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OPINION

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Plants and people: Our shared history and future

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Societal Impact Statement

Humans and plants have a complex relationship extending far back into our joint evolutionary history. This legacy can be seen today as plants provide nutrition, fiber, pharmaceuticals, and energy for people and animals across the globe. Plant domestication and agriculture allowed human society to develop and our settlements to become more complex. As such, our modern cities and cultures rely in part on the stable and reliable production and distribution of food. This work examines how changes affecting the globe may impact upon the plant–human relationship, and how plant science can approach future change as both a challenge and an opportunity.

Summary

Hominids have coevolved with plants for millions of years; the skulls of ancient hominids reflect the nature of the plant species they ate, while more recently we domesticated plants to suit our needs, leading to a dramatic cultural shift from hunter-gatherer to agricultural societies. Our deep relationship with, and understanding of, plants has enabled us to harness their nutritional, medicinal, and aesthetic benefits. Here, I describe how science can facilitate the further exploration of plant species, providing the information we need to adapt plants to enable us to meet the demands of the growing population or to identify novel plant-derived compounds with important medical applications. Many of the major global challenges we face will also impact our relationship with plants; we must protect their biodiversity, which holds vital information and solutions that will help us to cope with these problems. Discoveries arising from the research pipeline of basic and applied research will yield new technologies to both utilize and protect our relationship with plants in the future.

KEYWORDS
agriculture, biodiversity, humans and plants, joint evolutionary history, plant domestication, plant–human relationship, plants and people

1 | INTRODUCTION

Plants are central to our well-being, not only as food, but also as key components of our cultures, religions, and medicines. This can be seen in way that the beautiful curve of a tendril inspires art, or in the fact that indigenous forest peoples collect plant materials for medicinal use or for religious practices. We do not just get nourishment from plants, they are central to our societies.

We can see the importance of our relationship with plants in ancient art. Ancient petroglyphs carved by the Pueblo Native Americans depict maize (*Zea mays*), illustrating how important this particular plant is to their culture. Paintings from the Minoan civilization (2600–1100 BC) portray papyrus (*Cyperus papyrus*), while lychees (*Litchi chinensis*) are often represented in the exquisite art of China. Plants have inspired humans for a long time.

2 | COEVOLUTION

The evolutionary relationships between plants and people are complex. Peter Raven, one of the most important figures in plant biology and whose work is also featured in this issue (Raven, 2019), determined the term "coevolution" together with colleague Paul R. Ehrlich (Ehrlich & Raven, 1964). Coevolution is the process by which species interact with and respond evolutionarily to each other—a definition that encompasses several relationships between plants and humans.

Australopithecus africanus was a hominid that lived around three million years ago that is believed to be very similar to our human ancestors. *Australopithecus* lived in forest regions and survived on a challenging diet of hard nuts and the tough underground storage organs of plants, which were both difficult to chew and to extract nutrients from. The skull of *Australopithecus* possessed a very large jaw with large teeth covered in thick enamel, and was highly ridged for large muscles to attach to the jaw. The morphology of the *Australopithecus* skull enabled the chewing of tough plant material, and was an evolutionary response to its diet. In addition, *Australopithecus* had a very long gastrointestinal system to facilitate the digestion of plant material.

Moving forward 1.5 million years to *Homo erectus*, a recent ancestor of humans, the skull was much lighter (Figure 1), with smaller teeth and thinner enamel than *Australopithecus;* these hominids also had a much shorter gastrointestinal system. *H. erectus* is believed to have foraged on the savannah for grasses and grass seeds, which are a better food source than the plants eaten by *Australopithecus*, and are less difficult to digest. As such, *H. erectus* did not require the same musculature or gastrointestinal system as *Australopithecus* to survive.

In addition to these morphological adaptations, hominids also adapted biochemically to ingestion of plant material. Probably one of the most important biochemical pathways in plants is the shikimic acid (SA) pathway, through which plants biosynthesize three of the nine essential amino acids that are not produced in the human body. Humans have evolved to require derivatives of the SA pathway, and therefore to depend on plants. Moreover, the SA pathway gives us flavonoids and alkaloids, many of which are used as medicines; for example, star anise (*Illicium verum*) and sweetgum (*Liquidambar styraciflua*) are sources of SA as the basis for Tamiflu, which is used to prevent the serious symptoms of influenza. These dietary and medical applications are another example of the close evolutionary relationship between plants and humans rooted in biochemistry.

Humans have also evolved to have more taste buds with increasing functional diversity. This is another example of the very important interconnection between plants and people, but it could be considered almost a cultural connection rather than an evolutionary one. In addition to diversity of taste, the diet of many cultures traditionally consists of a grain, such as rice (*Oryza sativa*), wheat (*Triticum aestivum*), maize, or teff (*Eragrostis tef*), combined with a legume, including peanuts (*Arachis hypogaea*), broad beans (*Vicia faba*), or chickpeas (*Cicer arietinum*). We cannot biosynthesize all the amino acids our bodies require, and cannot make the complete proteins necessary for our bodies to function without acquiring the essential amino acids from our diet. Legumes are very high in certain amino acids and low in others, while cereals have exactly the opposite composition. By combining these two plant types, we can obtain a complete set of amino acids, which is a remarkable dietary feature that has arisen many times in diverse human cultures. Another interesting example in this vein is ascorbate (vitamin C). Humans are not able to synthesize their own vitamin C, so early cultures adopted citrus fruits, and other species to avoid ascorbate deficiency, which can result in scurvy (Martin & Li, 2017).

3 | DOMESTICATION

Plant domestication is one of the most important processes in human history. Over 20,000 years ago, there were no cultivated plants; hunter-gatherers relied on wild plants. Over the course of their association with humans, those wild species became domesticated, that is to say, altered genetically, and eventually converted into crop species that are very different from their wild ancestors.

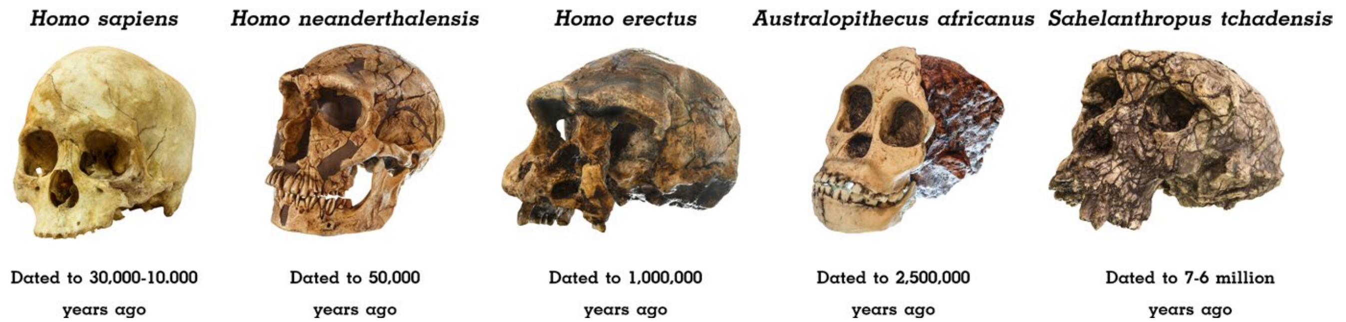

FIGURE 1 Comparison of hominid skulls over the last three million years. *Australopithecus africanus* had large teeth and grinding molars in the back of the jaw, while modern humans (*Homo sapiens*) have much smaller teeth and jaws. These skull shapes are a direct evolutionary consequence of the diet of these hominids, particularly in terms of the plants they ate. Image courtesy of Puwadol Jaturawutthicha

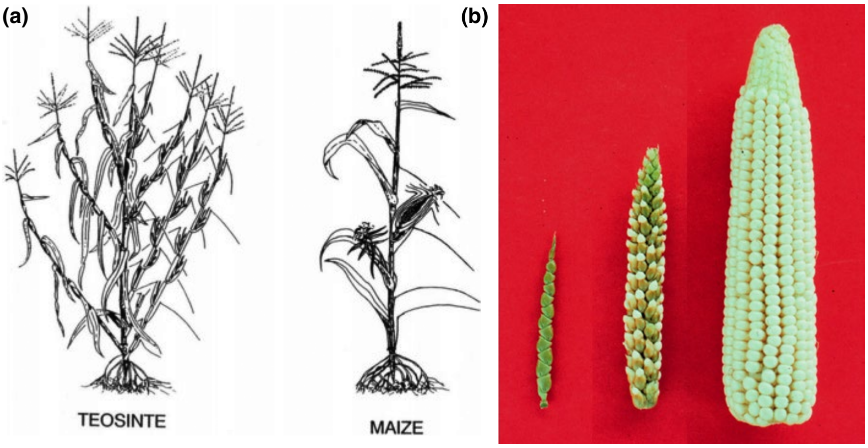

FIGURE 2 (a) A comparison of teosinte and modern domesticated maize. Image by Doebley et al. (1995), reproduced with permission; (b) variation in ear size of Teosinte (*Zea mays* ssp. *mexicana*, left), maize (right), and an ear of their F1 hybrid (center). Photograph by John Doebley, available at https://teosinte.wisc.edu/images.html

Oryza rufipogon is a wild ancestor of cultivated rice; however, the two plants are vastly different. *O. rufipogon* produces very large anthers for cross pollination and long awns to aid seed dispersal, both of which are missing in the modern crop. In most cultivated rice varieties the seeds are fertilized before the flower opens, so these massive changes in appearance are associated with domestication. The genetic changes associated with domestication in many species makes them unable to survive and compete in the wild. Thus, they have become dependent on humans.

Domestication has occurred repeatedly across the globe. There are many centers of domestication; for example, Asia is the home of domesticated rice and soya bean (*Glycine max*). Examples of domestication in Africa include yam (*Dioscorea* sp.), while the Fertile Crescent was the site of wheat and barley (*Hordeum vulgare*) domestication, and the Americas are the home of cultivated maize and potatoes (*Solanum tuberosum*). In the eastern United States, a whole suite of species were domesticated by the indigenous native peoples of America. Jared Diamond (1997) considers domestication to be the most significant technological development of the last 15,000 years. Our ability to domesticate and cultivate plants close to where we live changed the way our ancestors occupied the environment. As food became more reliable, they began to settle into permanent towns, populations grew and the division of labor was established. Not everyone was a hunter-gatherer and not everyone produced food, and this produced a cultural shift.

Teosinte (*Z. mays* ssp. *parviglumis*), the wild ancestor of maize, was domesticated in Mesoamerica. Like *O. rufipogon* and rice, maize and teosinte have dramatically different fruiting structures (Figure 2). Teosinte is a very large perennial with many flowers and flowering branches, while the domesticated maize plant has a few large leaves, two ears and a single stalk; thus, domestication again resulted in remarkable morphological changes.

The differences between domesticated crops and wild relatives can be attributed to human-mediated selection (the "artificial selection" described by Darwin). Humans took seeds from wild plants and grew them close to their homes, and the very early farmers observed that some plants had more favorable characteristics than others, such as better-tasting or more numerous or retained seeds, or were easier to grow, or were more vigorous. Early farmers collected the seeds of the best plants to grow the next year, and this domestication process happened year after year, generation after generation, until the nature of the plant was changed.

4 | THE GENETIC BASIS OF DOMESTICATION

Whole suites of characteristics are associated with crop domestication. Seed dispersal is often lost in domesticated plants, particularly when the seeds are the part we eat and they must therefore remain on the plant to be harvested. Wild plants disperse their seeds to find and colonize new sites; however, farmers do not want seeds to fall from the maternal plant, so dispersal mechanisms were quickly eliminated during domestication. Various rice varieties in Thailand display intermediate domestication, and some seeds retain their long awns for dispersal. Domesticated plants also need to flower at the same time so they can be harvested simultaneously. Wild plants tend to be taller than domesticated varieties, with multiple stems and few seeds. Often, humans selected plants to be tastier but also safer; for example, many SA-derived compounds can be bitter and can interfere with digestion, so over the course of domestication these characteristics were eliminated.

We now know a great deal about the genetic basis of domestication. Teosinte has a very hard kernel because of the activity of the gene *Teosinte Glume Architecture* (*TGA1*); however, a *tga1* mutation was harnessed during the domestication process, which resulted in the glumes of maize becoming softer and smaller, making the kernels much easier to harvest and eat (Dorweiller, Stec, Kermicle, & Doebley, 1993). Another gene involved in maize domestication is *Teosinte Branched1* (*TB1*), which controls the dominance of the apical meristem. Teosinte produces multiple branches with several inflorescences, but a mutation in *TB1* prevents the occurrence of lateral branches, resulting in a single stalk in maize (Doebley, Stec, & Gustus, 1995). This enables all of the plant's energy to go into the production of the single ear of corn present in maize, rather than the massive vegetative state observed in teosinte. Jaenicke-Després and co-workers (2003) surveyed traditional varieties of maize in Mexico, as well as modern and ancient DNA in this lineage, and identified three genes involved in domestication. Teosinte had much more genetic variation than modern maize. By comparing some of the traditional varieties and the ancient DNA, the researchers were able to determine the course of maize domestication; the wild ancestor had multiple alleles at a single locus, which enabled humans to select the most desirable characteristics (Xue, Bradbury, Casstevens, & Holland, 2016).

5 | THE FUTURE OF PEOPLE AND PLANTS

How can we continue to reap new benefits from plants in the future? We live in a particularly challenging time; our technology is changing, we have environmental degradation, and the human population is rapidly expanding with many more mouths to feed. How do we manage all this and look to the future with optimism? One important difference from earlier times, in which most traditional crops were domesticated, is that we no longer live in isolated communities, but in a global community. We must therefore think globally about plant conservation, the environment, and developing nutritious food. This global approach is important as we consider new challenges and opportunities.

What are the challenges facing our relationship with plants? For agriculture, the most obvious challenge is that we need to produce enough nutritious food to sustainably feed a growing global population. The United Nations estimates that the human population will grow to 8.6 billion by 2030 (Figure 3; United Nations, 2017), which will put tremendous strain on our relationship with plants, as well as our natural and urban environments more generally. Not all parts of the globe have the same trajectory for population growth, however; the population of Europe is expected to stabilize or decline, while in other areas, such as Africa and Latin America, there is a tremendous potential for population growth over the coming decades (United Nations, 2017). This is a potential concern, as the largest population growth is predicted in areas which often have food insecurity.

Another challenge for food systems is not only the number of calories we can produce, but also the nutrition and safety of the food. Plant-derived amino acids, micronutrients, and vitamins are required for good health. Food must also be safe, free from contaminants, and resistant to fungal growth, bacteria and other diseases. Two types of malnutrition exist around the world; some people do not have access to enough food, while others are challenged by excess calories. One goal is to produce plant-based food that provides complete nutrition in terms of micronutrients and vitamins. Another goal is to provide enhanced nutrition in developed countries, where we can substitute one lipid for another to produce food that is more healthy. We need to provide nutritious food and new crop varieties that give us the right kind of nutrition and enough total calories. Producing enough of the right kinds of food is a challenge, but our future depends upon it.

Stunting in children is highest in sub-Saharan Africa and in south Asia (de Onis, Blössner, & Borghi, 2012). Many of those affected also have cognitive limitations that can also be associated with nutritional inadequacies. The areas with the highest incidences of these developmental issues are those where rapid population growth is expected; therefore, it is imperative for plant scientists, governments and society to work together to enhance nutrition in these regions.

The plant kingdom represents many opportunities to meet these nutritional challenges. It contains around 20,000 edible plant species, of which only 30 are widely used (Levetin & McMahon, 2015). There is substantial potential for the discovery of new types of food that can enhance health, a truly exciting opportunity. The work described at the XIX International Botanical Congress in Shenzhen, China, including the conservation, exploration, systematics, and

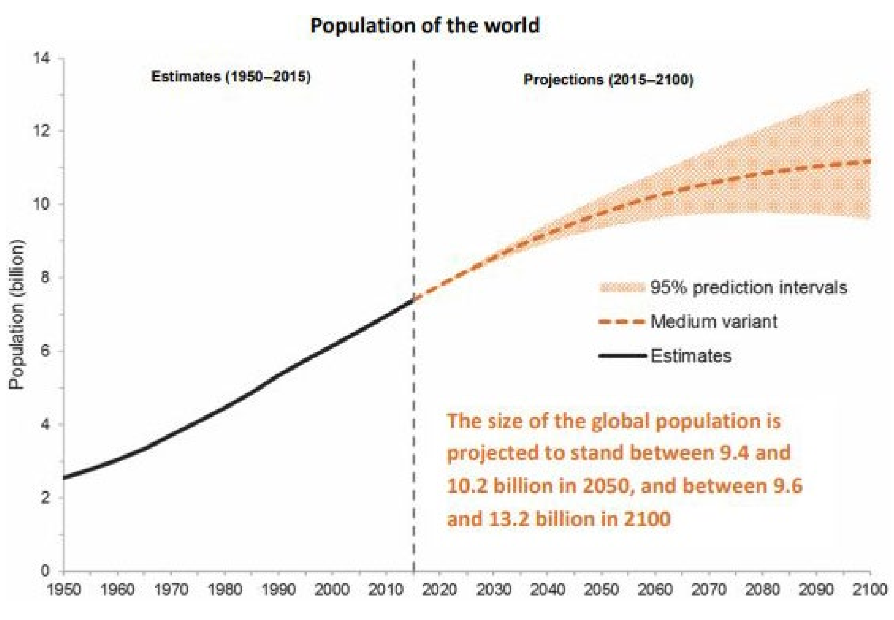

FIGURE 3 A projection of the human population until 2100, as determined by the United Nations (2017). From *World Population Prospects 2017 – Data Booklet (ST/ESA/SER.A/401)* by United Nations, Department of Economic and Social Affairs, Population Division, © 2017 United Nations. Reprinted with the permission of the United Nations

taxonomy of plants, is extraordinarily important. Not only will this work enhance our knowledge of plants, an important goal in itself, but it will also provide potential new benefits for humankind, including new food crops with improved nutritional quality. Plant biodiversity can also lead to better health. Traditionally, plants have been the source of medicines; for example, aspirin was first extracted from willow (*Salix* sp.) trees. Foxgloves (*Digitalis* sp.) are an early and effective source of medicine for congestive heart failure. Compounds first identified in the Madagascan periwinkle (*Catharanthus roseus*) are used to treat some cancers, while the antimalarial compound artemisinin was discovered in extracts of sweet wormwood (*Artemisia annua*). A vast number of plants with sophisticated biochemistries involving multiple pathways have been analyzed, providing hope that we will identify more plant-derived cures for diseases in the future.

Another important aspect of the plant–human connection is biodiversity. Biodiversity is vital for the preservation of our biosphere, the performance of ecosystem services, psychological wellbeing, culture and pleasure. Conserving plants is important for a number of reasons. A sustainable environmental footprint is a major consideration for the future, particularly regarding agriculture. Agriculture has a large impact on the environment. In the USA, agriculture accounts for 80% of freshwater use; conserving water means rethinking agriculture and developing water-conserving crop varieties, developing precision agriculture practices as well as conserving soils. Modern agriculture often involves a portfolio of agrichemicals, which can pollute streams and aquatic systems and may have long-term environmental consequences. Reducing agrichemicals is an important part of ensuring a sustainable environmental footprint. The majority of land suitable for agriculture is already under cultivation, and needs to be used more effectively and efficiently in the future, as well as adapting plants to tolerate marginal habitats. In addition to conserving land, we must conserve biodiversity in the soil. One area of research receiving a great deal of attention focuses on gaining a better understanding of the dynamics of complex soil ecosystems and how these contribute to plant health and productivity.

Our global transportation network has helped rapidly spread human diseases. Our crop plants are also affected by the spread of pests and pathogens as well as the emergence of new diseases. In part, this is the result of the ongoing evolutionary relationship between plants and their pathogens. At the same time, climate change is also altering the range of pests and pathogens and introducing them to new geographical areas. For example, wheat stem rust (*Puccinia graminis* f. sp. *tritici*) is beginning to emerge in Europe and the USA after spreading rapidly across Africa and Asia, an epidemic that has been partially driven by changes in the climate. Climate change also presents direct challenges to agriculture. Some of the crops currently grown in a region will likely face altered temperature and rainfall regimes. Adapting crops to new climate patterns will be an ongoing activity for crop breeders.

One area for optimism is the many opportunities for new plant-based products. Work is underway to develop products such as precursors for medicines, industrial products, biofuels, or disposable plastics through biotechnological approaches. These developments could enable the production of new products in an environmentally sustainable way, reducing our footprint while meeting future economic demand. Again, this must be achieved in the context of changing world temperatures and climate change.

6 | THE RESEARCH ECOSYSTEM

Facing the challenges of the future requires a vibrant research ecosystem, scientific programs that provide the understanding, applied knowledge, and new technologies required to meet future needs. Agriculture, medicine, aviation, computing, information technology, and nanomaterials are all the result of scientific research and its development into products. For example, the increase in maize yields over the last century was the result of practically applying our scientific understanding of genetics and how plants function. We know that science can be of tremendous benefit to humans; in fact, its justification is twofold: (1) as humans, we want to understand our natural world, which is important on its own, and (2) science serves society, and has enabled modern developments that have increased our well-being.

Science comprises basic research, where people seek to better understand the world, and applied research, which takes the knowledge gained in basic research and applies it to achieve a particular goal. Developing new technologies and better products is not possible without a deep understanding of nature, achieved through a vigorous system of fundamental research. After World War II, Vannaver Bush convinced US President Franklin D. Roosevelt to invest resources toward basic science, which led to the establishment of the United States' National Science Foundation, the goal of which is to understand the world better through widespread basic research.

A vibrant research ecosystem supports investigations into many areas; one cannot predict what particular investigation will result in a new technology that improves health or develops a product that will lead to a new economic sector. Basic science, including the deep understanding of plants, is an essential component of the research ecosystem and we must accept that some discoveries will never lead to applications, while others will become central for new technologies and the growth of industry.

A classic example of the importance of fundamental research is the identification of the mechanism by which *Agrobacterium tumefaciens* induces the formation of galls on plant stems. This work at first seems like an esoteric and far from useful activity, but has led to much of our modern crop varieties. *Agrobacterium* takes over the metabolic machinery of plant cells by inserting a plasmid into the plant's DNA, inducing it to form a gall and to provide food for the pathogen. This fundamental discovery provided the basis of the genetic modification of plants, which can be achieved by adding a gene of interest to the plasmid and using it to transfer the gene into the plant's genome. This technique and those derived from it have led to pest- and herbicide-resistant varieties of many crops. This basic research in a plant pathology laboratory led to a monumentally important discovery with unexpected applications. Today, basic research into CRISPR/Cas9 and other gene-editing technologies is generating truly exciting discoveries, which have the potential to be applied to the development of cancer therapies, the improvement of agriculture and the facilitation of synthetic biology in the future. The need for basic, fundamental research, especially in plants, has never been greater and politicians ignore at their peril the importance of this research for the future of our planet and its people.

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