sup> )
<i>Agave americana</i> L. <sup>a</sup>	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
<i>Agave angustifolia</i> Haw. <sup>b</sup>	>20	Mescal, brooms, fiber or textiles, pulque, rope	22-38	5-50		125-1680	Unknown, not usually applied	Oaxaca	No	~249	206
<i>Agave fourcroydes</i> Lem. <sup>c</sup>	3	Fiber for textiles, rope, fuel, sandals, construction	18-36	-2-40		500-1000	Unknown, leaves and bagasse	Yucatan	No	~15 000	12.6
<i>Agave mapisaga</i> Trel. <sup>d</sup>	1	Pulque, fiber, cattle feed, food, construction	12-16		700		Unknown, manure	Central Mexico	No	None commercial	Unknown
<i>Agave salmiana</i> Otto ex Salm-Dyck <sup>e</sup>	4	Pulque, mescal, food, jewellery, toys, decoration, ornamentals, fuel, poultice	12-16			125-800	Unknown	San Luis Potosi and Hidalgo	No	~59 000	0.063
<i>Agave sisalana</i> Perrine <sup>f</sup>	2	Fiber for textiles, ornamental, medicine	35-40	5-40	1200	500-800	Variable	Unknown, introduced from Mexico	No	331 330	111
<i>Agave tequilana</i> Weber var. azul <sup>g</sup>	7	Tequila, fuel, sweeteners	30 day/15 night	-3->50		700	40-60 kg N ha <sup>-1</sup> year <sup>-1</sup> , other nutrients depend on soils	Jalisco	No	330 000	314
<i>Aloe</i> spp. <sup>h</sup>	360 species	Burns, digestion, inflammation, wounds, diabetes, immunity, antitumorogenic, cosmetics, ornamental, phytotherapy	Variable	Variable	150 ml kg <sup>-1</sup> plant	>100	Manure used at 5-10 Mg ha <sup>-1</sup>	Southern Africa, Arabian peninsula	Partially		100 (raw) 125 000 (in products)
<i>Aloe barbadensis</i> <sup>i</sup>			19-27	10-30	1900-3000		80-40-80 or NPK		Partially		
<i>Ananas comosus</i> (L.) Merrill <sup>j</sup>	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 <sup>-1</sup> to soil, 200-600 kg N ha <sup>-1</sup> year <sup>-1</sup> to leaves; 25-100 kg P ha <sup>-1</sup>	Guiana Shield in South America	Partially	1 122 520	3351
Cactaceae family (except <i>Opuntia</i> ) <sup>k</sup>	>>100 wild species, 12 domesticated, many man-aged	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

Table 1. Continued

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 <sup>-1</sup> )
<i>Opuntia ficus-indica</i> <sup>i</sup>	81	Food, beverages, cosmetics, forage, pharmaceuticals	25 day/15 night	−7–65	500		50–100 kg N ha <sup>-1</sup> year <sup>-1</sup> , 10–30 kg P ha <sup>-1</sup> year <sup>-1</sup> , 20–50 kg K ha <sup>-1</sup> year <sup>-1</sup> , 10–50 kg ha <sup>-1</sup> year <sup>-1</sup> , Ca at planting	Central Mexico	No	>600 000	2520
Orchidaceae family <sup>m</sup>	>29 000 species	Ornamental (both cut flowers and potted plants), food, medicinal use, ceremonial use	Variable	Variable	Variable	Variable	Variable	Tropical humid climates	Only for ornamental		
<i>Vanilla</i> Mill. <sup>n</sup>	107 species	Food, spice, medicine, woven figures and baskets	21–32	10–33	>1500	>1500	Unknown, mulch and compost	Central Mexico	No	93 119	762

<sup>a</sup> Gentry, 1982; Ocaña-Nava et al., 2007; Escamilla-Treviño, 2012; Hamissa et al., 2012.  
<sup>b</sup> Gentry, 1982; Colunga-GarcíaMarín et al., 1999; Aguirre et al., 2001; Bautista-Cruz et al., 2007; Eguiarte and Souza, 2007; Palmirino et al., 2007; Zizumbo-Villarreal and Colunga-GarcíaMarín, 2007; Rivera-Lugo et al., 2018.  
<sup>c</sup> Colunga-GarcíaMarín et al., 1993; Colunga-GarcíaMarín and May-Pat, 1993; Irish and Irish, 2000.  
<sup>d</sup> Cruz-Ramírez et al., 2006; Aguilar-Juárez et al., 2014.  
<sup>e</sup> Gentry, 1982; Ocaña-Nava et al., 2007; Aguilar-Juárez et al., 2014; Esparza-Ibarra, 2015.  
<sup>f</sup> Gentry, 1982; Debnath et al., 2010.  
<sup>g</sup> Valenzuela-Zapata, 1994; Valenzuela-Zapata, 1997; Mancilla-Margalli and López, 2006; Bautista-Cruz et al., 2007; Pimental-Barrios et al., 2007; Holtum et al., 2011; Núñez et al., 2011.  
<sup>h</sup> Grindlay and Reynolds, 1986; Ahlawat and Khatkar, 2011; Liontakis et al., 2016; Katerere, 2018.  
<sup>i</sup> Saha et al., 2005; Ahlawat and Khatkar, 2011.  
<sup>j</sup> Bartholomew et al., 2002; Ming et al., 2015; FAOSTAT, 2018.  
<sup>k</sup> Casas and Barbera, 2002; Nerd et al., 2002.  
<sup>l</sup> Nobel and Israel, 1994; Nobel, 2002; Nobel and De la Barrera, 2003; Griffith, 2004; Stintzing and Carle, 2005; Feugang et al., 2006; Aguilera-Barreiro et al., 2013; Yang et al., 2015a; Arba et al., 2017; Inglesse et al., 2017.  
<sup>m</sup> Arditti, 1992; De La Cruz Medina et al., 2009; Silvera et al., 2009; Swarts and Dixon, 2009; De et al., 2014; Fay, 2018.  
<sup>n</sup> Fouché and Jouve, 1999; Cameron, 2011.



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. mapisaga*, *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 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. vivipara* L.) in Sonora, *A. salmiana* in Zacatecas, San Luis Potosí, and Guanajuato (Aguirre *et al.*, 2001; Aguilar-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<sup>-1</sup> year<sup>-1</sup> (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 by 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 (Zuñiga-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 *Phyllophaga* spp., *Pseudococcus* spp., *Acutaspis 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*, *Metarhizium anisopliae*, and *Chilocorus 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 (*Erwinia* 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 sisal, 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 Yucatán 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 decortication 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. kewensis* (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* × *A. angustifolia*) × *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<sup>-1</sup> year<sup>-1</sup> 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 (Bunyaphatsara 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 (Liontakis 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  $\delta^{13}\text{C}$  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. *natalensi* Berger (Eshun and He, 2004; Nejatzadeh-Barandozi et al., 2012; Sánchez-Machado et al., 2017), that is poorly understood.

## *Aloe barbadensis* Miller

*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; Añez and Vázquez, 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 year<sup>-1</sup>. 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 (Nayanakantha *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 Opuntoid 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 Hylocereae) 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 opuntoid 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 cacti 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 cacti 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 *sahuero*, 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 Guarijío, the *etcho* (*Pachycereus pecten-aboriginum*) is of paramount importance, and the *sahuira* (*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 *copao* (*Eulychnia acida*) from northern Chile have less than 1% sugar content (Salvatierra *et al.*, 2010) and the fruit of *Jasminocereus thouarsii*, endemic to the Galápagos Islands, is less than 3% sugar (AB, pers. obs.). The *pasakanas* and *cardón* fruits of *Echinopsis* spp., *Corryocactus* spp., and *Browningia candelaris* among other South American species are eaten with sugar added, and the acidity of the fruit of *pichaja* (*Oreocereus 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 *pitaya* fruits, mainly from *Stenocereus pruinosus*, *S. queretaroensis*, 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* Salm-Dyck, *O. amyclaea* Tenore, *O. streptacantha* Lemaire, *O. stricta* Haw, *O. dilennei* (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 Metzger, 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 *nopales*) 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 ca 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<sup>-1</sup> year<sup>-1</sup> of water (Dubeux *et al.*, 2017).

The commercial varieties produced in Mexico for human consumption include Milpa Alta, COPENA V-1, COPENA



F-1, Atlixco, Jalpa, Esmeralda, and Blanco de Valtierra. This crop is ranked sixth in volume of production of vegetables and eighth in value of the production after the tomato, green chili, potato, onion, zucchini, and asparagus. The fresh product is sold in the domestic market with a consumption per capita of  $6.4 \text{ kg year}^{-1}$ , and used in different foods such as creams, soups, salads, stews, sauces, drinks, and desserts (Berger *et al.*, 2013; Dubeux *et al.*, 2017).

The cladodes are harvested between 1 and 3 years after the 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  $15\text{--}95 \text{ kg day}^{-1}$  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  $47.3 \text{ Mg ha}^{-1} \text{ year}^{-1}$  (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 (Brulfert *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 predominantly in arid and semi-arid zones tolerating temperatures up to  $65^\circ\text{C}$ , 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  $100 \text{ mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ , compared with  $\text{C}_3$  and  $\text{C}_4$  plants ( $1\text{--}1.5$  and  $2\text{--}3 \text{ mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ , respectively), allowing growth in zones with a mean annual precipitation of 250–700 mm (Yahia and Sáenz, 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 (Pimienta-Barrios, 1994; Yahia and Sáenz, 2011).

The average yield of the commercially produced fruit (prickly pear) in Mexico is around  $7 \text{ tons ha}^{-1}$  with a range across different producing regions of  $5\text{--}20 \text{ tons ha}^{-1}$  (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; Mejía 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; Wongsheree *et al.*, 2013).

Considerable research has been done on curing to improve vanillin production and relevant biochemical pathways are well defined (Dignum *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. Díez *et al.*, 2017; Ramírez-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 Philippines, 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 (Coppens d'Eckenbrugge and Leal, 2002). In fact, pineapples are still harvested in the wild and intercropped with other plants in Brazil (Malezieux *et al.*, 2002). There are five varieties of the species *Ananas comosus* currently recognized (Coppens 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  $\delta^{13}\text{C}$  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  $\text{C}_3$  or  $\text{C}_4$  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  $\text{C}_3$  and  $\text{C}_4$  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 direct

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  $\text{C}_3$ ,  $\text{C}_4$ , CAM, and  $\text{C}_3/\text{CAM}$  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 aided selection 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  $\text{C}_3$  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 *C<sub>3</sub>* *Arabidopsis* (Abraham et al., 2016) provides valuable insights for the engineering of CAM into *C<sub>3</sub>* 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 *C<sub>3</sub>*-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 *C<sub>3</sub>* 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 *C<sub>3</sub>* systems, representing crucial candidates for engineering CAM into plants with *C<sub>3</sub>* 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 *C<sub>3</sub>* to CAM in the weak CAM plant *Talinum triangulare* are also demonstrated in Brilhaus et al. (2016). Cascading transcriptional changes are further described as fundamental for the expression of CAM in *Erycina* spp. (Heyduk et al., 2018). Experimental approaches are now required to investigate the effects of the *C<sub>3</sub>*-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 *C<sub>3</sub>* and *C<sub>4</sub>* 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 *C<sub>3</sub>* and *C<sub>4</sub>* crop species, making these attractive agricultural commodities that can be expanded as climate change continues to progress.

## Acknowledgements

We would like to acknowledge and thank all of the participants of The Biology of CAM Plants conference that convened at the Desert Botanical Gardens on 9–13 April 2018. This conference was sponsored by the *Journal of Experimental Botany*. EvT was supported by the Netherlands Organization for Scientific Research (NWO), Anthura, Signify, Imac and B-Mex. *Agave* research by JSW and KCGV is supported by CONACYT Grant 220339. AB received funding from Programa de Apoyos a Proyectos de Investigación e Innovación Tecnológica PAPIIT-DGAPA IN-213814 and The Consortium for Arizona-Mexico Arid Environments during a sabbatical leave supported by DGAPA-Universidad Nacional Autónoma de México. NHC was funded by a grant from Colciencias, Colombia. LVD was funded by the Department of Energy (DOE) Office of Science, Genomic Science Program under award number DE-SC0008834.

## References

- Abraham PE, Yin H, Borland AM, et al. 2016. Transcript, protein and metabolite temporal dynamics in the CAM plant *Agave*. *Nature Plants* **2**, 16178.
- Aguilar-Juárez B, Enríquez del Valle JR, Rodríguez-Ortiz G, Granados Sánchez D, Martínez Cerero B. 2014. The current state of *Agave salmiana* and *A. mapisaga* in the Valley of Mexico. *Revista Mexicana de Agroecosistemas* **1**, 106–120.
- Aguilera-Barreiro MA, Rivera-Márquez JA, Trujillo-Arriaga HM, Tamayo y Orozco JA, Barreira-Mercado E, Rodríguez-García ME. 2013. Intake of dehydrated nopal (*Opuntia ficus indica*) improves bone mineral density and calciuria in adult Mexican women. *Food & Nutrition Research*, **57**, 19106.
- Aguirre RJR, Charcas SH, Flores FJL. 2001. El maguey mezcalero potosino. Consejo Potosino de Ciencia y Tecnología. San Luis Potosí, México: Universidad Autónoma de San Luis Potosí. México.
- Ahluwat KS, Khatkar BS. 2011. Processing, food applications and safety of aloe vera products: a review. *Journal of Food Science and Technology* **48**, 525–533.
- Albert VA, Carretero-Paulet L. 2015. A genome to unveil the mysteries of orchids. *Nature Genetics* **47**, 3–4.
- Albesiano S, Kiesling R. 2012. Identity and neotypification of *Cereus macrogonus*, the type species of the genus *Trichocereus* (Cactaceae). *Haseltonia* **17**, 24–34.
- Amin AB, Rathnayake KN, Yim WC, Garcia TM, Wone B, Cushman JC, Wone BW. 2019. Crassulacean acid metabolism abiotic stress-responsive transcription factors: a potential genetic engineering approach for improving crop tolerance to abiotic stress. *Frontiers in Plant Science* **10**, 129.
- Añez B, Vásquez J. 2005. Efecto de la densidad de población sobre el crecimiento y rendimiento de la zábila (*Aloe barbadensis* M.). *Revista de la Facultad de Agronomía de la Universidad del Zulia* **22**, 1–12.



- Anneck DP, Moran VC. 1978. Critical review of biological pest control in South Africa. 2. The prickly pear, *Opuntia ficus-indica* (L.) Miller. *Journal of the Entomological Society of Southern Africa* **41**, 161–188.
- Arba M, Falisse A, Choukr-Allah R, Sindic M. 2017. Biology, flowering and fruiting of the cactus *Opuntia* spp.: a review and some observations on three varieties in Morocco. *Brazilian Archives of Biology and Technology* **60**, <http://dx.doi.org/10.1590/1678-4324-2017160568>.
- Arditti J. 1992. *Fundamentals of orchid biology*. New York: John Wiley & Sons.
- Bartholomew DP, Paull RE, Rohrbach KG, eds. 2002. *The pineapple: botany, production, and uses*. Wallingford, UK: CABI Publishing.
- Bautista-Cruz A, Carrillo-González R, Arnaud-Viñas MR, Robles C, de León-González F. 2007. Soil fertility properties on *Agave angustifolia* Haw. Plantations. *Soil & Tillage Research* **96**, 342–349.
- Berger H, Rodríguez-Félix A, Galletti L. 2013. Field operations and utilization of cactus cladodes. In: Saenz C, ed, *Agro-industrial utilization of cactus pear*. Rome: Food and Agriculture Organization of the United Nations, 21–29.
- Bernal SJ, Orozco Hernández A, del Real Laborde JI, González Hernández H, eds. 2006. *Estado Actual del Manejo de Plagas y Enfermedades del Agave Tequilero: Memorias Simposio Prioridades Fitosanitarias Actuales en el cultivo de Agave tequilana* Weber var. Azul. XXIX Congreso Nacional de Control Biológico. Jalisco, Mexico: Colegio de Posgraduados and Tequila Sauza SA de CV.
- Borland AM, Griffiths H, Hartwell J, Smith JA. 2009. Exploiting the potential of plants with crassulacean acid metabolism for bioenergy production on marginal lands. *Journal of Experimental Botany* **60**, 2879–2896.
- Borland AM, Hartwell J, Weston DJ, Schlauch KA, Tschaplinski TJ, Tuskan GA, Yang X, Cushman JC. 2014. Engineering crassulacean acid metabolism to improve water-use efficiency. *Trends in Plant Science* **19**, 327–338.
- Borland AM, Wulschleger SD, Weston DJ, Hartwell J, Tuskan GA, Yang X, Cushman JC. 2015. Climate-resilient agroforestry: physiological responses to climate change and engineering of crassulacean acid metabolism (CAM) as a mitigation strategy. *Plant, Cell & Environment* **38**, 1833–1849.
- Bos JJ, Lensing FHG. 1973. A new cultivar in sisal from East Africa: *Agave sisalana* Perr. Ex Engelm. Cv. Hildana. *East African Agricultural and Forestry Journal* **39**, 17–25.
- Boudreau MD, Olson GR, Tryndyak VP, Bryant MS, Felton RP, Beland FA. 2017. From the cover: aloin, a component of the aloe vera plant leaf, induces pathological changes and modulates the composition of microbiota in the large intestines of F344/N male rats. *Toxicological Sciences* **158**, 302–318.
- Boxall SF, Dever LV, Kneřová J, Gould PD, Hartwell J. 2017. Phosphorylation of phosphoenolpyruvate carboxylase is essential for maximal and sustained dark CO<sub>2</sub> fixation and core circadian clock operation in the obligate crassulacean acid metabolism species *Kalanchoe fedtschenkoi*. *The Plant Cell* **29**, 2519–2536.
- Brewbaker JL, Gorrez DD. 1967. Genetics of self-incompatibility in the monocot genera *Ananas* (pineapple) and *Gasteria*. *American Journal of Botany* **80**, 41–44.
- Brilhaus D, Bräutigam A, Mettler-Altmann T, Winter K, Weber AP. 2016. Reversible burst of transcriptional changes during induction of crassulacean acid metabolism in *Talinum triangulare*. *Plant Physiology* **170**, 102–122.
- Brink M, Achigan-Dako EG. 2012. *Plant resources of tropical Africa*, Vol. 16, *Fibres*. Wageningen, Netherlands: PROTA Foundation.
- Bruhn J. 1971. *Carnegiea gigantea*; the saguaro and its uses. *Economic Botany* **25**, 320–329.
- Bulfert J, Kluge M, Guerrier D, Queiroz O. 1987. Characterization of carbon metabolism in *Opuntia ficus-indica* Mill. exhibiting the idling mode of Crassulacean acid metabolism. *Planta* **170**, 92–98.
- Bunyapraphatsara N, Yongchaiyudha S, Rungpitarangsi V, Chokechaijaroenporn O. 1996. Antidiabetic activity of *Aloe vera* L. juice II. Clinical trial in diabetes mellitus patients in combination with glibenclamide. *Phytomedicine* **3**, 245–248.
- Cai J, Liu X, Vanneste K, et al. 2015. The genome sequence of the orchid *Phalaenopsis equestris*. *Nature Genetics* **47**, 65–72.
- Cameron K. 2011. *Vanilla orchids: natural history and cultivation*. Portland: Timber Press.
- Casas A, Barbera G. 2002. Mesoamerican domestication and diffusion. In: Nobel PS, ed. *Cacti: biology and uses*. Berkeley, CA, USA: University of California Press, 143–162.
- Chandra D, Choudhary P. 2014. Diversity analysis of different accessions of *Aloe barbadensis* Mill.(syn. *Aloe vera* L.) collected from Rajasthan using RAPD marker system. *The Bioscan* **9**, 7–10.
- Choi SW, Son BW, Son YS, Park YI, Lee SK, Chung MH. 2001. The wound-healing effect of a glycoprotein fraction isolated from aloe vera. *The British Journal of Dermatology* **145**, 535–545.
- Citlali F-G, Desgarenes D, Flores-Núñez VM, Partida-Martínez LP. 2018. The microbiome of desert CAM plants: lessons from amplicon sequencing and metagenomics. *Metagenomics, Perspectives, Methods and Applications* **12**, 231–254.
- Colunga-GarcíaMarín P. 2003. The domestication of henequen (*Agave fourcroydes* Lem.) In: Gomez-Pompa A, Allen M, Fedick S, Jimenez-Osorio J, eds. *The lowland Maya area: three millennia at the human-wildland interface*. New York: Food Products Press, 439–446.
- Colunga-GarcíaMarín P, Coello-Coello J, Eguarte LE, Piñero D. 1999. Isozymatic variation and phylogenetic relationships between henequen (*Agave fourcroydes*) and its wild ancestor *A. angustifolia* (Agavaceae). *American Journal of Botany* **86**, 115–123.
- Colunga-GarcíaMarín P, Coello-Coello J, Espejo-Peniche L, Fuente-Moreno L. 1993. Agave studies in Yucatan, Mexico II. Nutritional value of the inflorescence peduncle and incipient domestication. *Economic Botany* **47**, 328–334.
- Colunga-GarcíaMarín P, May-Pat F. 1993. Agave studies in Yucatan, Mexico I. Past and present germplasm diversity and uses. *Economic Botany* **47**, 312–327.
- Copetti D, Búrquez A, Bustamante E, et al. 2017. Extensive gene tree discordance and hemiplasy shaped the genomes of North American columnar cacti. *Proceedings of the National Academy of Sciences, USA* **114**, 12003–12008.
- Coppens d'Eckenbrugge G, Leal F. 2002. Morphology, anatomy, and taxonomy. In: Bartholomew DP, Paull RE, Rohrbach KG, eds. *The pineapple: botany, production, and uses*. Wallingford, UK: CABI Publishing, 13–32.
- Crayn DM, Winter K, Schulte K, Smith JAC. 2015. Photosynthetic pathways in Bromeliaceae: phylogenetic and ecological significance of CAM and C<sub>3</sub> based on carbon isotope ratios for 1892 species. *Botanical Journal of the Linnean Society* **178**, 169–221.
- CRT. 2018. Consejo Regulador del Tequila. <https://www.crt.org.mx/>.
- Cruz-García H, Enríquez-del Valle JR, Velasco Velasco VA, Ruiz Luna J, Campos Ángeles GV, Aquino García DE. 2013. Nutrients and carbohydrates in plants from *Agave angustifolia* Haw. and *Agave karwinskii* Zucc. *Revista Mexicana de Ciencias Agrícolas* **6**, 1161–1173.
- Cruz-Ramírez LA, Valdez-Morales M, Chacón-López MA, Rosas-Cárdenas FF, Cruz-Hernández A. 2006. Mexican Crops of agroalimentary importance. In: Guevara-González RG, Torres-Pacheco I, eds. *Advances in agricultural and food biotechnology*. Trivandrum, Kerala, India: Research Signpost, 35–53.
- Cushman JC, Davis SC, Yang X, Borland AM. 2015. Development and use of bioenergy feedstocks for semi-arid and arid lands. *Journal of Experimental Botany* **66**, 4177–4193.
- Davis SC, Dohleman F, Long S. 2010. The global potential for *Agave* as a biofuel feedstock. *GCB Bioenergy* **3**, 68–78.
- Davis SC, Kloepper JE, Mayer JA, Cushman JC. 2018. Diversifying agriculture with novel crop introductions to abandoned lands with sub-optimal conditions. In: Benkeblia N, ed. *Climate change and crop production*. Foundations for Agroecosystem Resilience. Boca Raton: CRC Press, 163–172.
- Davis SC, Kuzmick ER, Niechayev NA, Hunsaker DJ. 2016. Productivity and water use efficiency of *Agave americana* in the first field trial as bio-energy feedstock on arid lands. *GCB Bioenergy* **9**, 314–325.
- Davis SC, LeBauer DS, Long SP. 2014. Light to liquid fuel: theoretical and realized energy conversion efficiency of plants using crassulacean acid metabolism (CAM) in arid conditions. *Journal of Experimental Botany* **65**, 3471–3478.
- Davis SC, Ming R, LeBauer DS, Long SP. 2015. Toward systems-level analysis of agricultural production from crassulacean acid metabolism (CAM): scaling from cell to commercial production. *New Phytologist* **208**, 66–72.

- De LC, Pathak P, Rao AN, Rajeevan PK.** 2014. Commercial orchids. Berlin, Boston: De Gruyter.
- Debnath M, Pandey M, Sharma R, Thakur GS, Lal P.** 2010. Biotechnological intervention of *Agave sisalana*: a unique fiber yielding plant with medicinal property. *Journal of Medicinal Plants Research* **4**, 177–187.
- De La Cruz Medina J, Rodriguez Jiménez GC, García HS.** 2009. Vanilla: post-harvest operations. Rome: Food and Agriculture Organization of the United Nations.
- Dever LV, Boxall SF, Kneřová J, Hartwell J.** 2015. Transgenic perturbation of the decarboxylation phase of Crassulacean acid metabolism alters physiology and metabolism but has only a small effect on growth. *Plant Physiology* **167**, 44–59.
- Díez MC, Moreno F, Gantiva E.** 2017. Effects of light intensity on the morphology and CAM photosynthesis of *Vanilla planifolia* Andrews. *Revista Facultad Nacional de Agronomía* **70**, 8023.
- Dignum MJW, Kerler J, Verpoorte R.** 2001. Vanilla production: technological, chemical, and biosynthetic aspects. *Food Reviews International* **17**, 119–120.
- Duarte O, Paull RE.** 2015. Exotic fruits and nuts of the new world, Chapter 2, Calophyllaceae, Clusiaceae and Cactaceae. Wallingford, UK: CABI.
- Dubeux JCB, dos Santos MVF, de Andrade Lira M, dos Santos DC, Farias I, Lima LE, Ferreira RLC.** 2006. Productivity of *Opuntia ficus-indica* (L.) Miller under different N and P fertilization and plant population in north-east Brazil. *Journal of Arid Environments* **67**, 357–372.
- Dubeux JCB Jr, Salem HB, Nefzaoui A.** 2017. Forage production and supply for animal nutrition. In: Inglese P, Mondragon-Jacobo C, Nefzaoui A, eds, Crop ecology, cultivation and uses of cactus pear. Rome: Food and Agriculture Organization of the United Nations and International Center for Agricultural Research in the Dry Areas, 73–92.
- Edwards EJ, Ogburn RM.** 2012. Angiosperm responses to a low CO<sub>2</sub> world: CAM and C<sub>4</sub> photosynthesis as parallel evolutionary trajectories. *International Journal of Plant Science* **173**, 724–733.
- Eguiarte LE, Souza V.** 2007. Historia natural del Agave y sus parientes: Evolución y Ecología. In: Colunga-GarcíaMarín P, Eguiarte L, Larqué-S. A y Zizumbo-Villareal D, eds, En lo ancestral hay futuro: del tequila, los mezcales y otros agaves. México City: CICY-CONACYT-CONABIO-INE, 3–22.
- Escalante A, López Soto DR, Velázquez Gutiérrez JE, Giles-Gómez M, Bolívar F, López-Munguía A.** 2016. Pulque, a traditional Mexican alcoholic fermented beverage: historical, microbiological, and technical aspects. *Frontiers in Microbiology* **7**, 1026.
- Escamilla-Treviño LL.** 2012. Potential of plants from the genus *Agave* as bioenergy crops. *Bioenergy Research* **5**, 1–9.
- Eshun K, He Q.** 2004. *Aloe vera*: A valuable ingredient for the food, pharmaceutical, and cosmetic industries – A review. *Critical Reviews in Food Science and Nutrition* **44**, 91–96.
- Esparza-Ibarra EL, Violante-González J, Monks S, Iñiguez JC, Araujo-Andrade C, Rössel-Kipping ED.** 2015. Los agaves mezcaleros del altiplano Potosino y Zacatecano. In: Pulido-Flores G, Monks S, López-Herrera M, eds. Estudios en biodiversidad. Lincoln, NE, USA: Zea Books, 227–245.
- Evans S.** 2007. Bound in twine: the history and ecology of the henequen-wheat complex for Mexico and the American and Canadian Plains, 1880–1950. College Station: Texas A&M University Press.
- FAO.** 2018. FAOSTAT. Rome: Food and Agriculture Organization of the United Nations. [www.fao.org/faostat/](http://www.fao.org/faostat/)
- Fay MF.** 2018. Orchid conservation: how can we meet the challenges in the twenty-first century? *Botanical Studies* **59**, 16.
- Felger RS, Moser MB.** 1985. People of the desert and sea. Ethnobotany of the Seri Indians. Tucson, AZ, USA: University of Arizona Press.
- Feugang JM, Konarski P, Zou D, Stintzing FC, Zou C.** 2006. Nutritional and medicinal use of Cactus pear (*Opuntia* spp.) cladodes and fruits. *Frontiers in Bioscience* **11**, 2574–2589.
- Fouché JG, Jouve L.** 1999. *Vanilla planifolia*: history, botany and culture in Reunion island. *Agronomie* **19**, 689–703.
- Galizzi FA, Felker P, González C, Gardiner D.** 2004. Correlations between soil and cladode nutrient concentrations and fruit yield and quality in cactus pears, *Opuntia ficus indica* in a traditional farm setting in Argentina. *Journal of Arid Environments* **59**, 115–132.
- García-Mendoza A.** 2007. Los agaves de México. *Ciencias* **87**, 14–23.
- Gentry SH.** 1982. Agaves of Continental North America. Tucson, AZ, USA: University of Arizona Press.
- Giannakoudakis DA, Hosseini-Bandegharai A, Tsafrakidou P, Triantafyllidis KS, Kornaros M, Anastopoulos I.** 2018. *Aloe vera* waste biomass-based adsorbents for the removal of aquatic pollutants: a review. *Journal of Environmental Management* **227**, 354–364.
- Gibson AC, Nobel PS.** 1986. The cactus primer. Cambridge: Harvard University Press.
- Grace OM, Buerki S, Symonds MR, et al.** 2015. Evolutionary history and leaf succulence as explanations for medicinal use in aloes and the global popularity of *Aloe vera*. *BMC Evolutionary Biology* **15**, 29.
- Greene RA.** 1936. The composition and uses of the fruit of the giant cactus, *Carnegiea gigantea* and its products. *Journal of Chemical Education* **13**, 309–312.
- Griffith MP.** 2004. The origins of an important cactus crop, *Opuntia ficus-indica* (Cactaceae): new molecular evidence. *American Journal of Botany* **91**, 1915–1921.
- Grindlay D, Reynolds T.** 1986. The *Aloe vera* phenomenon: a review of the properties and modern uses of the leaf parenchyma gel. *Journal of Ethnopharmacology* **16**, 117–151.
- Gross SM, Martin JA, Simpson J, Abraham-Juarez MJ, Wang Z, Visel A.** 2013. De novo transcriptome assembly of drought tolerant CAM plants, *Agave deserti* and *Agave tequilana*. *BMC Genomics* **14**, 563.
- Guevara JC, Silva Colomer JH, Juárez MC, Estevez OR.** 2003. *Opuntia ellisiana*: cold hardiness, above-ground biomass production and nutritional quality in the Mendoza plain, Argentina. *Journal of Professional Association for Cactus Development* **5**, 55–64.
- Guzmán Loayza D, Chávez J.** 2007. Estudio bromatológico del cladodio del nopal (*Opuntia ficus-indica*) para el consumo humano. *Revista de la Sociedad Química del Perú* **73**, 41–45.
- Hamissa AMB, Seffen M, Aliakbarian B, Casazza AA, Perego P, Converti A.** 2012. Phenolics extraction from *Agave americana* (L.) leaves using high-temperature, high-pressure reactor. *Food and Bioproducts Processing* **90**, 17–21.
- Hartwell J, Dever LV, Boxall SF.** 2016. Emerging model systems for functional genomics analysis of Crassulacean acid metabolism. *Current Opinion in Plant Biology* **31**, 100–108.
- Hartzell S, Bartlett MS, Porporato A.** 2018. Unified representation of the C<sub>3</sub>, C<sub>4</sub>, and CAM photosynthetic pathways with the Photo3 model. *Ecological Modelling* **384**, 173–187.
- Havkin-Frenkel D, Belanger FC.** 2011. Handbook of vanilla science and technology. Oxford: Wiley-Blackwell.
- Heyduk K, Hwang M, Albert V, Silvera K, Lan T, Farr K, Chang TH, Chan MT, Winter K, Leebens-Mack J.** 2018. Altered gene regulatory networks are associated with the transition from C<sub>3</sub> to crassulacean acid metabolism in *Erycina* (Oncidiinae: Orchidaceae). *Frontiers in Plant Science* **9**, 2000.
- Hinsley A, de Boer HJ, Fay MF, et al.** 2017. A review of the trade in orchids and its implications for conservation. *Botanical Journal of the Linnean Society* **186**, 435–455.
- Hinsley A, Verissimo D, Roberts DL.** 2015. Heterogeneity in consumer preferences for orchids in international trade and the potential for the use of market research methods to study demand for wildlife. *Biological Conservation* **190**, 80–86.
- Hodgson WC.** 2001. Food plants of the Sonoran Desert. Tucson, AZ, USA: The University of Arizona Press.
- Holtum JA, Chambers D, Morgan T, Tan DK.** 2011. Agave as a biofuel feedstock in Australia. *GCB Bioenergy* **3**, 58–67.
- Holtum JAM, Hancock LP, Edwards EJ, Winter K.** 2017. Optional use of CAM photosynthesis in two C<sub>4</sub> species, *Portulaca cyclophylla* and *Portulaca digyna*. *Journal of Plant Physiology* **214**, 91–96.
- Huazano GA, López MG.** 2015. Agavins reverse the metabolic disorders in overweight mice through the increment of short chain fatty acids and hormones. *Food & Function* **12**, 3720–3727.
- Hussain A, Sharma C, Saniyah K, Kruti S, Shafiul H.** 2015. *Aloe vera* inhibits proliferation of human breast and cervical cancer cells and acts synergistically with cisplatin. *Asian Pacific Journal of Cancer Prevention* **16**, 2939–2946.



- Irish G, Irish M.** 2000. Agaves, yuccas and related plants. A gardener's guide. Portland, Oregon: Timber Press.
- Inglese P, Barbera G, La Mantia T.** 1995. Research strategies for the improvement of cactuspear (*Opuntia ficus-indica*) fruit quality and production. *Journal of Arid Environments* **29**, 455–468.
- Inglese P, Mondragon C, Nefzaoui A, Saenz C.** 2017. Crop ecology, cultivation and uses of cactus pear. Advance draft prepared for the IX International Congress on Cactus Pear and Cochineal: CAM crops for a hotter and drier world, Coquimbo, Chile, 26–30 March 2017. Rome: Food and Agriculture Organization of the United Nations and the International Center for Agricultural Research in the Dry Areas. <http://www.fao.org/3/a-i7012e.pdf>
- Javed S, Atta-ur-Rahman.** 2014. Aloe vera gel in food, health products, and cosmetics industry. *Studies in Natural Products Chemistry* **41**, 261–285.
- Jin ZM, Wang CH, Liu ZP, Gong WJ.** 2007. Physiological and ecological characters studies on *Aloe vera* under soil salinity and seawater irrigation. *Process Biochemistry* **42**, 710–714.
- Katerere R.** 2018. Commercialization of plant-based medicines in South Africa. In: Wambebe C, ed. African indigenous medical knowledge and human health. Boca Raton: CRC Press, 143–150.
- Kiesling R, Metzger D.** 2017. Origin and taxonomy of *Opuntia ficus-indica*. In: Inglese P, Mondragon-Jacobo C, Nefzaoui A, Saenz C, eds, Crop ecology, cultivation and uses of cactus pear. Rome: Food and Agriculture Organization of the United Nations and International Center for Agricultural Research in the Dry Areas, 13–20.
- Kirtman B, Power SB, Adedoyin JA, et al.** 2013. Near-term climate change: projections and predictability. In: Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM, eds, Climate change 2013: the physical science basis. Contribution of Working Group I to the fifth assessment report of the intergovernmental panel on climate change. Cambridge, New York: Cambridge University Press, 953–1028.
- Kluge M, Ting IP.** 1978. Crassulacean acid metabolism. Analysis of an ecological adaptation. Berlin: Springer-Verlag.
- Koch K, Kennedy RA.** 1980. Characteristics of crassulacean acid metabolism in the succulent  $C_4$  dicot, *Portulaca oleracea* L. *Plant Physiology* **65**, 193–197.
- Kole C, Muthamilarasan M, Henry R, et al.** 2015. Application of genomics-assisted breeding for generation of climate resilient crops: progress and prospects. *Frontiers in Plant Science* **6**, 563.
- Koyyappurath S, Atuahiva T, Le Guen R, et al.** 2016. *Fusarium oxysporum* f. sp. *radicis-vanillae* is the causal agent of root and stem rot of vanilla. *Plant Pathology* **65**, 612–625.
- Lim SD, Lee S, Choi WG, Yim WC, Cushman JC.** 2019. Laying the foundation for crassulacean acid metabolism (CAM) biodesign: expression of the  $C_4$  metabolism cycle genes of CAM in *Arabidopsis*. *Frontiers in Plant Science* **10**, 101.
- Liontakis A, Tzouramani I, Liontakis A, Tzouramani I.** 2016. Economic sustainability of organic *Aloe vera* farming in Greece under risk and uncertainty. *Sustainability* **8**, 338.
- Liu D, Palla KJ, Hu R, et al.** 2018. Perspectives on the basic and applied aspects of crassulacean acid metabolism (CAM) research. *Plant Science* **274**, 394–401.
- Liu H, Luo Y-B, Heinen J, Bhat M, Liu Z-J.** 2014. Eat your orchid and have it too: a potentially new conservation formula for Chinese epiphytic medicinal orchids. *Biodiversity and Conservation* **23**, 1215–1228.
- Lopez RG, Runkle ES.** 2005. Environmental physiology of growth and flowering of orchids. *HortScience* **40**, 1969–1973.
- López-García JJ, Fuentes-Rodríguez JM, Rodríguez RA.** 2001. Production and use of *Opuntia* as forage in northern Mexico. In: Mondragon-Jacobo C, Pérez-González S, eds, Cactus (*Opuntia* spp.) as forage. Rome: Food and Agriculture Organization of the United Nations, 29–36.
- Luque D, Martínez-Yrizar A, Búrquez A, López-Cruz GL, Murphy AD.** 2017. Complejos bioculturales de Sonora: pueblos y territorios indígenas. Hermosillo, Mexico: Centro de Investigación en Alimentación y Desarrollo.
- Majure LC, Puente R, Griffith MP, Judd WS, Soltis PS, Soltis DE.** 2012. Phylogeny of *Opuntia* s.s. (Cactaceae): clade delineation, geographic origins, and reticulate evolution. *American Journal of Botany* **99**, 847–864.
- Malezieux E, Cote F, Bartholomew DP.** 2002. Crop environment, plant growth, and physiology. In: Bartholomew DP, Paull RE, Rohrbach KG, eds, The pineapple: botany, production, and uses. Wallingford, UK: CABI Publishing, 69–108.
- Mancilla-Margalli NA, López MG.** 2006. Water-soluble carbohydrates and fructan structure patterns from *Agave* and *Dasyllirion* species. *Journal of Agricultural and Food Chemistry* **54**, 7832–7839.
- Martínez-Palacios A, Eguiarte LE, Fournier GR.** 1999. Genetic diversity of the endangered endemic *Agave victoriae-reginae* (Agavaceae) in the Chihuahuan Desert. *American Journal of Botany* **86**, 1093–1098.
- Mason PM, Glover K, Smith JAC, Willis KJ, Woods J, Thompson IP.** 2015. The potential of CAM crops as a globally significant bioenergy resource: moving from 'fuel or food' to 'fuel and more food.' *Energy & Environmental Science* **8**, 2320–2329.
- Mauseth JD.** 2017. Are some cacti the fastest growing plants in the world? *Cactus and Succulent Journal* **89**, 4–10.
- Mazzeo G, Russo A, Suma P, Longo S.** 2018. The history of *Dactylopius coccus* (Costa) (Hemiptera: Dactylopiidae) in the Mediterranean basin: the Sicilian episode. *Entomologica* **47**, 55–55.
- Mejía A, Cantwell M.** 2003. Prickly pear fruit development and quality in relation to gibberellic acid applications to intact and emasculated flower buds. *Journal of the Professional Association for Cactus Development* **5**, 72–85.
- Méndez Gallegos SJ, García-Herrera J.** 2006. La tuna: producción y diversidad. *CONABIO. Biodiversitas* **68**, 1–5.
- Ming R, VanBuren R, Wai CM, et al.** 2015. The pineapple genome and the evolution of CAM photosynthesis. *Nature Genetics* **47**, 1435–1442.
- Mondragon-Jacobo C, Bordelon BB.** 1996. Cactus Pear (*Opuntia* spp. Cactaceae) breeding for fruit production. *Journal of the Professional Association for Cactus Development* **1**, 19–35.
- Murillo-Amador B, Cortes-Avila A, Troyo-Díez E, Nieto-Garibay A, Jones HG.** 2001. Effects of NaCl salinity on growth and production of young cladodes of *Opuntia ficus-indica*. *Journal of Agronomy and Crop Science* **187**, 269–279.
- Naumann G, Alfieri L, Wyser K, Mentaschi L, Betts RA, Carrao H, Feyen L.** 2018. Global changes in drought conditions under different levels of warming. *Geophysical Research Letters* **45**, 3285–3296.
- Nadakuduti SS, Buell CR, Voytas DF, Starker CG, Douches DS.** 2018. Genome editing for crop improvement – Applications in clonally propagated polyploids with a focus on potato (*Solanum tuberosum* L.). *Frontiers in Plant Science* **9**, 1607.
- Nayankantha NMC, Singh BR, Gupta AK.** 2010. Assessment of genetic diversity in Aloe germplasm accessions from India using RAPD and morphological markers. *Ceylon Journal of Science* **39**, 1–9.
- Nejatzadeh-Barandozi F, Akbari L.** 2013. Karyotypic variation of the *Aloe vera* L. and *Aloe littoralis* Baker in Iran. *Iranian Journal of Biotechnology* **11**, 233–237.
- Nejatzadeh-Barandozi F, Naghavi MR, Enferadi ST, Mousavi A, Mostofi Y, Hassani ME.** 2012. Genetic diversity of accessions of Iranian *Aloe vera* based on horticultural traits and RAPD markers. *Industrial Crops and Products* **37**, 347–351.
- Nerd A, Karadi A, Mizrahi Y.** 1991. Salt tolerance of prickly pear cactus (*Opuntia ficus-indica*). *Plant and Soil* **137**, 201–207.
- Nerd A, Raveh E, Mizrahi Y.** 1993. Adaptation of five columnar cactus species to various conditions in the Negev Desert of Israel. *Economic Botany* **43**, 31–41.
- Nerd A, Tel-Zur N, Mizrahi Y.** 2002. Fruits of vine and columnar cacti. In: Nobel PS, ed, Cacti: biology and uses. Berkeley, CA, USA: University of California Press, 184–197.
- Niechayev N, Jones A, Rosenthal D, Davis SC.** 2019. A model of environmental limitations on production of *Agave americana* L. grown as a biofuel crop in semi-arid regions. *Journal of Experimental Botany* **70**, 6549–6559.
- Nobel PS.** 1984. Productivity of *Agave deserti*: measurement by dry weight and monthly prediction using physiological responses to environmental parameters. *Oecologia* **64**, 1–7.
- Nobel PS** (ed). 2002. Cacti: biology and uses. Berkeley, CA, USA: University of California Press.

- Nobel PS, De la Barrera E.** 2003. Tolerances and acclimation to low and high temperatures for cladodes, fruits and roots of a widely cultivated cactus, *Opuntia ficus-indica*. *New Phytologist* **157**, 271–279.
- Nobel PS, Bobich EG.** 2002. Environmental biology. In: Nobel PS, ed. *Cacti: biology and uses*. Berkeley, CA, USA: University of California Press, 57–74.
- Nobel PS, Cui M.** 1992. Shrinkage of attached roots of *Opuntia ficus-indica* in response to lowered water potentials—predicted consequences for water uptake or loss to soil. *Annals of Botany* **70**, 485–491.
- Nobel PS, Garcia-Moya E, Quero E.** 1992. High annual productivity of certain agaves and cacti under cultivation. *Plant, Cell and Environment* **15**, 329–335.
- Nobel PS, Israel AA.** 1994. Cladode development, environmental responses of CO<sub>2</sub> uptake, and productivity for *Opuntia ficus-indica* under elevated CO<sub>2</sub>. *Journal of Experimental Botany* **45**, 295–303.
- Núñez HM, Rodríguez LF, Khanna M.** 2011. Agave for tequila and bio-fuels: an economic assessment and potential opportunities. *GCB Bioenergy* **3**, 43–57.
- Nyffeller R, Eggli U, Ogburn M, Edwards E.** 2008. Variations on a theme: repeated evolution of succulent life forms in the Portulacineae (Caryophyllales). *Heseltonia* **14**, 26–36.
- Ocaña-Nava D, García-Mendoza A, Larson J.** 2007. Modelación supervisada de la distribución de magueyes mezcaleros en México. In: Colunga-GarcíaMarín P, Eguiarte L, Larqué-S. A y Zizumbo-Villareal D, eds, *En lo ancestral hay futuro: del tequila, los mezcales y otros agaves*. México: CICY-CONACYT-CONABIO-INE, 153–174.
- Olatunya OS, Olatunya AM, Anyabolu HC, Adejuyigbe EA, Oyelami OA.** 2012. Preliminary trial of aloe vera gruel on HIV infection. *Journal of Alternative and Complementary Medicine* **18**, 850–853.
- Orozco UCM.** 2007. El pitayo (*Stenocereus thurberi*) un elemento de conservación y sustentabilidad. Bachelor thesis. Centro de Estudios Superiores del Estado de Sonora, Hermosillo, Mexico.
- Owen NA, Griffiths H.** 2013. A system dynamics model integrating physiology and biochemical regulation predicts extent of crassulacean acid metabolism (CAM) phases. *New Phytologist* **200**, 1116–1131.
- Owen N, Griffiths H.** 2014. Marginal land bioethanol yield potential of four crassulacean acid metabolism candidates (*Agave fourcroydes*, *Agave salmiana*, *Agave tequilana*, and *Opuntia ficus-indica*) in Australia. *GCB Bioenergy* **6**, 687–703.
- Palomino G, Martínez J, Méndez I.** 2007. Variación inter e intraespecífica en especies de Agave por citometría de flujo y análisis de sus cromosomas. In: Colunga-GarcíaMarín P, Eguiarte L, Larqué-S. A y Zizumbo-Villareal D, eds, *En lo ancestral hay futuro: del tequila, los mezcales y otros agaves*. México: CICY-CONACYT-CONABIO-INE, 41–65.
- Pareek OP, Sharma BD, Nath V, Singh RS, Bhargava R.** 1999. Effect of nitrogen and phosphorus fertilizers and organic manure on growth and yield of Indian aloe (*Aloe barbadensis* Mill.). *Annals of Arid Zone* **38**, 85–86.
- Peña-Valdivia CB, Trejo C, Arroyo-Peña VB, Sánchez Urdaneta AB, Balois Morales R.** 2012. Diversity of unavailable polysaccharides and dietary fiber in domesticated nopalito and cactus pear fruit (*Opuntia* spp.). *Chemistry & Biodiversity* **9**, 1599–1610.
- Pérez-Negrón E, Dávila P, Casas A.** 2014. Use of columnar cacti in the Tehuacán Valley, Mexico: perspectives for sustainable management of non-timber forest products. *Journal of Ethnobiology and Ethnomedicine* **10**, 79.
- Pimienta-Barrios E.** 1994. Prickly pear (*Opuntia* spp.): a valuable fruit crop for the semi-arid lands of Mexico. *Journal of Arid Environments* **28**, 1–11.
- Pimienta-Barrios E, Zañudo-Hernández J, Nobel PS, García-Galindo J.** 2007. Ecofisiología del agave azul (*Agave tequilana* Weber). In: Colunga-GarcíaMarín P, Eguiarte L, Larqué-S. A y Zizumbo-Villareal D, eds, *En lo ancestral hay futuro: del tequila, los mezcales y otros agaves*. México: CICY-CONACYT-CONABIO-INE, 67–82.
- Pinaria AG, Liew ECY, Burgess LW.** 2010. Fusarium species associated with vanilla stem rot in Indonesia. *Australasian Plant Pathology* **39**, 176–183.
- Ramachandra Rao S, Ravishankar G.** 2000. Vanilla flavour: production by conventional and biotechnological routes. *Journal of the Science of Food and Agriculture* **80**, 289–304.
- Ramírez-Mosqueda MA, Iglesias-Andreu LG, Luna-Sánchez IJ.** 2017. Light quality affects growth and development of in vitro plantlet of *Vanilla planifolia* Jacks. *South African Journal of Botany* **109**, 288–293.
- Rana S, Sharma D, Bakshi N.** 2018. A mini review on morphological, biochemical and molecular characterization of *Aloe vera* L. *International Journal of Chemical Studies* **4**, 3109–3115.
- Rao S, Hegde S, Baliga-Rao M, et al.** 2017. An *Aloe vera*-based cosme-ceutical cream delays and mitigates ionizing radiation-induced dermatitis in head and neck cancer patients undergoing curative radiotherapy: a clinical study. *Medicines* **4**, 44.
- Rao X, Krom N, Tang Y, Widiez T, Havkin-Frenkel D, Belanger FC, Dixon RA, Chen F.** 2014. A deep transcriptomic analysis of pod development in the vanilla orchid (*Vanilla planifolia*). *BMC Genomics* **15**, 964.
- Rathod AH, Parmar SK, Vaghela PO, Sheikh WA, Shinde AS, Kalaskar SR.** 2014. Floral and reproductive phenology of *Aloe vera*. *Bioscan* **9**, 723–726.
- Reyes-Aguero JA, Aguirre-Rivera JR.** 2011. Agrobiodiversity of cactus pear (*Opuntia*, Cactaceae) in the Meridional Highlands Plateau of Mexico. *Journal of Natural Resources and Development* **1**, 1–9.
- Rivera-Lugo M, García-Mendoza A, Simpson J, Solano E, Gil-Vega K.** 2018. Taxonomic implications of the morphological and genetic variation of cultivated and domesticated populations of the *Agave angustifolia* complex (Agavoideae, Asparagaceae) in Oaxaca, Mexico. *Plant Systematics and Evolution* **304**, 969–979.
- Rohrbach KG, Leal F, Coppens d'Eckenbrugge G.** 2002. History, distribution, and world production. In: The pineapple: botany, production, and uses. Bartholomew DP, Paull RE, Rohrbach KG, eds, Wallingford, UK: CAB International, 1–12.
- Royal Flora Holland.** 2018. Annual Report 2017. Aalsmeer, Netherlands: Royal Flora Holland. <https://www.royalfloraholland.com/media/12324292/royal-floraholland-annual-report-2017-en.pdf>
- Rulfo VFO, Pérez Domínguez JF, del Real Laborde JI, eds.** 2007. Conocimiento y Prácticas Agronómicas para la Producción de *Agave tequilana* Weber en la Zona de Denominación de Origen del Tequila. Sagarpa, Jalisco, Mexico: Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias: Centro de Investigación Regional del Pacífico Centro.
- Russell CE, Felker P.** 1987. The prickly-pears (*Opuntia* spp., Cactaceae): A source of human and animal food in semiarid regions. *Economic Botany* **41**, 433–445.
- Saha R, Palit S, Ghosh BC, Mitra BN.** 2005. Performance of *Aloe vera* as influenced by organic and inorganic sources of fertilizer supplied through fertigation. *Acta Horticulturae* **676**, 171–175.
- Salvatierra González A, Masson Salau L, Encina Acosta C, Osorio Ulloa A.** 2010. Copao (*Eulychnia acida* Phil.), cactácea endémica de Chile: Información nutricional de los frutos y recomendaciones generales. Boletín W212. La Serena, Chile: Instituto de Investigaciones Agropecuaria. Centro Regional de Investigaciones Intihua.
- Sánchez J, Sánchez F, Curt MD, Fernández J.** 2012. Assessment of the bioethanol potential of prickly pear (*Opuntia ficus-indica* (L.) Mill.) biomass obtained from regular crops in the province of Almería (SE Spain). *Israel Journal of Plant Sciences* **60**, 301–318.
- Sánchez-Machado DI, López-Cervantes J, Sendón R, Sanches-Silva A.** 2017. *Aloe vera*: Ancient knowledge with new frontiers. *Trends in Food Science & Technology* **61**, 94–102.
- Santos TN, Dutra ED, Gomes do Prado A, et al.** 2016. Potential for bio-fuels from the biomass of prickly pear cladodes: challenges for bioethanol and biogas production in dry areas. *Biomass and Bioenergy* **85**, 215–222.
- Santos Díaz MS, Barba de la Rosa AP, Héliès-Toussaint C, Guéraud F, Nègre-Salvayre A.** 2017. *Opuntia* spp.: characterization and benefits in chronic diseases. *Oxidative Medicine and Cellular Longevity* **17**, 8634249.
- Schartel TE, Brooks CP.** 2018. Biotic constraints on *Cactoblastis cactorum* (Berg) host use in the southern US and their implications for future spread. *Food Webs* **15**, e00083.
- Segura S, Fresnedo J, Mathuriau C, López J, Andrés J, Muratalla A.** 2018. The edible fruit species in Mexico. *Genetic Resources and Crop Evolution* **65**, 1767–1793.
- Shackleton S, Kirby D, Gambiza J.** 2011. Invasive plants – friends or foes? Contribution of prickly pear (*Opuntia ficus-indica*) to livelihoods in Makana Municipality, Eastern Cape, South Africa. *Development Southern Africa* **28**, 177–193.
- Shalabi M, Khilo K, Zakaria MM, Elsebaei MG, Abdo W, Awadin W.** 2015. Anticancer activity of *Aloe vera* and *Calligonum comosum* extracts



separately on hepatocellular carcinoma cells. *Asian Pacific Journal of Tropical Biomedicine* **5**, 375–381.

**Sidana J, Singh B, Sharma OP.** 2016. Saponins of *Agave*: chemistry and bioactivity. *Phytochemistry* **130**, 22–46.

**Silva H, Sagardia S, Seguel O, Torres C, Tapia C, Franck N, Cardemil L.** 2010. Effect of water availability on growth and water use efficiency for biomass and gel production in *Aloe Vera* (*Aloe barbadensis* M.). *Industrial Crops and Products* **31**, 20–27.

**Silva MA, Trevisan G, Hoffmeister C, et al.** 2014. Anti-inflammatory and antioxidant effects of *Aloe saponaria* Haw in a model of UVB-induced paw sunburn in rats. *Journal of Photochemistry and Photobiology. B, Biology* **133**, 47–54.

**Silvera K, Neubig KM, Whitten WM, Williams NH, Winter K, Cushman JC.** 2010. Evolution along the crassulacean acid metabolism continuum. *Functional Plant Biology* **37**, 995–1010.

**Silvera K, Santiago LS, Cushman JC, Winter K.** 2009. Crassulacean acid metabolism and epiphytism linked to adaptive radiations in the Orchidaceae. *Plant Physiology* **149**, 1838–1847.

**Simpson J, Martinez Hernandez A, Abraham Juarez M, Delgado Sandoval S, Sanchez Villarreal A, Cortes Romero C.** 2011. Genomic resources and transcriptome mining in *Agave tequilana*. *GCB Bioenergy* **3**, 25–36.

**Snyman HA.** 2006. Root distribution with changes in distance and depth of two-year-old cactus pears *Opuntia ficus-indica* and *O. robusta* plants. *South African Journal of Botany* **72**, 434–441.

**Snyman HA.** 2013. Growth rate and water-use efficiency of cactus pears *Opuntia ficus-indica* and *O. robusta*. *Arid Land Research and Management* **27**, 337–348.

**Stintzing FC, Carle R.** 2005. Cactus stems (*Opuntia* spp.): a review on their chemistry, technology, and uses. *Molecular Nutrition & Food Research* **49**, 175–194.

**Swarts ND, Dixon KW.** 2009. Perspectives on orchid conservation in botanic gardens. *Trends in Plant Science* **14**, 590–598.

**Tabatabaei SRF, Ghaderi S, Bahrami-Tapehebur M, Farbood Y, Rashno M.** 2017. *Aloe vera* gel improves behavioral deficits and oxidative status in streptozotocin-induced diabetic rats. *Biomedicine & Pharmacotherapy* **96**, 279–290.

**Tawaray K, Turjaman M, Ekamawanti HA.** 2007. Effect of arbuscular mycorrhizal colonization on nitrogen and phosphorus uptake and growth of *Aloe vera* L. *Hortscience* **42** 1737–1739.

**Thackery FA, Leding AR.** 1929. The giant cactus of Arizona: the use of its fruit and other cactus fruits by the Indians. *Journal of Heredity* **20**, 401–414.

**Ticktin T, Johns T, Chapol Xoca V.** 2003. Patterns of growth in *Aechmea magdalenae* (Bromeliaceae) and its potential as a forest crop and conservation strategy. *Agriculture, Ecosystems & Environment* **94**, 123–139.

**Tripathi N, Saini N, Tiwari S.** 2011. Assessment of genetic diversity among *Aloe vera* accessions using amplified fragment length polymorphism. *International Journal of Medicinal and Aromatic Plants* **1**, 115–121.

**Tsai WC, Dievart A, Hsu CC, Hsiao YY, Chiou SY, Huang H, Chen HH.** 2017. Post genomics era for orchid research. *Botanical Studies* **58**, 61.

**USDA.** 2015. Census of horticultural specialties (2014). 2012 Census of Agriculture, Volume 3, Special Studies, Part 3. Report No. AC-12-SS-3. Washington, DC: United States Department of Agriculture National Agricultural Statistics Service. [https://www.nass.usda.gov/Publications/AgCensus/2012/Online\\_Resources/Census\\_of\\_Horticulture\\_Specialties/HORTIC.pdf](https://www.nass.usda.gov/Publications/AgCensus/2012/Online_Resources/Census_of_Horticulture_Specialties/HORTIC.pdf)

**USDA NASS.** 2018. Census of agriculture statistics. Washington, DC, USA: United States Department of Agriculture National Agricultural Statistics Service. <https://www.nass.usda.gov/>.

**Valenzuela-Zapata AG.** 1994. El agave tequilero: Su cultivo e industrialización. Guadalajara, México: Monsanto.

**Valenzuela-Zapata AG.** 1997. El agave tequilero, su cultivo e industria, 2nd edn. Guadalajara, México: Monsanto.

**van der Knaap N.** 2005. Cultivation guide phalaenopsis: knowledge for professionals. Bleiswijk, The Netherlands: Anthura.

**Vázquez B, Avila G, Segura D, Escalante B.** 1996. Antiinflammatory activity of extracts from *Aloe vera* gel. *Journal of Ethnopharmacology* **55**, 69–75.

**Villagrán C, Castro V.** 2003. Ciencia indígena de los Andes del norte de Chile. Santiago, Chile: Editorial Universitaria S.A., Universidad de Chile.

**Walton NJ, Mayer MJ, Narbad A.** 2003. Vanillin. *Phytochemistry* **63**, 505–515.

**Winter K, Aranda J, Holtum JAM.** 2005. Carbon isotope composition and water-use efficiency in plants with crassulacean acid metabolism. *Functional Plant Biology* **32**, 381.

**Winter K, Smith JAC.** 1996. Crassulacean acid metabolism: current status and perspectives. In: Winter K, Smith JAC, eds. *Crassulacean acid metabolism*. Berlin, Heidelberg: Springer-Verlag, 389–426.

**Wongsheree T, Wongs-Aree C, Srilaong V, Jitareerat P.** 2013. Vanilla cultivation and curing in Thailand. *Acta Horticulturae* **1011**, 213–218.

**Xu C, Ding C, Zhou N, Ruan XM, Guo BX.** 2016. A polysaccharide from *Aloe vera* L. var. *chinensis* (Haw.) Berger prevents damage to human gastric epithelial cells in vitro and to rat gastric mucosa in vivo. *Journal of Functional Foods* **24**, 501–512.

**Yepes L, Días M, Granadillo E, Chacin F.** 1993. Frecuencia óptima de riego y fertilización en *Aloe vera*. *Turrialba* **43**, 261–267.

**Yahia EM.** 2012. Prickly pear fruit and cladodes. In: Rees D, Farrell G, Orchard J, eds. *Crop post-harvest: science and technology*. UK: Blackwell Publishing Ltd, 264–285.

**Yahia EM, Sáenz C.** 2011. Cactus pear (*Opuntia* species). In: Yahia EM, ed. *Postharvest biology and technology of tropical and subtropical fruits*. Sawston, UK: Woodhead Publishing, 290–331e.

**Yan X, Tan D, Inderwildi O, Smith JAC, King D.** 2011. Life cycle energy and greenhouse gas analysis for agave-derived bioethanol. *Energy & Environmental Science* **4**, 3110–3121.

**Yang H, Barros-Rios J, Kourteva G, et al.** 2017. A re-evaluation of the final step of vanillin biosynthesis in the orchid *Vanilla planifolia*. *Phytochemistry* **139**, 33–46.

**Yang L, Lu M, Carl S, Mayer JA, Cushman JC, Tian E, Lin H.** 2015a. Biomass characterization of *Agave* and *Opuntia* as potential biofuel feed-stocks. *Biomass and Bioenergy* **76**, 43–53.

**Yang X, Cushman JC, Borland AM, et al.** 2015b. A roadmap for research on crassulacean acid metabolism (CAM) to enhance sustainable food and bioenergy production in a hotter, drier world. *New Phytologist* **207**, 491–504.

**Yang X, Hu R, Yin H, et al.** 2017. The *Kalanchoë* genome provides insights into convergent evolution and building blocks of crassulacean acid metabolism. *Nature Communications* **8**, 1899.

**Yetman D.** 2007. The great cacti: ethnobotany and biogeography. Tucson, AZ, USA: University of Arizona Press.

**Yetman DA, Búrquez A.** 1996. A tale of two species: speculation on the introduction of *Pachycereus pringlei* in the Sierra Libre, Sonora, Mexico by *Homo sapiens*. *Desert Plants* **12**, 23–32.

**Zhou WZ, Zhang YM, Lu JY, Li JF.** 2012. Construction and evaluation of normalized cDNA libraries enriched with full-length sequences for rapid discovery of new genes from *Sisal* (*Agave sisalana* Perr.) different developmental stages. *International Journal of Molecular Sciences* **13**, 13150–13168.

**Zizumbo-Villarreal D, Colunga-GarcíaMarín P.** 2007. La introducción de la destilación y el origen de los mezcales en el occidente de México. In: Colunga-GarcíaMarín P, Eguiarte L, Larqué-S. A y Zizumbo-Villareal D, eds. *En lo ancestral hay futuro: del tequila, los mezcales y otros agaves*. México: CICY-CONACYT-CONABIO-INE, 85–112.

**Zuñiga-Estrada L, Rosales Robles E, Yáñez-Morales MJ, Jacques-Hernández C.** 2018. Características y productividad de una planta MAC, *Agave tequilana* desarrollada con fertigación en Tamaulipas, México. *Revista Mexicana de Ciencias Agrícolas* **9**, 553–564.