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RESEARCH ARTICLE

An Aridamerican model for agriculture in a hotter, water scarce world

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Societal Impact Statement

Climate change is dramatically restructuring agriculture and damaging crops, food security, and human health, especially in deserts. To radically redesign food systems to buffer against climatic disruptions, we focus on agroecological function, human health, and community well-being. Using arid North America ("Aridamerica") as a laboratory for the future, we employed 18 criteria to select 17 desert plant genera with high potential as food crops. When integrated into perennial polycultures modeled after arid ecosystems and traditional knowledge, desert plants can stabilize yields, produce disease-preventing foods, and generate rural livelihoods. We envision food systems that can reduce disparities while enhancing resilience in a hotter, drier world.

Summary

Climate disruptions and water scarcity are threatening food security and human well-being. We provide a framework for selecting a more diverse set of arid-adapted food crops to reduce food system vulnerabilities to climate change, climate-related illness, and economic disparities in arid lands. We constructed a list of candidate crops based on the diets of the Comcaac, O'odham, and Pima Bajo peoples of the Sonoran Desert. Representative genera were then screened for traits related to agroecological functionality, human health, community well-being, and agronomic suitability. Of the 154 species (86 genera) used by these Sonoran Desert Indigenous cultures, 101 species (80 genera) were more broadly used in Aridamerica, suggesting wide acceptability and value of desert plants for arid-adapted agriculture in North America. We highlight 17 genera with high potential to simultaneously improve agricultural resilience, human health, and community prosperity in the face of climate change, over a third of which are water-use efficient crassulacean acid metabolism (CAM) succulents. Assembling these candidate crops into perennial polycultures coupled with solar energy and rainwater harvesting

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Dedicated to desert botanist Richard S. Felger, who pioneered research in arid land food crops and envisioned their potential before others.

systems can maximize yield reliability while minimizing fossil fuel, agrichemical, and surface and groundwater use. Now is the time to invest in desert-adapted farming and food systems, with climate change already accelerating damages to agricultural landscapes. Biomimicry and traditional knowledge can aid in designing co-located food, water, and energy provisioning systems adapted to arid climates and scarce resources that improve agroecological and human health. Adopting such designs will require transdisciplinary integration of plant, environmental, social, and health sciences.

KEYWORDS

agroecosystem, biomimicry, climate change, desert ecology, food systems, human health, traditional knowledge

1 | INTRODUCTION

Climate change and water scarcity are dramatically restructuring agriculture and degrading arable lands while placing food security, human health, and community well-being at risk (IPCC, 2019; Porter et al., 2014; Smith et al., 2014; Wheeler & von Braun, 2013). Maintaining food security without further compromising natural resources requires holistic but pragmatic approaches that meet increasing food demands while reducing energy and water demands (e.g., Barron-Gafford et al., 2019) and address agroecological health, human health, and rural poverty (Zimmerer & de Haan, 2017). Arid and semi-arid lands are on the frontlines of the climate change food security crisis, currently experiencing challenges that much of the earth's population could soon face (Huang, Yu, Guan, Wang, & Guo, 2016).

Climate change is already impacting global food security through increasing temperatures, changing precipitation patterns, and increased frequency of extreme events, including heatwaves, drought, floods, and fires (IPCC, 2019; Porter et al., 2014). According to the World Resources Institute, food systems in 17 countries around the world are already under extreme water stress (Hofste et al., 2019), currently using almost all their available water to feed a quarter of the planet's population. Major climate-driven challenges to food production include:

1. Greater frequency of temperatures exceeding thermal thresholds for photosynthesis, flowering, and fruiting of many crops including beans, canola, groundnuts, maize, millets, rice, and tomatoes (Lobell & Gourdji, 2012; Luo, 2011);
2. Greater frequency and severity of drought (Naumann et al., 2018);
3. Increasing rates of anthropogenic soil erosion (Nearing, Xie, Liu, & Ye, 2017);
4. Diminished groundwater and surface water availability for crop irrigation (Mann & Gleick, 2015); and
5. Salinization of arable lands due to sea level rise, saltwater intrusion in aquifers, and inadequate irrigation management (Mann & Gleick, 2015; Squires & Glenn, 2011).

These pressures will only intensify in the years to come. If global warming continues at the present rate, water supply-demand deficits could increase five-fold, resulting in prolonged socioeconomic impacts (Naumann et al., 2018). Arid and semi-arid lands, which currently cover approximately 40% of the Earth's land surface, could expand to 50% or more by the end of the 21st century (Huang et al., 2016). Thus, today's arid zones are laboratories for the future. Here, climate change already poses an imminent threat to water availability, food security, ecosystem services, economic security, and human health (Gonzalez et al., 2018).

Without radical changes in current food production and arable land management practices, we face widespread hunger and inequity in a hotter, drier future (IPCC, 2019). Our current food production systems not only contribute to climate change, producing 19%–29% of global anthropogenic greenhouse gas emissions, but also drive widespread environmental degradation, socioeconomic inequalities, and negative health impacts (Horrigan, Lawrence, & Walker, 2002; Vermeulen, Campbell, & Ingram, 2012). Climate change exacerbates these disparities, disproportionately affecting marginalized populations, such as the poor, communities of color, and Indigenous populations (Olsson et al., 2014; WHO, 2018). Climate-related illness and health care costs are already rising (Box 1), especially for rural agricultural workers (Jackson & Rosenberg, 2010). We predict that the rise of climate-exacerbated illnesses will pose one the most daunting public health dilemmas that has ever affected the economies of rural and Indigenous communities in arid zones.

Agricultural visionaries from Argentina, Australia, North America, and elsewhere have been calling for “new roots for agriculture” for more than 40 years (Felger, 1975; Jackson, 1980). Their visions favor high biodiversity-low input agroecosystems, with greater emphasis on perennial polycultures. To quote pioneering desert botanist Richard Felger, to whom this article is dedicated, we must “fit the crops to the environment rather than remaking the environment to fit the crops.” Yet, to date few agronomists have given sufficient attention to effective means to reduce heat or moisture stress in crops and livestock, or in the humans who struggle to manage them (Nabhan, 2013).

We present a conceptual framework to evaluate and select desert plants for arid-adapted agriculture in arid North America (“Aridamerica,” Figure 1), modeled after the native ecosystems (“biomimicry” in Baumeister, Tocke, Dwyer, Ritter, & Benyus, 2014) and traditional knowledge of the Sonoran Desert. Here, plants have evolved

BOX 1 Health toll of climate change

Climate change is considered the greatest public health challenge of the 21st century (WHO, 2018). Human diseases and mortality linked to climate change are on the rise, including kidney, cardiovascular, and respiratory disease exacerbated by extreme heat and air pollution; vector-borne infectious diseases; and malnutrition due to crop failure (Smith et al., 2014; WHO, 2018). Among those most vulnerable are poor populations, including Indigenous peoples and rural outdoor agricultural workers (Jackson & Rosenberg, 2010; McMichael, Friel, Nyong, & Corvalan, 2008; Smith et al., 2014), for whom climate change exacerbates existing chronic stressors and socioeconomic inequalities. Climate-related health issues bring a significant economic toll, including loss of productivity and employment, costly hospitalizations and emergency room visits, and even loss of human life (Johnson et al., 2019; Limaye, Max, Constible, & Knowlton, 2019). Nutrient-dense, plant-based diets high in antioxidant diversity and other chemo-preventative compounds, however, may alleviate rising medical costs by enhancing human health (Soldati et al., 2018). Bioactive secondary compounds are particularly prevalent in plants adapted to deserts and other extreme environments, where they provide defense against solar radiation, high heat, desiccation, or herbivory (Rinnan, Steinke, McGenity, & Loreto, 2014). Climate change intensifies environmental stressors contributing to oxidative stress in humans—an imbalance between antioxidant and free radicals or reactive oxygen species in the body that causes tissue damage. Oxidative stress triggers or exacerbates many pathological conditions, including asthma, cancer, diabetes, hypertension, and renal, neurological, and pulmonary diseases (Birben, Shahiner, Sackensen, Erzurum, & Kalavc, 2012), which generate high healthcare costs for desert dwellers worldwide.

a remarkable number of strategies to cope with the combined stresses of intense solar radiation, heat, drought, and highly variable precipitation (Box 2). Many wild plants in the region have a long history of human foraging and cultivation (Hodgson, 2001) and potential for direct or indirect use in modern food crop development, especially for arid-adapted agriculture (Felger, 1975; Felger & Nabhan, 1978; Nabhan & Felger, 1985; Riordan & Nabhan, 2019). We define arid-adapted agriculture in Aridamerica as a low-input farming system dominated by desert-adapted perennial plants (including succulents) and their soil microbes that produce higher and more reliable crop yields with less water than can most conventional annual crops.

We begin by constructing a list of arid-adapted wild food plants based on the historic and prehistoric diets of Indigenous Sonoran Desert cultures that relied primarily on local water, energy, and plant resources: the Comcaac (Seri people) of coastal Sonora, Mexico (Felger & Moser, 1985; Felger & Wilder, 2012) and the O'odham and Pima Bajo of Arizona, USA, and Sonora, Mexico (Rea, 1997). We then screen representative Aridamerican food plant genera for traits related to agroecological functions, human health, community well-being, and agronomic and agroforestry system suitability. Using plants with high rankings across our selection criteria, we integrate these potential crops into two agroecosystem models for application in Aridamerica. These arid-adapted designs have the potential to not only weather climate change, but also to improve agroecological functionality, human health, and community well-being in economically and ecologically sustainable fashion.

2 | MATERIALS AND METHODS

2.1 | Indigenous desert food plants

We constructed a list of potential food crops based on the diets of Indigenous Sonoran Desert cultures in the heart of Aridamerica: the Comcaac (Seri people), O'odham, and Pima Bajo peoples. The Comcaac are the last remaining foraging-hunting-fishing culture in the deserts of North America (Felger & Moser, 1985). They inhabit the arid coastal desert bordering the Gulf of California and at one time had perhaps the largest range of desert hunter-gatherers in Mexico. The O'odham and Pima Bajo peoples—including the Pima Bajo of Sonora, the Hia C-ed O'odham and Tohono O'odham of southwestern Arizona and Sonora, and the Akimel O'odham or River Pima of central Arizona—farmed and field-foraged the semi-arid and arid reaches of the Sonoran Desert, adjacent subtropics, and desert grasslands (Rea, 1997). These cultures have inhabited landscapes receiving just 100–250 mm of annual precipitation for millennia, evolving subsistence strategies based on arid-adapted food plants and selected animal foods, largely without dependence on groundwater or fossil fuel.

We reviewed major ethnobotanical, ethnographical, archeological, and botanical literature (Tables S1 and S2) to document the historical use of wild and semi-domesticated native food plants in the Sonoran Desert, excluding introduced species and incidental-famine foods. Plant taxonomy follows current nomenclature in TROPICOS (https://www.tropicos.org/) and the International Plant Name Index (IPNI; https://www.ipni.org/). For each species, we determined the photosynthetic pathway (C_3, C_4, CAM) and categorized water-acquisition strategy as extensive exploiter (e.g., *Prosopis*/mesquite), intensive exploiter (e.g., *Salvia columbariae*/chia, *Phaseolus acutifolius*/wild tepary bean), or water storer (e.g., *Agave*/agave, *Opuntia*/prickly pear) following Burgess (1995). We then documented breadth of Indigenous food plant use in Aridamerica in (a) Baja California to the west, (b) the Chihuahuan Desert to the east, and (c) the most arid reaches of Mesoamerica (Table S3).

2.2 | Evaluation of desert crop potential

We used 18 selection criteria to assess candidate crops for agroecological functions, human health, and community well-being, as

FIGURE 1 Map of America and the Sonoran Desert. See Supporting Information for further details on defining Aridamerica

well as agronomic suitability (Figure 2). Agroecological functions criteria evaluate potential to reduce agroecosystem vulnerability to soil loss, increasing abiotic stresses, and damaged agroecosystem services. Human health criteria evaluate potential to benefit physical well-being through chemo-preventative compounds that support multiple body systems, aid in glycemic control for type 2 diabetes, and increase resilience to environmental stress. Community well-being criteria evaluate potential to improve economic prosperity through rural job creation, and enhanced environmental quality of living and working conditions. Agronomic suitability criteria evaluate feasibility of new crop development, such as their inclusion in existing genomic research on domesticated crops; prior successful propagation, and established scalability of their harvest. A detailed description of individual crop selection criteria and scoring methods can be found in Supporting Information.

BOX 2 Desert plants as food crops

The majority of widespread crops (e.g., rice, wheat, soybean) are C_3 plants with low water-use efficiency and reduced photosynthetic efficiency under high temperatures. C_4 crops (e.g., corn, sorghum, sugarcane) have higher heat tolerance but usually require reliable irrigation in arid and semi-arid land settings. As temperatures increase, so do evapotranspiration and water input required to maintain crop yields. Thus, even drought- and heat-tolerant varieties of conventional C_3 and C_4 crops may be unable to weather—let alone mitigate—the stressful agronomic conditions predicted for arid zones over the coming century. In contrast, wild desert plants have evolved multiple strategies to cope with heat and drought (Gibson, 1996). Desert plants with the crassulacean acid metabolism (CAM) pathway uptake CO_2 nocturnally when temperatures are cooler, thereby optimizing water-use efficiency (Nobel, 2010). In succulents like cacti and agaves, the CAM pathway is accompanied by multiple adaptations to extreme heat and intense solar radiation. The small leaves of many non-succulent desert C_3 and C_4 perennials remain below lethal temperature with minimal water loss, enabling desert plants to maximize CO_2 uptake even under high temperatures (Gibson, 1996). Deep-rooted phreatophytes tap subsurface perennial watercourses, whereas ephemeral annuals track the desert's variable precipitation, enduring adverse conditions as seeds. With their low input requirements and yield reliability even under drought conditions, desert plants hold high potential for a new model of arid-adapted agriculture that can both weather and mitigate climate change (Davis et al., 2019; Nabhan, 2013; Nobel, 2010; Stewart, 2015).

We chose 36 Aridamerican food plant genera representative of desert-adapted life-history strategies to evaluate against the selection criteria. To score genera, we reviewed information on plant traits related to ecological, agronomic, nutritional, medicinal, and economic benefits. We summed individual criteria scores by selection category (agroecological functions, human health, community well-being, and agronomic suitability) and by genus. Category totals were then standardized to ensure equal weighting and summed for an overall score used to rank genera by their potential value for arid-adapted crop development. To demonstrate feasibility of crop development, we determined whether candidate crop genera contain wild species that have already been advanced as arid-adapted crops and evaluated the accessibility of germplasm accessions for crop research in regional botanical and research collections.

Collectively, these criteria provide a framework for evaluating selecting candidate food crops that simultaneously address agroecological functionality and resilience, human health, and community well-being in the context of climate change. Evaluation was performed at the genus level, as many species had incomplete or missing data across our criteria categories. However, criteria and rankings can be refined iteratively as additional data (e.g., carbon sequestration) become available for a wider range of desert plants.

3 | RESULTS

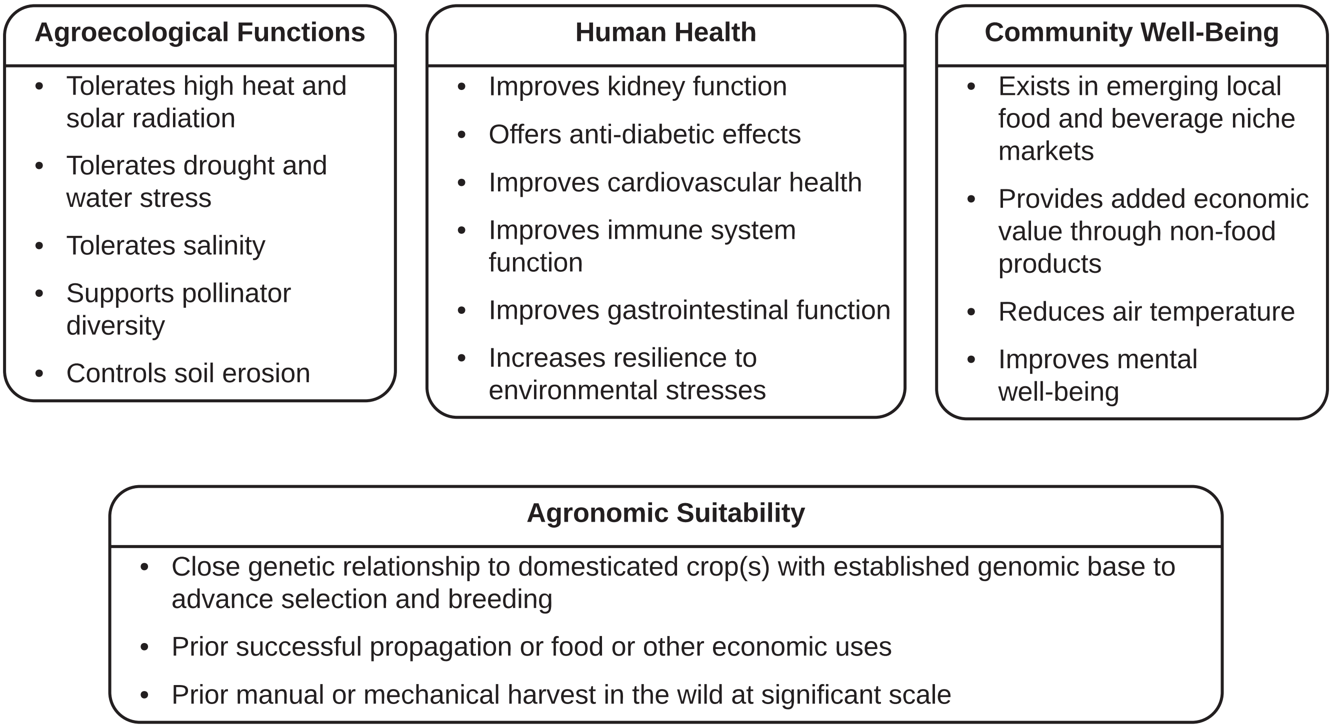
3.1 | Indigenous desert food plants

In the Sonoran Desert, the Comcaac, O'odham, and Pima Bajo Indigenous cultures historically used a diversity of wild and semi-cultivated food plants, including arid-adapted annuals, geophytes, perennial shrubs, legume trees, and succulents. Of the 86 native plants consumed as food and drink by the Comcaac, 36% (31 species) are water-use efficient CAM succulents (Table S1). Several have noteworthy salt tolerance including *Distichlis palmeri*, which was also used by other Indigenous groups in the Sonoran Desert (Pearlstein et al., 2012). By comparison, the O'odham and Pima Bajo peoples foraged and farmed over a wider range of habitats, accessing as many as 115 wild or semi-domesticated native plant species (Table S2). CAM succulents were commonly used as foods and beverages with probiotic properties, comprising 29% (34 species) of the plant species in their diet. When combined, these inventories form a core component of an Aridamerican diet, 154 species in 86 genera, with long tenure in the Sonoran Desert (Table S3). The genera of approximately one-third of the taxa have been identified in archaeological contexts. Over 90% of all genera have broader use in Aridamerica with at least 101 species historically used as food plants by Indigenous cultures in Baja California, the Chihuahuan Desert, or Mesoamerica (Table S3).

3.2 | Evaluation of desert crop potential

Applying the selection criteria, we identified 17 priority genera in nine families with high potential as new desert crops to improve agroecological functionality, human health, and community well-being (Table 1). These include: *Agave* (*maguey*/century plant), *Atriplex* (*chamizo*/saltbrush), *Capsicum* (*chiltepín*/wild chile), *Carnegiea* (*sahuaro*/saguaro), *Celtis* (*garambullo*/hackberry), *Cylindropuntia* (*choya*/cholla), *Ficus* (*higuera*/wild fig), *Opuntia* (*nopal*/*tuna*/prickly pear cactus), *Lippia* (*orégano*/Mexican oregano), *Pachycereus* (*sahueso*/cardón cactus), *Phaseolus* (*frijol*/bean), *Prosopis* (mesquite), *Salvia* (chia), *Sambucus* (*tápiro*/elderberry), *Sarcomphalus* (*Ziziphus*) (*bachata*/graythorn), *Stenocereus* (*pitaya*/organpipe cactus), and *Yucca* (*sota*/*yuca*/yucca). Six genera are perennial, water-storing CAM succulents. Also notable are deep-rooted trees (*Prosopis*) able to exploit and redistribute deep soil moisture.

The majority of the 36 screened genera offer potential benefits for agroecological functionality, human health, and community well-being. With respect to agroecological functions, 29 genera



Agroecological Functions

- Tolerates high heat and solar radiation
- Tolerates drought and water stress
- Tolerates salinity
- Supports pollinator diversity
- Controls soil erosion

Human Health

- Improves kidney function
- Offers anti-diabetic effects
- Improves cardiovascular health
- Improves immune system function
- Improves gastrointestinal function
- Increases resilience to environmental stresses

Community Well-Being

- Exists in emerging local food and beverage niche markets
- Provides added economic value through non-food products
- Reduces air temperature
- Improves mental well-being

Agronomic Suitability

- Close genetic relationship to domesticated crop(s) with established genomic base to advance selection and breeding
- Prior successful propagation or food or other economic uses
- Prior manual or mechanical harvest in the wild at significant scale

FIGURE 2 Candidate crop selection criteria to evaluate potential for agroecological functions, human health, and community well-being

have moderate to high heat tolerance and 22 genera have moderate to high drought tolerance (Table S4). Cacti and agave CAM succulents (six genera) have both high heat and drought tolerance. In addition, candidate crops in several other plant genera (e.g., *Atriplex*, *Chenopodium*, *Sporobolus*) are true halophytes having potential for saline agriculture (Aronson, 1989; Santos, Al-Azzawi, Aronson, & Flowers, 2016). Long-lived woody shrubs and nurse trees, perennial grasses, and arborescent cacti have the greatest capacity to control soil erosion. Most genera provide pollinator services, with *Agave*, *Carnegiea*, and *Stenocereus* supporting the greatest richness of higher taxonomic groups of pollinators, and *Prosopis* the greatest species richness of native bees.

Many of the screened genera also have the potential to support multiple aspects of human health (Table S5 and S6). Nearly all (33 of 36) may improve nutrition and insulin metabolism, potentially aiding glycemic control of type 2 diabetes, the costliest nutrition-related disease to treat in Aridamerica. For example, the galactomannan gums of complex polysaccharides in mesquite pods slow the digestion and absorption of sugar and increase insulin sensitivity (Brand, Snow, Nabhan, & Truswell, 1990). Antioxidant, anti-inflammatory, and other chemo-preventative compounds in desert plants potentially support immune system function (27 genera), cardiovascular health (27 genera), kidney function (23 genera), and resilience to environmental stress and pathogens (24 genera). Twenty-five genera may support gastrointestinal health through improved food digestion and enhanced gut microbiome. These include fermented cactus fruit in *Carnegiea*, *Opuntia*, *Stenocereus*, *and Pachycereus*, roasted leaf bases or fermented sap of *Agave*, and the mucilaginous seeds of chia. Notably, 10 genera have potential benefits across all six health criteria, including *Agave*, *Cylindropuntia*, *Prosopis*, *Salvia* (chia), and *Capsicum*.

For community well-being (Table S7), desert trees and arborescent cacti (e.g., *Carnegiea*, *Prosopis*, *Celtis*) provide shade that reduces ambient air temperatures, potentially enhancing comfort in living and outdoor working conditions and reducing energy costs. Twenty genera have aromatic flowers or resinous leaves that imbue the atmosphere with biogenic volatile organic compounds (BVOCs) and may promote a sense of well-being through reduction of cortisol and other stress hormones (Song, Ikei, & Miyazaki, 2016). Many desert plants already exist in emerging food and beverage niche markets (27 genera) or have additional non-food use and economic value (26 genera) that generate livelihoods, potentially reducing economic disparities in and among rural communities.

New desert food crops need not be domesticated from scratch. All 36 genera include species having prior successful propagation (Table S8). Many have been included in genomic research on domesticated crops (23 genera) or have been shown to have scalable harvests (27 genera). At least 26 desert-adapted species in the 36 screened genera have been subject to preliminary agronomic research into their potential as new crops. Botanical gardens and research institutes in the Sonoran Desert provide critical ex situ conservation and access to living materials of candidate desert crops (Table S9).

4 | DISCUSSION

The vulnerabilities of our present food, energy, and water supplies make building climate resilience into food systems daunting and

TABLE 1 Aridamerican candidate desert crop scores for improving agroecological functionality, human health, and community well-being. The 17 top-scoring genera are highlighted in gray

Family	*Genus*	Agroecological functions	Human health	Community well-being	Agronomic suitability	Total score	Priority
Amaranthaceae	*Amaranthus*	3.1	8.3	5.0	10.0	26.4	19
Amaranthaceae	*Atriplex*	5.4	8.3	5.0	10.0	28.7	14
Amaranthaceae	*Chenopodium*	3.8	6.7	5.0	10.0	25.5	21
Asparagaceae	*Agave*	7.7	10.0	7.5	10.0	35.2	1
Asparagaceae	*Dasylirion*	4.6	10.0	5.0	6.7	26.3	20
Asparagaceae	*Yucca*	4.6	10.0	5.0	10.0	29.6	11
Bixaceae	*Amoreuxia*	3.1	5.0	2.5	3.3	13.9	35
Cactaceae	*Carnegiea*	10.0	8.3	10.0	3.3	31.6	6
Cactaceae	*Cylindropuntia*	6.9	10.0	5.0	6.7	28.6	15
Cactaceae	*Echinocereus*	6.2	10.0	0.0	3.3	19.5	32
Cactaceae	*Ferocactus*	6.9	5.0	2.5	6.7	21.1	29
Cactaceae	*Opuntia*	6.9	10.0	7.5	10.0	34.4	2
Cactaceae	*Pachycereus*	9.2	10.0	7.5	3.3	30.0	9
Cactaceae	*Stenocereus*	10.0	8.3	5.0	10.0	33.3	4
Cannabaceae	*Celtis*	4.6	5.0	10.0	10.0	29.6	12
Caprifoliaceae	*Sambucus*	3.1	6.7	10.0	10.0	29.8	10
Cucurbitaceae	*Cucurbita*	6.2	6.7	2.5	10.0	25.4	22
Fabaceae	*Parkinsonia*	6.2	6.7	7.5	3.3	23.7	26
Fabaceae	*Phaseolus*	4.6	8.3	5.0	10.0	27.9	17
Fabaceae	*Prosopis*	7.7	10.0	10.0	6.7	34.4	3
Lamiaceae	*Salvia*	3.1	10.0	5.0	10.0	28.1	16
Liliaceae	*Allium*	1.5	6.7	2.5	10.0	20.7	30
Martyniaceae	*Proboscidea*	3.8	3.3	5.0	6.7	18.8	33
Moraceae	*Ficus*	5.4	3.3	10.0	10.0	28.7	13
Plantaginaceae	*Plantago*	3.1	6.7	5.0	10.0	24.8	23
Poaceae	*Panicum*	2.3	3.3	5.0	10.0	20.6	31
Poaceae	*Sporobulus*	3.1	1.7	5.0	3.3	13.1	36
Portulaceae	*Portulaca*	3.1	6.7	5.0	10.0	24.8	24
Rhamnaceae	*Sarcomphalus* (*Ziziphus*)	5.4	8.3	10.0	6.7	30.4	8
Rubiaceae	*Randia*	4.6	8.3	5.0	3.3	21.2	28
Sapotaceae	*Sideroxylon*	4.6	8.3	2.5	3.3	18.7	34
Solanaceae	*Capsicum*	3.1	10.0	7.5	10.0	30.6	7
Solanaceae	*Lycium*	6.9	5.0	5.0	10.0	26.9	18
Solanaceae	*Physalis*	3.8	5.0	5.0	10.0	23.8	25
Solanaceae	*Solanum*	3.1	1.7	7.5	10.0	22.3	27
Verbenaceae	*Lippia*	6.2	8.3	7.5	10.0	32.0	5

immediate challenges. Climate change will likely exacerbate interannual yield instability and frequency of failure of conventional annual and perennial crops (Lobell & Gourdji, 2012; Luo, 2011), forcing us to reconsider food system designs not just in Aridamerica, but in arid and semi-arid regions worldwide. Shifting from resource-consumptive monocultures to desert-adapted perennial polycultures can reduce dependence on costly water and energy inputs. We provide a conceptual framework for evaluating and selecting plants suited to arid conditions that enhance agroecological functionality, human health, and community well-being in the face of climate change (Figure 3).

As a laboratory for the future, Aridamerica is an ideal pool from which to select candidate crops. Its native plants exhibit a diversity of adaptive strategies that spatially and temporally complement one another and have extensive traditional knowledge of use and cultivation for food (Felger, 1975; Felger & Moser, 1985; Hodgson, 2001;

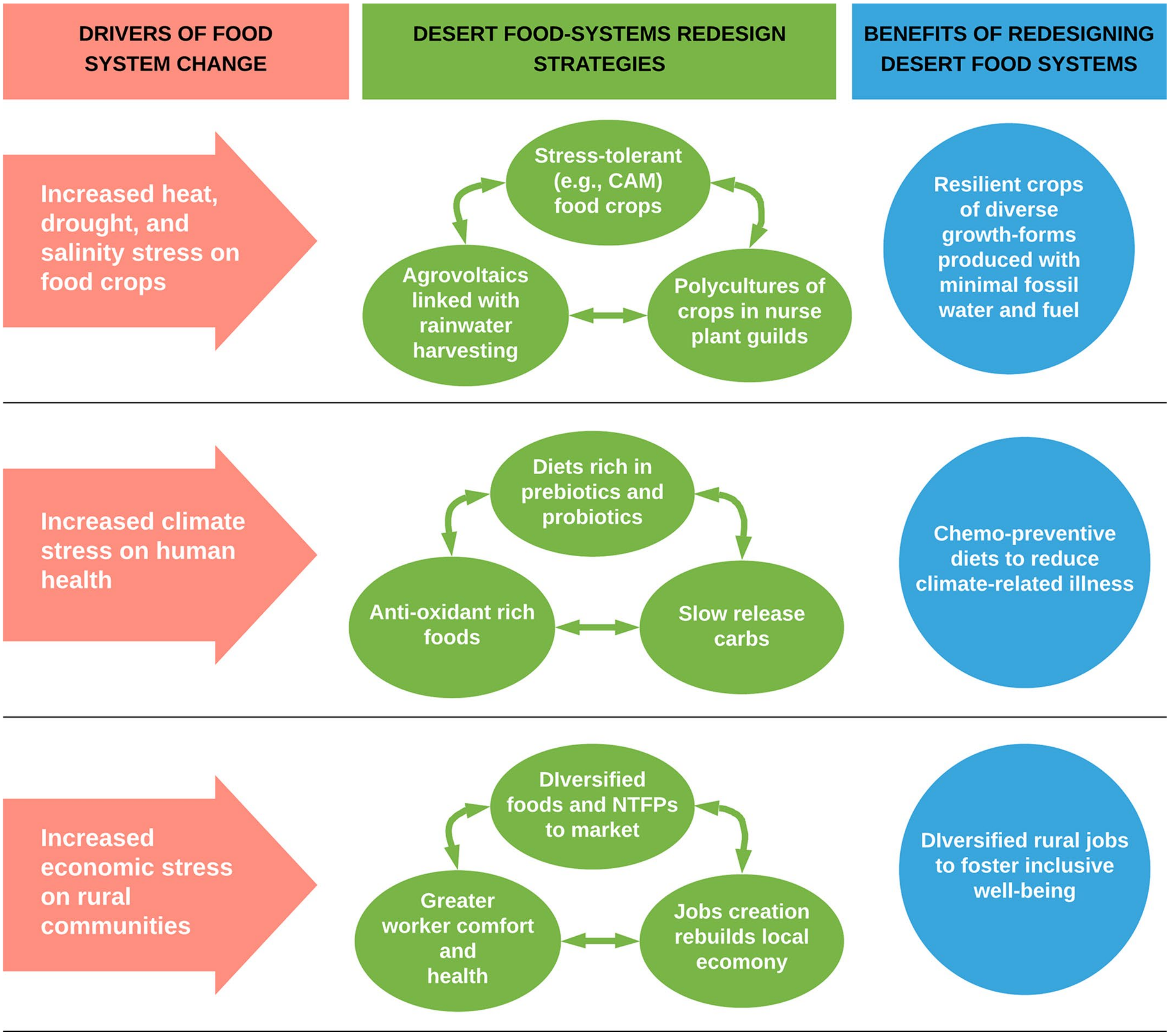


FIGURE 3 Arid-adapted agriculture model that simultaneously fosters agroecological functioning and resilience, human health, and community well-being in the face of climate change. NTFP, non-timbre food product

Rea, 1997). For centuries, traditional farming in dryland Mexico has taken advantage of two contrasting plant life-history strategies: low-variance environmental "averagers" and high-variance environmental "trackers" (Recer et al., 1987). Low-variance CAM succulents (e.g., agaves and cacti) can withstand drought and highly variable precipitation. Their fairly constant standing biomass across time functioned in many traditional cultures as a form of insurance against environmental vagaries. In contrast, the biomass and yield of high-variance annual species (e.g., amaranth and beans) are tightly linked to the precipitation in a given season and year. Coupling low-variance CAM succulents and high-variance seasonal annuals provides yield reliability in the face of highly variable and unpredictable water availability. When rainfall was plentiful, annual plants were primarily consumed, but in periods of drought, agaves and cacti were consumed.

The broad culinary use of many Sonoran Desert plants demonstrates their adaptability across desert environments and cultures, suggesting considerable potential as new, or in some cases resurrected, food crops for Aridamerica. Pods of mesquite and seeds of cacti, herbaceous annuals, and perennial grasses became ubiquitous in Sonoran and Chihuahuan Desert archaeological contexts as early as 5,000–4,000 years ago, suggesting these plants were managed in a form of "proto-agriculture" (Doolittle & Mabry, 2006; Leach & Sobolik, 2010). The Hohokam culture of the northern Sonoran Desert extensively cultivated and harvested rainwater for several *Agave* species for long-term food security (Fish & Fish, 2014). Decades of investment in perennial, water-saving, crops produced stable yields with greater nutrient density compared to many annual crops (Leach & Sobolik, 2010; Pailes, Martínez-Tagüeña, & Doelle, 2018). Indeed, the historical Aridamerican dietary dependence on CAM succulents for both nutrient-dense foods and probiotic beverages is perhaps the highest for any region in the world (Leach & Sobolik, 2010).

Today, desert plants, especially CAM succulents, are receiving renewed interest as resilient crops and natural capital under climate change (Davis et al., 2019; Grace, 2019; Owen, Fahey, & Griffiths, 2016; Stewart, 2015). Compared to conventional C_3 and C_4 crops, CAM plants require tenfold less water per unit dry biomass produced (Mason et al., 2015). Their high water-use efficiency allows reliable yield, even under drought conditions (Davis et al., 2019; Ezcurra, 2007; Stewart, 2015). In the Sonoran Desert, prickly pear (*Opuntia*) fruit are already harvested on large-scale and processed into syrups, jellies, candies, and probiotic fermented beverages (Nabhan & Mabry, 2016). Additionally, CAM cactus crops can reduce soil CO_2 emissions by maintaining organic carbon in soil, even in agricultural zones with declining soil fertility (De León-González et al., 2018). Mesquite (*Prosopis*) trees are managed for honey and for flour (milled from their pods) for low glycemic soft drinks, breads, beers, and tortillas. Ranchers in northwestern Mexico continue to harvest large stands of agaves in restored rangelands to make *bacanora*, *lechuguilla*, and other spirits, demonstrating that traditional knowledge of their value in Aridamerica has not been lost (Gardea et al., 2011).

We propose a new system of arid-adapted agriculture based on perennial polycultures modeled after the native ecosystems and informed by the traditional ecological knowledge of Indigenous desert cultures (Nabhan, 2013). Sonoran Desert nurse plant guilds provide a point of departure for designing multiple-strata agroforestry systems that can weather current and future climatic changes (Nabhan, 2013). Species-specific positive interactions among nurse and understory plants facilitate seedling survival (Gómez-Aparicio, Zamora, Castro, & Hódar, 2008). When applied to polyculture assembly (Table 2), ecological principles of species complementarity (Cardinale et al., 2007), and functional diversity (Cadotte, Carscadden, & Mirotchnick, 2011) facilitate niche partitioning and positive species interactions, thereby promoting agroecosystem services and more efficient use of limiting resources (Faucon, Houben, & Lambers, 2017; Moonen & Bàrberi, 2008). Our desert crop selections for polycultures can be integrated into several agroecosystem designs adapted for arid land food production (Figure 4; Figure S1).

One agroecosystem design features desert legume trees (e.g., mesquite) that shade an understory of cacti, herbaceous perennials, and ephemeral annuals irrigated by active and passive rainwater harvesting systems (Lancaster, 2019; Nabhan, 2013). In these perennial polycultures, trees and shrubs serve as shade-bearing nurse plants (e.g., Suzán, Nabhan, & Patten, 1996), shielding understory plants from intense summer solar radiation, temperature stress, and evaporative water loss. Their root systems provide the entire guild with soil moisture, even during dry summer periods. Rainwater harvested from micro-catchments or small watersheds alleviates water stress while decreasing the need for additional input from groundwater. Legume trees have been shown to redistribute water and nutrients to their nearest neighbors (Barron-Gafford et al., 2017), enhancing underground biodiversity, improving soil microbial functionality, and increasing long-term carbon storage while also decreasing the need for fossil fuel-based fertilizers.

A second design applies the nurse plant concept to co-located renewable energy and food production systems. Instead of being placed under trees, heat-sensitive herbaceous crops are planted in the partial shade of solar photovoltaic arrays that also harvest rainwater. This “agrivoltaic” design couples food and renewable energy production, activities that often compete for available land. Growing crops beneath solar arrays produces notable benefits, including reduced plant drought stress, more stable soil moisture content, reduced photovoltaic panel heat stress, and increased production for some crops (Barron-Gafford et al., 2019). In the winter, insolation by solar arrays maintains warmer air and soil temperatures at night, lessening the frequency of freezing temperatures and helping protect cold-sensitive plants. In the summer, the combination of lower variation in daily temperature (reduced high temperatures) and

TABLE 2 Example of desert-adapted perennial polyculture assembly. Polyculture position: taxon primally grown with other lifeforms in alley cropping (AC), under photovoltaic array (UPA), alongside photovoltaic array (APA), or on terrace lip (TL)

Scientific name	Growth form	Polyculture position	Heat tolerance	Shade tolerance	Water use
Agave angustifolia	Succulent rosette	AC, UPA, TL	High	Tolerant	Storer
Opuntia engelmannii	Multi-stemmed cactus	AC, APA, TL	High	Tolerant	Storer
Stenocereus thurberi	Arborescent cactus	AC, APA	High	Tolerant	Storer
Celtis reticulata	Shrub to tree	AC, APA	Moderate	Provider	Extensive exploiter
Sambucus nigra	Shrub to tree	AC, APA	Low	Provider	Extensive exploiter
Prosopis velutina	Shrub to tree	AC, APA	High	Provider	Extensive exploiter
Sarcomphalus obtusifolius (syn. *Ziziphus obtusifolia*)	Shrub	AC, APA	High	Provider	Extensive exploiter
Capsicum annuum var. *glabriusculum*	Shrub	AC, UPA	Moderate	Tolerant	Intensive exploiter
Lippia palmeri	Shrub	AC, UPA	High	Provider	Intensive exploiter
Phaseolus acutifolius	Summer ephemeral	AC, UPA	Moderate	Tolerant	Intensive exploiter
Salvia columbariae	Winter ephemeral	UPA	Low	Tolerant	Intensive exploiter

FIGURE 4 Examples of arid-adapted agroecosystems. Clockwise from left: agrivoltaic design at Biosphere 2 outside Tucson, AZ, USA (image credit: Greg Barron-Gafford); intercropping of agave and columnar cacti near Las Canoas in Jalisco, Mexico (image credit: Bill Hatcher), perennial polyculture of columnar cacti, arborescent cacti, agave, and legume trees near Las Canoas in Jalisco, Mexico (image credit: Bill Hatcher)

relative humidity (increased humidity) decreases evapotranspiration for plants under the arrays, thereby lessening dependence on both fossil groundwater and the fossil fuel used to pump water (Barron-Gafford et al., 2019). Intercropping beneath and between arrays with plants with diverse low- and high-variance life-history strategies can further compensate for the increasing vagaries of weather.

Shifting from input-intensive conventional agriculture to regenerative, arid-adapted agroecosystem designs has the potential to improve biodiversity and food security while promoting rural livelihoods. Rural livelihoods are being hard hit by climate-related hazards including exposure to extreme weather, losses in crop yields, and food insecurity (Olsson et al., 2014). Indigenous populations are particularly vulnerable, with climate change exacerbating chronic stresses, such as extreme poverty and nutrition-related diseases. Agroecosystem- and agroforestry-based food production can restore self-reliance, improve access to culturally relevant and healthy foods, provide economic stability, and enhance resilience to climate change (Altieri & Toledo, 2011; Krishnamurthy, Krishnamurthy, Rajagopal, & Peralta Solares, 2019). Communities are already benefiting from research and community outreach promoting desert food plants to control an epidemic of nutrition-related diseases (e.g., diabetes) in Indigenous America (Brand et al., 1990; Nabhan, 2008). Across most of Latin America, food production approaches that integrate agroecological science and traditional knowledge are conserving natural resources, enhancing food security, and empowering rural communities and peasant organizations and movements (Altieri & Toledo, 2011).

By combining elements of traditional and high-tech agroecosystems, we illustrate how linking time-tested and novel practices can foster more resilient food systems. We envision deployment at smallholder or landscape scales for a net positive impact on environmental and ecosystem health. Systems can combine high- and low-tech designs, but ideally should be based on sound ecological and economic principles to foster sustainability. A number of candidate arid-adapted food plants have been subject to agronomic research into their potential as new crops (Felger, 1975). Within Sonora, Mexico, there are precedents to bring mesquite (*Prosopis*), wild oregano (*Lippia palmeri*), joboba (*Simmondsia chinensis*), and agaves (*Agave*), and wild chiles (*Capsicum annuum* var. *glabrisculum*) into small to medium scale cultivation. Perennial-based agroforestry designs can be economically competitive with annual row crops when mechanized and managed for scale (Gruley & Keeley, 2018), however, alternative desert crops have not benefited the decades-long efforts to scale harvesting and processing technologies or the long-standing federal government subsidies of conventional crops. In addition, new desert crop development should be coupled with in situ and ex situ conservation strategies to ensure the protection of wild genetic diversity (Riordan & Nabhan, 2019).

The success of regenerative arid-adapted agriculture will hinge upon the generation of collective knowledge and integration of plant, environmental, social, and health sciences research relevant to policy (Garibaldi et al., 2017; Šūmane et al., 2018; Zimmerer & de Haan, 2017). Additional research is needed to fill knowledge gaps, particularly with respect to belowground agroecological functioning (i.e., drylands soil carbon sequestration and microbiome diversity) and crop-specific benefits and constraints for agrivoltaics. We also need to better understand the factors that constrain the effectiveness and adoption of agroecological practices in order to inform sustainable agriculture and policy, create economic incentives, and generate new markets and consumer demand. The local food economy of Tucson, Arizona—the first UNESCO City of Gastronomy in the United States—is a promising example of a diverse market and growing consumer demand for sustainably grown, arid-adapted food crops (Nabhan & Mabry, 2016). Creating knowledge sharing networks (Šūmane et al., 2018), including extension programming for smallholder farmers and seed and cutting sharing networks, can foster collective knowledge about the cultivation and use of desert crops. These efforts should be coupled with efforts to ensure reciprocal sharing of knowledge, technologies, and resources with Indigenous communities and protections against biopiracy of Indigenous crops.

We put forward a new Aridamerican food production strategy, informed by centuries of rich traditional ecological knowledge from many desert cultures, that can benefit the health of our lands and communities. Climate change is already threatening crop yields and accelerating dryland expansion. We must consider a wider range of crop growth forms and agroecosystem designs to ensure future food security in the face of climate change. Novel food, water, and energy provisioning designs can incorporate deeper adaptations to aridity that not only deal with the symptoms of climate change but also help address its causes. Adopting such designs will require transdisciplinary integration of plant, environmental, social, and health sciences as well as key collaboration with smallholder and traditional farmers. Now is the time to champion desert-adapted crops for more resilient food systems.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

G.P.N. conceived the paper and facilitated group input. G.P.N. and E.C.R. wrote the manuscript. G.P.N., E.C.R., L.M., and A.B. developed the selection criteria. B.T.W., E.E., G.P.N., A.B., P.M., and E.C.R developed the conceptual map of Aridamerica. L.M., A.M.R., and W.C.H. contributed ethnobotanical data on Sonoran Desert food plants. W.C.H. checked taxonomy and provided food plant use in the Sonoran Desert. J.M. provided data on antiquity of historical and current plant use. G.P.N. and L.M. reviewed health benefits. T.M.C. provided perspectives on perennial polycultures. J.A. provided perspectives on halophytes and saline agriculture. J.G. provided Spanish common names and contemporary uses in Mexican deserts. G.B.-G. provided information on agrivoltaic design. J.G. and B.T.W. provided data on accessions from botanical garden and research institutions. All authors contributed ideas, reviewed, and approved the manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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