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Large variation in availability of Maya food plant sources during ancient droughts

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Paleoclimatic evidence indicating a series of droughts in the Yucatan Peninsula during the Terminal Classic period suggests that climate change may have contributed to the disruption or collapse of Classic Maya polities. Although climate change cannot fully account for the multifaceted, political turmoil of the period, it is clear that droughts of strong magnitude could have limited food availability, potentially causing famine, migration, and societal decline. Maize was undoubtedly an important staple food of the ancient Maya, but a complete analysis of other food resources that would have been available during drought remains unresolved. Here, we assess drought resistance of all 497 indigenous food plant species documented in ethnographic, ethnobotanical, and botanical studies as having been used by the lowland Maya and classify the availability of these plant species and their edible components under various drought scenarios. Our analysis indicates availability of 83% of food plant species in short-term drought, but this percentage drops to 22% of food plant species available in moderate drought up to 1 y. During extreme drought, lasting several years, our analysis indicates availability of 11% of food plant species. Our results demonstrate a greater diversity of food sources beyond maize that would have been available to the Maya during climate disruption of the Terminal Classic period than has been previously acknowledged. While drought would have necessitated shifts in dietary patterns, the range of physiological drought responses for the available food plants would have allowed a continuing food supply under all but the most dire conditions.

Maya | ethnobotany | agriculture | drought | sustainability

It is widely accepted that something significantly disrupted ancient Maya social order during the Terminal Classic period (ca. 750 to 900/1000 CE). Population growth and the accompanying environmental impacts of deforestation have historically been suggested as causes of the social decline during this period (1). In recent years, evidence for extended droughts in the Maya Lowlands have gained prominence in both popular and academic circles as a likely cause for the Terminal Classic decline. Paleoclimatic records derived from lake and marine sediment cores and speleothems have been interpreted as indicating multiple, often closely spaced, droughts of varying intensity across the Maya Lowlands during the Terminal Classic (2–4), suggesting to some that climate impacts contributed to the disruption of Classic Maya polities and economic organization, and led to a decline in health and population levels (5). However, complex human–environmental interactions and sociopolitical factors have also been advanced as causes for what is sometimes considered more of a "reorganization" than "collapse," in which droughts were potentially a contributing factor rather than a direct cause (6–13). We focus here on the events and processes of the Terminal Classic period, which have received the most attention regarding the possible impact of drought, while recognizing that severe droughts of both earlier and later periods would have necessitated responses by Maya groups. One of the keys for understanding the potential for drought to have destabilized ancient Maya society is whether the documented meteorological droughts led to agricultural drought and were severe enough to disrupt food production and cause food shortages. Meteorological drought refers to rainfall amounts, while agricultural drought is related to the availability of water for crops; specifically, water availability for a particular crop to grow at a particular time and place. Archaeologists have tended to equate agricultural drought directly with meteorological drought, with the assumption there is a direct causal/proportional relationship between rainfall deficit and agricultural drought. This relationship is, however, not a simple one, as we will explore in this study. Climatological publications on the Maya droughts often discuss links between droughts and the disruption of Classic Maya society, without specifically suggesting agricultural collapse (2, 14, 15), by briefly noting the potential impact on food production or agriculture (4, 16–18) or by discussing only maize in relation to drought impact on ancient agriculture (19, 20). Turning to the impact of droughts and associated famines suffered by the Maya during the Colonial period, Hoggarth and colleagues (21) use historic records to examine maize availability during droughts, while the only reference to other food plants used during droughts is a brief allusion to eating the bark of trees. Other approaches argue that droughts were a constant threat to Maya society, reaching the most disastrous levels of agricultural collapse and starvation during the Terminal Classic (22).

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Significance

The disruption of Classic Maya society coincided with extended droughts, as suggested by numerous paleoclimatic studies. However, the role of drought in civil upheaval and demographic decline is complicated by the difficulty of linking relatively coarse estimates of meteorological drought with fine-scale plant processes that underpin agriculture. Our analysis of drought resistance across the historically documented, indigenous food plants of ethnographic Maya groups shows a broad range of foods gradually dwindling through droughts of increasing severity. This finding implies that short to moderate droughts could have caused agricultural disruption but not subsistence collapse. However, multiyear extreme drought is consistent with agricultural collapse and the specter of starvation, unless mitigated by food storage or trade from areas less affected by drought.

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Human populations can respond to droughts and other food stresses in a number of ways (23–25), including reliance on stored foodstuffs, crop diversification, and trading nonfood materials for food available in neighboring communities or regions. Contemporary Maya people enhance food security by planting crops in contrasting soil types (26–30) and diversifying agricultural varieties and landraces capable of production in differing microenvironments (28–32). Archaeological evidence for food storage by the ancient Maya is scant (33–35), and there is no evidence of large-scale food storage, such as storehouses, as found in several other ancient cultures of the New World (e.g., ref. 36). Ethnographic studies for the Maya document only small-scale storage facilities associated with households (37).

While there is strong evidence that maize was important to the ancient Maya as both a staple food and symbolic touchstone, there has been growing evidence for and recognition of the contribution of many other crops for both their subsistence and symbolic values (38–44). Still, little attention has been given to the relative drought resistance of maize when compared to other crops. Maize is an annual herbaceous plant that gains some water conservation through the C_4 photosynthetic pathway (45) of which more drought tolerant landraces have been selected, but maize harvests can be significantly reduced during drought years (29, 46, 47). Ethnographic studies of food plant species used by contemporary Maya people during drought or food shortage indicate that many so-called famine foods are both cultivated and grow in a natural forest, representing a form of food storage through living plants. Until now, a broad analysis of the food resources that would have been available to Maya people during ancient droughts has not been undertaken. Here, we analyze the drought resistance of the 497 indigenous food plant species, documented ethnographically, as having been used by the lowland Maya (39) and estimate the range of crop and wildland plant food products that would have been available under varying levels of drought.

In the Maya Lowlands, annual rainfall is divided into a wet season, generally from June to October, and a drier season, generally from November to May. Rainfall fluctuation between seasons can be significant, as can rainfall patterns within the wet season. Reduction in annual rainfall due to drought can manifest in various ways, and plants have a high diversity of responses to drought (48–50). A short-term drought could have a catastrophic impact on rain-fed herbaceous crops without any effect on woody tree crops with roots that reach the water table. Lengthening the dry season could have significant impact on agriculture and plant growth, while decreasing rainfall during a rainy season of normal length could have little or no impact on agriculture or plant growth, as long as the ground retained enough moisture for the plants to grow. It should be noted that an excess of wet season rainfall, usually a result of hurricanes or tropical storms, can also severely impact crops and livelihoods of Maya farmers (51, 52). Much of this interseasonal rainfall variation can be masked by annual precipitation records. Globally, only ~33% of contemporary variation in crop production is explained by interannual climate variability (46). For the modern Maya, fine-scale daily rainfall variations within a growing season, rather than annual precipitation, are recognized as determining crop success or failure. Too much or too little rain within a growing season is the significant variable (53). Unfortunately, most paleoclimatological studies for the Maya region are not yet able to distinguish the seasonal distribution of rainfall reduction. One paleoclimatic study does suggest that rainfall reduction during the Terminal Classic period was likely due, primarily, to a decrease in frequency and intensity of summer season tropical rainstorms rather than a complete loss of summer tropical storm activity (15).

A key to understanding the potential role of drought in ancient Maya social history is whether the droughts were intense enough to affect food production. Our evaluation of indigenous food plants is aimed at determining what would have been available under varying levels of drought during any period of ancient Maya history, based on well-established plant functional traits (54, 55) and knowledge of nutritional value for the plant parts eaten (56, 57). Our definitions for levels of drought severity used in this study are provided below in *Materials and Methods*. Our main questions are the following:

1) What is the range of growth forms and drought survival traits found among Maya food plants?
2) How would the availability of food plants vary during different drought intensities?
3) What types of plant-based foods would have been available during the most severe drought scenarios?

Results

We found that of the 497 indigenous food plant species documented as having been used by the lowland Maya, 445 of these species have a total of 577 edible parts identified, such as fruits and roots, that would be available during a year of normal rainfall; the other 52 species of food plants do not have the specific edible parts reported.

During a short-duration drought, 84 species, essentially herbaceous C_3 plants, would not survive an extended dry season, leaving a total of 413 plant food species available for consumption (Fig. 1*A* and *SI Appendix*, Tables S1 and S2). In a short-duration drought, the most common form of drought, some annual staple crops, such as beans and squash, might not produce, but plenty of food would be available. During short-duration drought, a total of 458 edible parts would still be produced (Fig. 1*B* and *SI Appendix*, Tables S1 and S2). Of these, 119 species of tree fruits would be available, including domesticated species such as papaya (*Carica papaya*), mamey (*Pouteria sapota*), avocado (*Persea americana*), and hog plum (*Spondias purpurea*). Avocado stands out for its fat content, while carbohydrate content of hog plum approaches that of maize (Table 1). Also remaining available in short-duration droughts would be other crops that have been suggested as subsistence alternatives to maize, such as amaranth grain (*Amaranthus*); the nuts of the ramon tree (*Brosimum alicastrum*); productive root crops such as manioc (*Manihot esculenta*), malanga (*Xanthosoma violaceum* and *Xanthosoma yucatanense*), and sweet potato (*Ipomoea batatas*); and protein-rich leaves of chaya (*Cnidoscolus tubulosus*). These plants offer several carbohydrate-rich options and reasonable protein content in chaya and ramon, although not at the same protein levels as bean and squash seeds (Table 1).

During a moderate, year-long drought without summer season tropical storms, an additional 305 food plant species, including maize, would no longer produce food, leaving 108 productive species available (Fig. 1*A*). A total of 179 edible plant parts from the 108 species would still be available, representing an overall decrease of 69% of edible plant parts and 78% of species from years with normal rainfall (Fig. 1). The most notable drop in available food plants is seen in tree fruits/nuts, including ramon, available in a short-duration drought but eliminated in a drought of moderate duration. Additionally, other edible reproductive organs of all plants, as well as all edible oils produced from seeds/nuts, would cease to be available. However, all other plant parts available during a short-duration drought would continue to be available during a moderate-duration drought (Fig. 1*B*). This would include 43 species of leaves from C_4 herbaceous plants, crassulacean acid metabolism (CAM) plants, and C_3 plants with woody stems, including highly nutritious chaya. Root crops would continue to be

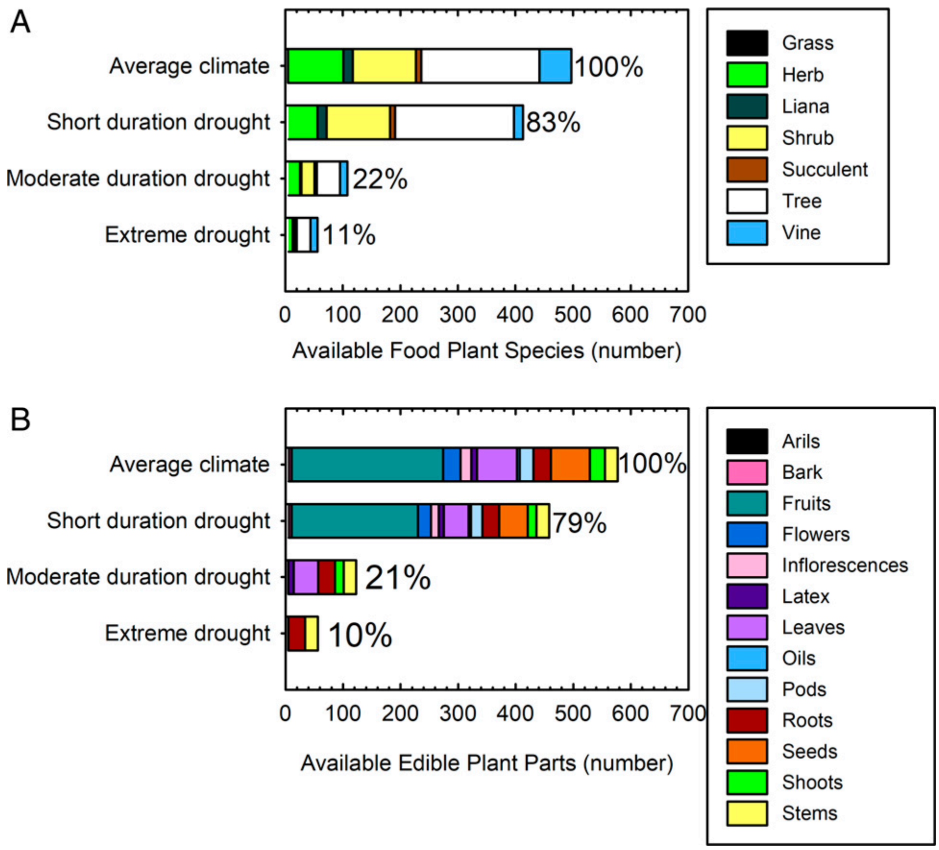

Fig. 1. Available edible plant organs (*A*) and available food plant species (*B*) during simulated climatic conditions, illustrating the dwindling breadth of food resources potentially available to ancient Maya as simulated drought proceeds.

available, with 29 species, including all those noted above, for short-duration droughts.

In an extreme multiyear drought, an additional 52 species would cease to be available as food sources, leaving 56 species with 56 edible parts that would still be harvestable. This number represents an overall decrease of 89% of species and 90% of edible plant parts from years with normal rainfall. Even among species with high-drought resistance, 296 of those species, or 91%, are likely to cease production of edible parts under conditions of extreme drought. This situation results in a precipitously narrow variety of food choices of roots, palm stems, and tree bark, many of them wildland plants with relatively high carbohydrate contents and some protein, as a last resort for harvest (Fig. 1 and Table 1 and *SI Appendix*, Tables S1 and S2).

Of the 29 edible roots that would probably be available into extreme drought, 25 of these species have low-drought tolerance (herbaceous stems), meaning no above-ground growth would occur (*SI Appendix*, Table S2). These roots would probably still be available to harvest through the first year of extreme drought, but how long they would survive in the ground beyond that is uncertain. However, four species that produce edible roots also have high-drought resistance and woody stems and would be the most likely to survive under multiple years of extreme drought. These plants are manioc (*M. esculenta*), papaya (*C. papaya*), yucca (*Yucca guatemalensis*), and the little known mata ratón (*Zamia polymorpha*), a rare cycad, the roots of which would probably need to be processed to remove toxins before eating. Of the root crops with high-drought resistance, manioc stands out as very nutrient dense (Table 1) and has recently been demonstrated to have been intensively cultivated by the ancient Maya (62). Manioc roots continue to grow for up to 2 y after planting, but after that age, the roots become tough and woody though still edible (63, 64). While manioc has several adaptations which promote survival during drought, how well the plant would continue to produce new growth, including roots, appears to depend on the seasonality of water availability during a drought year (65).

Edible plant stems, particularly heart of palm (Arecacae family), would be the most reliable and abundant plant food during extreme drought. The heart of palm, or palmito, consists of the actively growing portion of the meristem and tender undeveloped leaves, with a remarkably high carbohydrate content and a protein content approaching maize (Table 1). It is generally harvested by cutting off the upper part of the palm just below the oldest leaf. The leaves and outer growth are then cut away to reveal the tender, cylindrical heart. The volume of heart of palm increases with the size of the tree; young trees may produce only a finger-size portion, and larger palms can produce many pounds of a meaty, edible heart. While single stemmed palms would be killed by harvesting the heart, many palm species are multistemmed or clonal, and hearts of individual stems can be harvested through many years without killing the remaining clonal parent plant. Under conditions of extreme drought, the new growth of palms may slow or cease, with the hearts remaining in stasis for many years until adequate moisture is available to resume growth. Palms are extremely common throughout the Maya Lowlands and are found in nearly all local vegetation types. Most species of palm produce edible hearts, so the count of 18 species with documented use as food by Maya people (*SI Appendix*, Table S1) is probably a low estimate.

Table 1. Energy and nutritional content of Maya food plants per 100 g portion, comparing staple annual crops with the selected Maya alternative foods remaining available during increasing levels of drought intensity

Food	Energy (kcal)	Protein (g)	Fat (g)	Carbohydrate (g)
Staple annual food plants available during years of normal rainfall				
Maize*	89	3.27	1.35	18.70
Bean*	341	21.60	1.42	62.36
Squash (fruit)*	26	1.00	0.10	6.05
Squash (seed)*	559	30.23	49.05	10.71
Selected food plants remaining available during short drought				
Avocado*	160	2.00	14.66	8.53
Hog plum†	65	1.06	0.62	13.90
Mamey*	51	0.50	0.50	12.50
Papaya*	43	0.47	0.26	0.39
Amaranth (seed)*	317	13.56	7.02	65.25
Ramon (nut)*	217	5.97	0.99	46.28
Selected food plants remaining available during moderate drought				
Chaya (leaves)‡	32.25	5.70	0.40	4.20
Amaranth (leaves)*	23	2.46	0.33	4.02
Malanga (root)*	98	1.46	0.40	23.63
Sweet potato (root)*	86	1.57	0.05	20.12
Selected food plants remaining available during extreme drought				
Heart of palm*	115	2.70	0.20	25.61
Bark§	109	5.30	1.84	20.50
Cactus pad*	16	1.32	0.09	3.33
Manioc (root)*	160	1.36	0.28	38.06

*Ref. 57.
†Ref. 58.
‡Refs. 59 and 60.
§Ref. 61.

Cactus pads are another form of plant stem that could provide food well into an extreme drought. Four species in the Cactaceae family are reported as food sources for Maya people, *Nopalea cochenillifera*, *Opuntia dillenii*, *Opuntia guatemalensis*, and *Opuntia ficus-indica*, all commonly known as nopal or prickly pear. The young, tender pads are most commonly eaten, although the older pads are also edible, though they become more fibrous with age. Prickly pear is highly drought resistant, having a CAM photosynthetic pathway, and would likely survive and remain edible many years into extreme drought. These cacti are not common in the interior of closed forest but occur on sandy soils and other open vegetation types and increase in numbers moving northwest into more arid zones. Although potentially and locally abundant in some of the lowland Maya region, the nutritional content of the pads more closely resembles a sweet fruit than a carbohydrate-rich staple food (Table 1).

Bark is most often mentioned as the last resort food for Maya people during extreme drought (e.g., ref. 21). The edible portion is actually the inner bark or phloem, a thin layer of soft, spongy tissue between the cork cambium and the vascular cambium that functions to transport the carbohydrate-rich products of photosynthesis from leaves to roots. Even when trees become deciduous, most have scattered photosynthetic tissue in wood and can continue to transport carbohydrates in the phloem. The phloem can be harvested in patches from a tree without killing it, although removing phloem in a full circle around the trunk would effectively girdle the tree, likely killing it. Bark can be eaten raw or cooked and can be dried and ground into flour. Not much nutritional data are available on edible bark, but what exists shows relatively high carbohydrate and protein contents (Table 1). Ethnographic reports and field documentation of bark used as food by human groups is widespread (e.g., ref. 66). The bark from many species of trees is edible, and, like heart of palm, is probably underrepresented in reports of edible plants used by the Maya. Bark from five species of trees is documented as being used by the Maya as food (*SI Appendix*, Table S1). Three of these are in the Fabaceae family, with two known in English as cabbage bark (*Lonchocarpus castilloi* and *Lonchocarpus longistylus*) and the third as turtle bone (*Lepanthes guatemalensis*). The other two reported species are in the Malvaceae family, the ceiba (*Ceiba aesculifolia*) and the provision tree (*Pachira aquatica*).

Discussion

The Mesoamerican crop triad of maize (*Zea mays*), beans (*Phaseolus vulgaris* and *Phaseolus lunatus*), and squash (four species: *Cucurbita argyrosperma*, *Cucurbita lundelliana*, *Cucurbita moschata*, and *Cucurbita pepo*) are often equated with the core of Maya milpa agriculture, both ancient and modern (Fig. 2) (27, 67). Of these, only maize is likely to be productive into a short-duration drought, dependent on the maize landrace, planting location, and the timing of planting in relation to the reduced rainfall. Our analysis shows that none of the traditional milpa triad of species would produce food in moderate or extreme droughts. If droughts reached moderate or greater levels and ancient Maya people were dependent on maize, beans, and squash alone, starvation would set in rapidly; however, this is a highly unlikely scenario. Our analysis demonstrates that a great diversity of other food plants was available to ancient Maya people in times of drought (Figs. 1 and 2 and *SI Appendix*, Table S1), although we have not attempted to estimate population levels that could be sustained by these diverse

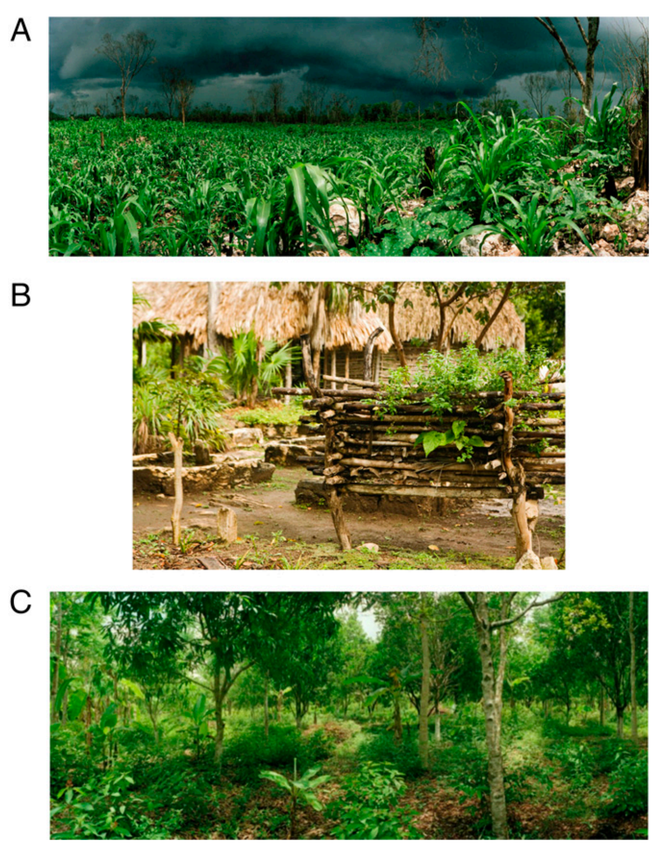

Fig. 2. Contexts of Maya food plants: milpa (*A*), home garden (*B*), forest garden (*C*). Photographs courtesy of and ©Copyright Macduff Everton.

food sources. It is interesting to note that many of the drought-resistant species are grown in the home garden (literally right outside the residence) and the outfield forest garden, while the key species of the outfield milpa are among the most drought-susceptible plants. Droughts would likely increase reliance on both close-to-residence home gardens and more distant forest gardens. As droughts intensified, people would have ventured deeper into the forest to forage for remaining food sources such as heart of palm and bark.

Decreasing the availability of plant foods through increasing the severity of drought represents a slow chipping away of resources. Our three discrete levels of drought severity and three classes of drought resistance for plants provide a framework for evaluating dwindling sources of plant foods and their edible parts with increasing drought. However, drought severity varies substantially, and responses by individual plant species will vary depending on the sum of all physiological survival traits employed by a plant, as well as other factors such as soil moisture availability in different physical settings (48, 49). Analyzed here are general trends in plant availability and use along a sliding scale that might be expected under varying drought conditions. Droughts of short or even moderate duration would have caused agricultural disruption and hardships but not subsistence collapse and starvation. Extreme drought, particularly lasting several years, could have caused agricultural collapse and the specter of starvation, unless mitigated by storage of foodstuffs, shifting of planting locations to soil environments with greater moisture retention, or access to food from areas less affected by drought. A discussion of which Maya plant foods might have served as commodities that could have been stored and transported has previously been presented by Fedick (40).

We caution here that interpretation of paleoclimatological data for meteorological drought does not translate simply into evidence for agricultural drought. The impact of meteorological droughts on agriculture is not certain or clear. Depending on the seasonality of rainfall during drought, there could have been a disruption of plant food availability, but the diversity of plants and their edible parts could have averted famine. It should not be assumed that the current paleoclimatological data indicates the severe impacts on plant food availability modeled here for extreme drought.

The resolution of climatological data is improving and, hopefully, will facilitate better characterization of the seasonal distribution of rainfall during ancient droughts, making the problem of predicting ancient food resources as a function of climate more tractable. This dataset, combined with ever-expanding botanical research, will help to identify particular drought survival strategies among species, as well as direct measures for each species of when hydraulic failure occurs (68, 69). The journey from maize to bark under conditions of increasing drought severity is nuanced and complex. A vast store of traditional knowledge about plant use held by contemporary Maya people reveals a great deal of flexibility in response to climate change in ancient times, as well as for the present and future.

Materials and Methods

We analyzed a database of 497 indigenous plant species, described as being used as food in the Maya Lowlands compiled by Fedick (39), based on reviews of 28 ethnographic, ethnobotanical, and botanical studies that contain taxonomic identifications of plants to the species level. The list is updated to current taxonomic nomenclature of the Angiosperm Phylogeny Group (*SI Appendix*) for both domesticated and nondomesticated food plant species. In the original database (39), 52 plant species were identified in the ethnographic record as being used as food by the contemporary Maya without specifying which part or parts of the plant were eaten. Those species are included here in the analysis of species survival under drought conditions but are not used here in the quantification and discussion of edible plant parts from the other 445 species. Also, only those plant parts identified in the ethnographic record as having been used by Maya people are utilized in this analysis, although other parts of plants may be reported as edible outside of the Maya cultural region.

The basis of this study is a list of indigenous food plants of the Maya Lowlands, as derived from modern ethnographic and ethnobotanical studies (39). While maize has a long history of recovery from Maya archaeological sites, it is well known that taphonomic processes result in the overrepresentation of maize in the paleoethnobotanical record when compared to other plant species (see ref. 70). Paleoethnobotany and methods for recovery and identification of ancient plant remains have advanced significantly over the last 20+ y (70–72). These recent advances now allow for recognition of many previously unidentifiable plant taxa of the Maya Lowlands, not only through long established recovery methods for pollen and carbonized macrobotanical remains but also through identification of phytoliths, starch grains, and chemical residues. The contexts for paleobotanical recovery in the Maya Lowlands have also expanded beyond middens and burials to include household floors, garden and field areas, residues adhering to cooking vessels and stone tools, and dental calculus. While a review of paleoethnobotanical plant identifications from ancient Maya sites is beyond the scope of this paper, it is worth noting that nearly all plants discussed here in the text have been identified in paleoethnobotanical studies of the Maya Lowlands.

In this study, we considered three levels of drought severity: 1) Short-duration drought, a year with the dry season extended in duration for up to an additional 3 mo. 2) Moderate-duration drought, up to a full year of dry season rainfall pattern, essentially missing a rainy season. 3) Extreme drought, multiple years without normal rainfall, basically a year-to-year pattern of only dry season precipitation. All these levels of drought have been historically documented in the region (73, 74).

We used growth form and photosynthetic pathway to classify each plant species into one of three drought resistance classes: 1) Low-drought resistance is assigned to plants that would fail to grow or live in short-duration droughts. 2) Moderate-drought resistance is assigned to plants that would continue to survive and grow under moderate-duration droughts. 3) High-drought resistance is assigned to plants that would survive and grow, even under extreme drought conditions. To assign plant species to a drought resistance class, species were first distinguished as woody or herbaceous based on botanical descriptions (75, 76) or familiarity with species (personal observation), with woody species being assigned to high-drought resistance (class 3), based on their trunk as a water storage organ (77, 78), and that roots of woody species are generally deeper than herbaceous species (79). Herbaceous plants were further divided into drought resistance classes, with C_3 plants assigned to low-drought resistance (class 1), C_4 plants assigned to moderate-drought resistance (class 2), and CAM plants assigned to high-drought resistance (class 3), based on differences in the water conservation benefits of their contrasting photosynthetic pathways (45). The drought resistance classes reflect the physiological ability of a plant to survive and grow under varying drought conditions but does not account for the availability of particular edible organs.

We also considered potential availability of the 13 classes of edible organs: fruits, flowers, pods, inflorescences, arils, seeds, oils, gums and latex, leaves, shoots, stems, roots, and bark, under the three defined levels of drought severity. The availability of edible plant parts under varying drought conditions are determined by growth form and known phenological cycles of crops and tropical plant species (80, 81).

Under short-duration droughts, plants with low-drought resistance (herbaceous stems, C_3 photosynthetic pathway) are expected to die, or at least cease new above-ground growth, including all edible reproductive organs (inflorescence, flower, fruit, pod, aril, and seed). Edible oils that otherwise could be processed from seeds/nuts would cease to be available, as would the edible sap produced by the herbaceous species *Costus pulverulentus* (Costaceae). Edible roots of low-drought resistance plants would probably continue to be available, with one exception: an annual (*Eleocharis geniculata*) with roots that are not considered available under drought conditions. All other edible portions of moderate- and high-drought resistance plants would continue to be available under short-duration drought. Plants with moderate-drought resistance (herbaceous stems, C_4 photosynthetic pathway) would likely continue to produce edible leaves and seeds/grains. Plants with high-drought resistance would likely continue to produce all edible portions with short-duration drought.

Under moderate-duration droughts, all of the edible reproductive organs (inflorescence, flower, fruit, pod, aril, and seed) available under normal rainfall or short-duration drought from plants of high-drought resistance would no longer be available. Edible roots and other edible portions from plants of moderate- to high-drought resistance consisting of leaves, shoots, and plant exudates, such as gums, sap, and latex, as well as stems, roots, and bark, would remain available.

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Under conditions of extreme drought, stems (specifically hearts of palm and cactus pads/cladodes) and bark would remain available, likely for multiple years. It is probable that edible roots of established perennial plants, even of low-drought resistance, would remain viable in the ground, potentially for multiple years, although new growth would probably not continue.

For this study, we assumed uniform soil nutrient and drainage conditions and depth to water table. We were only able to account for rain-fed cultivation and could not consider irrigation, channelized or raised fields, terracing, or other cultural practices. The current study does not distinguish between domesticated and "wild" plants, although plants of varying drought resistance (*SI Appendix*, Table S1) can be checked against the domestication status for all species, as provided in the original list (39). We also do not distinguish if plants are normally cultivated in formal agricultural fields, such as the milpa (e.g., ref. 67), in home gardens (e.g., ref. 82), or in managed forest gardens (e.g., ref. 38); they are all documented food plants, and many of them are found growing in multiple contexts. We also do not consider food storage, and we acknowledge that our estimates of food availability are therefore conservative, because some foods like grains and oils can be stored for long periods. We recognize that not all of these plants would have been equally available across the entire Maya Lowlands. However, environmental gradients across the Yucatan Peninsula primarily result in differences in relative frequency of species, rather than presence or absence (83).

Data Availability. All study data are included in the article and/or *SI Appendix*.

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