

The Fruits of Tropical Plant Genomics

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Abstract The richness of tropical biodiversity offers a corresponding wealth of opportunity for the application of genomic research strategies and technologies to address fundamental questions in agriculture, ecology, evolution, and medicine. Herein, we explore a tiny sampling of these opportunities in five taxa of special promise, foreshadowing a few possible outcomes of invigorated research into tropical plant biology. These and other equally attractive candidates for new research vary widely in the tools presently available for their study. However, technological progress sets the stage for choosing organisms for study based more heavily on their intrinsic ecological or evolutionary interest, reducing the need that they be facile for genomics.

Keywords *Carica* · *Saccharum* · *Psychotria* · *Opuntia* · *Prosopis* · Botanical diversity

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Introduction

Across a range of taxa, species richness is greater in tropical than temperate latitudes [100], and a host of major crops now adapted to temperate annual agriculture are of tropical or subtropical origin [153]. Accordingly, much of botanical diversity is encoded in the genomes of tropical plants. This diversity is transcribed and translated into a wide range of ecosystem services ranging from the provision of a host of specific foods, fibers and medicines, to macro-scale contributions to planetary metabolism—for example, tropical ecosystems appear to be stronger sinks for greenhouse gases (CO₂) than temperate ecosystems [159].

In that so much of botanical diversity is of tropical origin, the anticipated sequencing of the genomes of most major crops and botanical models over the next decade or so [127] will inevitably catalyze an explosion of knowledge about tropical plant biology. Technological progress in many areas, such as dramatically accelerated sequencing technologies [102, 151] together with efficient methods of sampling non-redundant sequence [138, 131], targeted approaches for identification of mutants useful to determine functions of specific genes [73], and high-throughput methods to identify functional elements in genomic sequence [13], set the stage for choosing organisms for study based on their intrinsic ecological or evolutionary interest rather than because they are facile for genomics. This is not to downplay the importance of botanical models, in which the groundwork has been laid for many pan-taxon goals such as determining the functions of many thousands of genes [2] and deducing the macroevolutionary history of angiosperms [16, 129]. However, major gaps remain, for example, in relating genetic mechanisms to evolutionary outcomes, and in understanding how this relationship is mediated by ecological factors. Genomic models, selected for small

genomes and short life cycles, present a biased picture of genome structure and evolution, and have intrinsic limitations as whole-organism-level study systems. Such gaps in knowledge will increasingly need to be filled by study of plants that are not traditionally viewed as botanical models.

Examples abound of tropical plant taxa with features that offer new opportunities to address fundamental questions in agriculture, ecology and evolution. Many of these features, for example the sex chromosomes of papaya [90], were discovered serendipitously, and we can only assume that still additional opportunities are as-yet undiscovered. Herein, we explore a tiny sampling of these opportunities in four taxa of special promise, foreshadowing a few possible outcomes of invigorated research into tropical plant biology.

Carica and the Evolution of Sex Determination

The Nature of the Opportunity Sexual reproduction is widespread in plants, animals, and to a lesser extent, fungi [21, 60, 182]. The multiple origins of sex chromosomes in each kingdom and even within some taxonomic families provide strong evidence of the evolutionary advantages of sex and recombination. The enormous diversity of life forms and their wide range of genome complexity [96] are made possible partly by sex.

Although the vast majority of flowering plants are hermaphrodites, monoecious and dioecious species occur in 75% of angiosperm families including all six dicotyledonous and all five monocotyledonous subclasses [140, 187]. Dioecious species accounted for 6% (14,620) of the estimated 250,000 species in 7.1% (959) of genera and 38% [174] of families of flowering plants [140]. Plants with unisexual flowers have evolved independently and multiple times from bisexual progenitors, which provides the opportunity to study diverse mechanisms of sex determination.

The formation of heteromorphic sex chromosomes ensures dioecy and enforces 1:1 segregation ratio of male and female individuals. Dioecy accompanied by sex chromosome dimorphism is common in animals but has evolved in only a limited number of angiosperms, only a subset of which have been characterized at the cytological and/or molecular levels [23]. Further study of angiosperm sex determination may offer the opportunity to gain insight into the earliest stages of the evolution of sex chromosomes from autosomes, with application across many eukaryotes [90].

A Facile Taxon Papaya sex determination (Fig. 1) has been a frequent subject of genetic analysis because it is directly related to efficient commercial fruit production. Two early studies [74, 75, 161] each concluded that sex in papaya was



Fig. 1 *Carica papaya*: **a** female flowers; **b** hermaphrodite flowers; **c** male flowers. Photos from R. Ming

determined by a single genetic locus with three alleles: M, male; M^h , hermaphrodite; m, female. Females (mm) are homozygous recessive. Males (Mm) and hermaphrodites (M^hm) are enforced sex heterozygotes. Hermaphrodites bear fruits typically containing 25% non-viable seeds, because all combination of dominant alleles, MM, MM^h , M^hM^h , are embryo-lethal. It was later suggested that M and M^h represent genetically inactive regions of the sex chromosomes from which vital genes are missing [76], and that the sex determining region includes a complex of genes regulating stamen and carpel development, a lethal factor, and a recombination-suppressing factor [162]. This



Fig. 1 (continued)

set of features is reminiscent of the conditions thought to be associated generally with sex chromosome evolution.

Curiously, DNA marker analysis revealed the papaya sex determination locus to be in a region of suppressed recombination and rapid divergence, with 225 (66%) of the 342 markers on linkage group 1 co-segregating with sex [99]. The polymorphism rate in this region is increased 14-fold compared with the remainder of the chromosome, suggesting enormously higher sequence divergence between the homologs in this region. Initial physical mapping of the non-recombining region resulted in an estimate of 4 to 5 Mb [90]. A more recent physical map consists of four contigs with a combined 8 Mb, and fluorescence in situ hybridization of male-specific bacterial artificial chromosomes (BACs) resulted in the estimation of the non-recombining region to be about 10–15% of the chromosome (Q. Yu, P. Moore, J. Jiang, A. Paterson, R. Ming, unpublished data). Selective sequencing of the BACs identified by male specific markers revealed decreased gene density and increased transposable element density [99].

Collectively, these findings suggest that a pair of incipient sex chromosomes has formed in papaya and that a primitive Y chromosome determines sex [89]. The papaya

male-specific Y region (MSY) may resemble the ancestor of the human Y chromosome, evolved from a common ancestral autosome shared with birds about 310 mya [180]. There is naturally a high level of interest in the exact genetic composition of the papaya MSY, and an NSF-funded project is identifying and sequencing a BAC tiling path of the region (DBI-0421803; www.nsf.gov).

Current State of Knowledge of the Taxon Papaya, *Carica papaya* L., belongs to the Caricaceae, a family composed of six genera and 35 species distributed in tropical and subtropical regions. Papaya has several characteristics that contribute to its promise as an experimental model for tree crops. Papaya trees are small, generally requiring less than 5 m² per plant for a field density of 1,600–2,000 trees per hectare. Papaya exhibits rapid growth and development with a 3- to 8-month juvenile phase (from germination to flowering) and a 9- to 15-month seed-to-seed generation time. Flowering and fruiting are continuous with the production of one to three ripe fruit per week and hundreds of fruit over the life of a tree. Although hermaphrodite trees are mostly selfing, the anthers and stigma are large, facilitating controlled crossing. Fruit mature in approximately 4–5 months and have up to 800–1,000 seeds (depending on the sex type, as 25% of seeds abort in hermaphrodites), providing an abundance of offspring for genetic studies. Genetic analyses are also facilitated by the fact that papaya is easily cloned from cuttings to allow replication of any genotype across multiple environments.

Papaya is also a favorable genomics system, being diploid with nine pairs of chromosomes, a smaller genome than rice (372 Mb [5]), and an established transformation system. The first papaya genetic map, reported more than 60 years ago, consisted of only three morphological markers: sex form, flower color, and stem color [73]. The present map includes 1,498 amplified fragment length polymorphism (AFLP) markers, the locus of the transgenically-inserted papaya ringspot virus coat protein, morphological sex type, fruit flesh color [97], and 706 BAC-end and whole genome shotgun sequence derived SSR markers [24]. This map is being used for molecular cytogenetic mapping of papaya chromosomes.

The genome of a female papaya plant has recently been sequenced to about 5-genome equivalent coverage (cgpb.hawaii.edu/papaya). Among the 200 longest papaya sequence scaffolds, 124 show colinearity with *Arabidopsis* using established criteria [178], with 26 corresponding to only one *Arabidopsis* segment, 41 to 2, 21 to 3, 30 to 4, and only 3 to more than 4. The fact that many papaya segments show colinearity with three or four *Arabidopsis* segments, reflects two genome duplications in the *Arabidopsis* lineage since its divergence from *Carica*. It was anticipated that the most recent *Arabidopsis* genome duplication, ‘alpha’ [16],

might affect only a subset of the Brassicales [148]. However, our phylogenetic dating [16] previously suggested the more ancient ‘beta’ duplication to precede the *Arabidopsis*–*Carica* divergence. Individual *Arabidopsis* genome segments correspond to only one *Carica* segment, showing that *Carica* has not duplicated since its divergence from *Arabidopsis* (Ming et al., submitted). *Carica* seems to parallel many mammals in association of sex chromosomes with a lack of genome duplication [125]—however, its sex chromosomes are thought to be too recently evolved [90] to attribute lack of genome duplication to this factor.

***Saccharum* and the Consequences of Polyploidy**

The Nature of the Opportunity The architecture and function of many higher eukaryotic genomes, including all angiosperms, has been shaped by genome duplication. Duplication and modification of existing genes is thought to be a primary source of genetic material available for the evolution of genes with new functions [124, 158], perhaps by mechanisms such as neo- or subfunctionalization [97] or transposon-based juxtaposition of previously unrelated exons [86].

Angiosperms are a singularly well-suited taxon in which to study the consequences of genome duplication for eukaryotes. Humans and other mammals are poorly suited to study of genome duplication, which can only be resolved over 1–5% of their genomes [10, 11, 27, 28, 169]. In contrast, it has long been suspected that many angiosperms are ancient polyploids [157]. The discovery that one polyploidization event (‘gamma’) appears to predate the monocot–eudicot divergence [16] arguably suggests that *all* angiosperms are ancient polyploids. Additional duplication events in the dicots [16], in the monocots before the divergence of the major cereals [129], and in many more recent branches of the angiosperm tree [14, 39, 132, 160, 168] offer opportunities to study ‘natural replicates’ for common features of genome duplications that have led to successful lineages.

While new data from microbes such as yeast [64, 147] and *Paramecium* [8] are shedding light on genome duplication and its consequences, these consequences are expected to be very different in organisms with much smaller effective population sizes such as angiosperms and other higher eukaryotes [95, 98]. For example, neofunctionalization is much more likely to occur in large populations, which contain more targets for mutations conferring new beneficial function. In contrast, subfunctionalization is improbable in large populations because a partially subfunctionalized allele (the first step in the process) is likely to be silenced by secondary mutations before reaching fixation by drift [98].

A Facile Taxon Saccharum genotypes are characterized by numerous (from 36 to more than 200) variably-sized chromosomes. *S. officinarum* has been defined as having $2n=80$, with clones having morphology of *S. officinarum* but higher chromosome numbers being considered atypical or hybrids (reviewed by 151). For *S. officinarum* and its wild progenitor, *S. robustum*, which exhibits from 60 to 200 chromosomes with major cytotypes of $2n=60$ or 80, the most likely basic chromosome number is $x=10$ based on quantitative karyotyping, fluorescence in situ hybridization, and periodicity among accessions for which chromosome numbers are known [82].

Both naturally occurring and human-mediated polyploidization have been central to the evolution and improvement of sugarcane. The closest relative of sugarcane is sorghum—the two grasses are thought to have diverged from a common ancestor as little as five million years ago [1] and some genotypes can still be crossed to one another [43]. Sorghum and sugarcane genomes share more extensive genome-wide colinearity, and fewer chromosomal rearrangements [47, 65, 107], than either share with any other known grass. The finding that many regions of the sorghum genome correspond to four or more homologous regions of sugarcane suggests that in the short period since their divergence from a common ancestor, sugarcane has been through at least two whole genome duplications [107]. The effects of these recent genome duplications are superimposed on the ancient duplication shared by most if not all cereals [129].

A further unusual feature of *Saccharum* transmission genetics has introduced still additional complexity into its genetic composition and genomic analysis. Modern cultivars are both polyploid and aneuploid with between 100 and 130 chromosomes [153], roughly 85–90% of which are from *S. officinarum* and 10–15% from *S. spontaneum*, derived from a few interspecific crosses performed a century ago. These interspecific crosses were followed by a few backcrosses to *S. officinarum* clones to recover types adapted to cultivation [4, 137]. During this process, a high frequency of transmission of $2n$ chromosomes by the female (*S. officinarum*) parent was discovered [18, 20], which facilitated the recovery of *S. officinarum* alleles associated with sugar production, while introgressing disease resistance, vigor, and adaptability from *S. spontaneum*. This ‘nobilitation’ process yielded composite interspecific genomes of a complexity which probably exceeds that of any other major crop.

Despite their high ploidies, both *S. officinarum* and *S. spontaneum* mainly form bivalents at meiosis [19, 151]. In interspecific cultivars, meiotic metaphase spreads reveal swarms of chromosomes that are difficult to interpret, but show mostly bivalents. Restriction fragment length polymorphism (RFLP) analysis using a singularly-informative

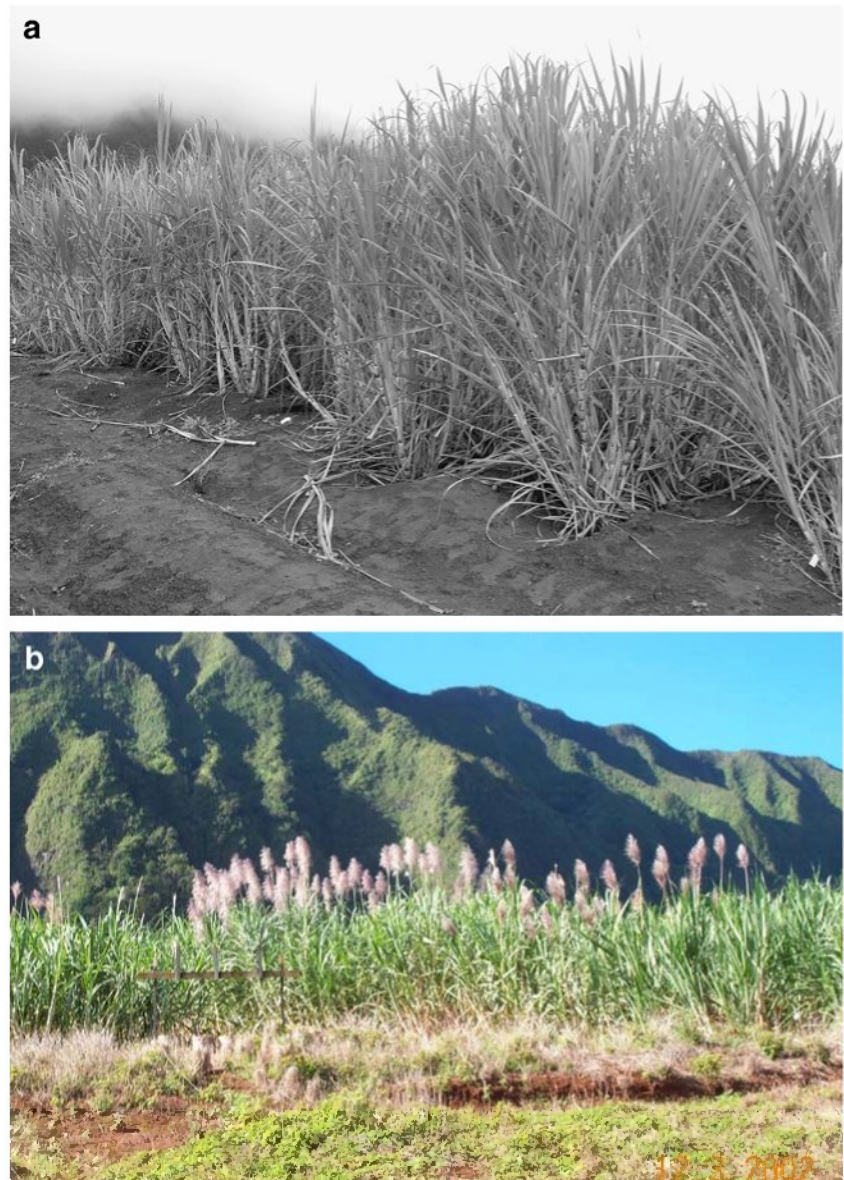
probe (BNL12.06) revealed a remarkable range of affinities among chromosomes within a single homologous group, from high levels of preferential pairing (although never true allelism), to frequent univalence for one chromosome that had a clear interspecific hybrid origin (noting that there was no evidence that interspecific hybridity was directly related to its univalence) [83].

Current State of Knowledge of the Taxon Sugarcane (*Saccharum* spp., Poaceae family, Fig. 2) is a perennial grass widely grown in a zone around the world within 30° of the equator, best known for its mature stalks which contain juice of 9–18% sucrose, providing about 75% of the world's sugar (sucrose). The plant in which C-4 photosynthesis was discovered [72], sugarcane has been reported to have carbon fixation rates as high as 28 mg CO₂ m⁻¹ s⁻¹ (63 μmol m⁻¹ s⁻¹)

[81]. For limited periods of time, the total dry matter produced by a sugarcane crop may reach 41 g m⁻¹ day⁻¹ [111]. If this rate of dry matter accumulation were constant for a year, it would attain a dry matter yield of 150 tons ha⁻¹ year⁻¹, about half of which would be partitioned into the harvested stalk. Consequently, it should be no surprise that sugarcane also is presently the world's leading biofuels crop.

There exists a range of well-developed genomics tools for *Saccharum* and a growing body of QTL data relating to measures of agricultural productivity and quality in elite sugarcanes (see [108] for a detailed review), but virtually no knowledge of the factors that have permitted this unusual genus to adapt to two whole-genome duplications in the short 5–10 my since its divergence from sorghum, or of the nature of differentiation within and among the chromosomes of *Saccharum* species. DNA marker-based

Fig. 2 **a** *Saccharum* production field. **b** Crossing block (partially in flower). Photos from P. Moore, Hawaii Agricultural Research Center



genetic maps have been made in numerous populations, but owing to the high chromosome numbers none of these are ‘complete’ in the sense of having a sufficient number and density of DNA markers to link into the expected chromosome number (indeed, because of heterozygosity and autopolyploidy, genetic mapping is done in the F1 progeny of heterozygous parents, resulting in a linkage group for each member of the somatic chromosome set). A clear need is a ‘complete’ genetic linkage map for each of the species in the genus, *S. spontaneum*, *S. robustum*, and *S. officinarum*.

As of this writing, 257,066 *Saccharum* ESTs are available in GenBank. Several expression profiling arrays have been developed, including one containing 8,236 *S.* probe sets to monitor gene expression for approximately 6,024 distinct genes (www.affymetrix.com), but none come close to coverage of even the existing unigene set. Moreover, because the levels and patterns of differentiation of homologous alleles remains largely unknown, it is unclear how many alleles are assayed by any one feature of any chip.

One BAC library is known to be available [166], characterized by hybridization-based anchoring to many thousands of DNA markers [15], and with end-sequencing in progress. The BAC library, from elite cultivar R570, provides about 14 times coverage of the basic chromosome set but only 1.2 times coverage of each homolog, thus is insufficient for many purposes. DNA fingerprinting by traditional methods [103] has shown the different members of a homologous group to be too differentiated from one another for contig assembly. A small sampling of BACs have been fully sequenced, with more in progress. Sequencing of two homologous BACs from *S. officinarum* and *S. spontaneum* revealed 96.5% DNA sequence identity between these two sugarcane species and 88.9% identity between sugarcane and sorghum, while the DNA sequence identities within the coding regions were 98.0% between sugarcane species and 94.5% between sugarcane and sorghum [84]. This high degree of gene structure conservation reinforces the notion that sorghum is the best model for sugarcane genomic research. A high-coverage BAC library is needed for each of the major species in the genus, particularly *S. spontaneum*, *S. robustum*, and *S. officinarum*.

The sequencing of the genome of a homozygous inbred representative of the sister species *Sorghum bicolor*, now complete (A.H.P. et al, in preparation), is expected to enable sugarcane researchers to gain much new insight into the biology of their complex subject. While both sorghum and sugarcane share an ancient polyploidization that affected a common ancestor of most if not all cereals about 60 mya [129], *S. bicolor* has not undergone any further whole-genome duplication. Thus, sorghum provides a virtually ideal outgroup for deducing the ancestral state,

and accordingly the derived consequences, of duplication and divergence of sugarcane chromosomes. Further, the formation of *Sorghum halepense*, a naturally-occurring tetraploid thought to be derived from crossing between *S. bicolor* and closely-related *S. propinquum* ((both of which remain extant, and are readily studied genetically at the diploid level—[15, 128]), provides a means to compare and contrast the consequences of recent but independent genome duplications in closely-allied lineages.

***Psychotria* and the Components of Phenotypic Plasticity**

The Nature of the Opportunity Ever since the pioneering common-garden experiments of Clausen et al. [29], evolutionary ecologists have been attempting to understand the genetic and environmental components of phenotypic plasticity in plants in relation to environmental gradients, and the adaptive significance of plasticity. A fundamental but still unresolved question about the evolution of adaptation is the extent to which species are composed of genetically polymorphic populations of individuals, or of phenotypically plastic but genetically similar individuals across variable environments [88, 104, 167, 163]. This is of course not an either–or question but a quantitative one. More recently, a new perspective on plasticity has emerged, namely that plasticity is not always adaptive, but instead often reflects non-adaptive responses to stress [94, 173]. Understanding adaptation and plasticity is difficult at best, and progress toward understanding the genetic basis of adaptation in particular has been hindered by inadequate methods.

While genomics is no panacea, our newfound ability to ask how individual plants (clones) respond at the whole genome level to environmental gradients promises to deliver potentially much faster progress towards a more mechanistic understanding of adaptation. From an ecological perspective, this question is key to understanding the differences between generalist and specialist species, one of the major unresolved problems in ecology [163, 174]. For example, genomic tools and approaches offer the possibility of quantifying both gene expression variation and coding sequence variation at the whole genome level, in multiple taxa and environments, to address the relative roles of responses to stress (acclimation) and genetic polymorphism (adaptation), in phenotypic plasticity.

A Facile Taxon A promising model system for dissecting the components of phenotypic plasticity is the genus *Psychotria* (Fig. 3), one of the ecologically best known genera of tropical woody plants. *Psychotria* is well represented in the world’s largest databank on natural plant populations, consisting of individually mapped, identified,

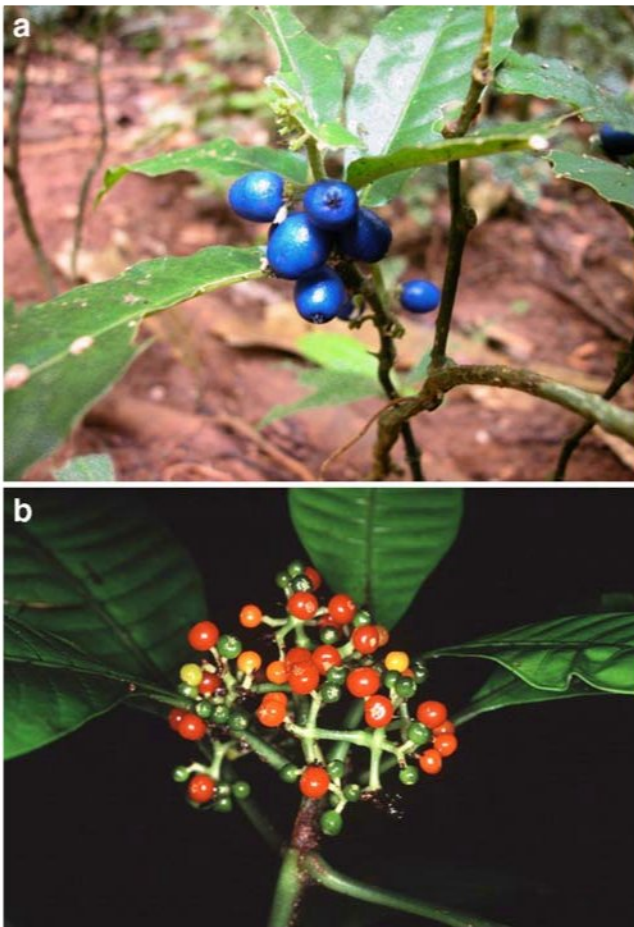


Fig. 3 **a** *Psychotria emetica* (blue berries), used commercially as an emetic. **b** *Psychotria limonensis* (red berries). Photos from J. Wright, Smithsonian Tropical Research Institute

and monitored tropical trees and shrubs in a global network of large (0.5 km²) plots managed by the Center for Tropical Forest Science (CTFS), a multinational consortium of >100 collaborating scientists and their students who maintain and do research in the plots, based at the Smithsonian Tropical Research Institute (STRI). There are now 17 plots worldwide in 14 countries that contain >5,000 tropical tree species, about 8% of the world's total tree flora. *Psychotria* occurs in 14 of the 17 plots. These plots are field “biodiversity laboratories” in which ecological and evolutionary questions could be addressed in known biotic and physical environments. The first of the plots, on Barro Colorado Island (BCI), Panama, was established in 1980, and is a model for the rest of the network [30, 79]. Complete data are currently available on 12 of the plots, which collectively contain 980 genera in 123 plant families. The plots are re-censused every 5 years to maintain the living databanks current.

The species of *Psychotria* are ecologically diverse, and appear to be rapidly evolving with regard to habitat

adaptation. They vary in growth form from semi-herbaceous shrubs <20 cm in height to trees >10 m tall. They inhabit dry to wet habitats from lowland to mid elevation montane tropical forests, and vary greatly in their light requirements. Some are light-demanding pioneer species found only in light gaps in primary forest; many others are highly shade-tolerant species that inhabit the understory of old-growth tropical rain forests; still others are weedy or invasive species that colonize disturbed habitats. Some species are ecological generalists and occur in a wide variety of habitats; others are highly restricted in their habitat distributions. In several instances, these adaptations to water and light regimes, presumed to be genetically complex, differentiate between closely-related, even sister species—for example *P. marginata* tolerates dry conditions while its sister *P. graciliflora* does not, and each of these tolerate understory conditions while sister *P. micrantha* is an ‘edge’ species [173]. Many *Psychotria* species exhibit dimorphic heterostyly, presumably to promote outcrossing. Insects, mainly bees, pollinate *Psychotria* species and have berries dispersed by understory frugivorous birds [36, 91, 92, 135]. Studies on allozyme variation in two Costa Rican *Psychotria* species indicate relatively high levels of genetic diversity [93], comparable to the high levels seen in surveys of tropical tree species [66, 67].

Several *Psychotria* species have been studied intensively, including studies of leafing phenology, flowering synchrony, and fruit set [6, 112, 135, 186], water relations [112, 113, 183, 186], whole-plant carbon gain in relation to architecture [130], growth and survival responses to light [3, 7, 42], phenotypic responses to variation in light [173], and defensive responses to herbivore damage [145, 146]. The long-term (20 years) population dynamics of *Psychotria* species in the BCI 50 ha plot have also been documented [31, 32].

Current State of Knowledge of the Taxon The genus *Psychotria* subgenus *Psychotria* (Rubiaceae), is a pantropical speciose, monophyletic but ecologically diverse group of shrubs and small trees, with more than 1,600 species worldwide. The molecular phylogeny of the genus as a whole is reasonably well known, and is very well known for the Panamanian species. *Psychotria* is attractive for study at the whole plant level, because it has a remarkable natural capacity for vegetative reproduction via the rooting of abscised, fallen leaves and pieces of stem, which make them ideal candidates for cloning experiments. Sagers [145] concluded that this mode of vegetative reproduction was very important in *Psychotria*. Censuses of small plants in *P. horizontalis* indicated that 92% originated from vegetative sprouting of plant fragments, not from seed. Sagers also found that nitrogen retention by the abscised leaves was unusually high. J. Wright (unpublished) has recorded

successful vegetative reproduction of wildings of all species of subgenus *Psychotria* found on BCI. Natural selection in *Psychotria* may have favored the ability to survive fragmentation from the impact of falling debris. This reproductive trait makes *Psychotria* an easy system in which to generate large cloned populations for common-garden experiments. Also *Psychotria* offers the potential to do crossing experiments relatively rapidly (for a woody plant) to obtain F₂ populations for genetic mapping of QTL traits. For example, seedlings of *P. horizontalis* from one genet can be grafted onto the crowns of other adult genets and induced to flower within 12–24 months (S. Hubbell, unpublished).

Psychotria is an excellent example of a tropical taxon that shows much promise for addressing fundamental questions in ecology and evolution, but which has been almost completely ignored by genetics and genomics researchers. We are not aware of a comprehensive set of chromosome counts for the members of the genus, although $2n=22$ has been reported for *Psychotria ligustrifolia* (Northrop) Millsp. *P. undata* Jacq. [89] and *P. hoffmannseggiana* [33] and $2n=32$ for *Psychotria deflexa* [33]. No estimates of *C*-value for *Psychotria* are available in the Kew database (www.kew.org/cval), and only 379 sequence reads are available for the entire genus in GenBank, with a maximum of 15 for any one species (*P. mariniana*), mostly comprising ribosomal RNA and chloroplast-related sequences used in molecular systematics. This glaring need is only partly mitigated by the availability of more than 62,000 ESTs for another member of the Rubiaceae, *Coffea* (coffee).

Opuntia and Adaptation to Water Deficit

The Nature of the Opportunity An accelerating worldwide water crisis threatens the food security of many of the world's poorest citizens. Rainfall is chronically inadequate for agriculture on about one-third of the world's arable land [17], and agriculture uses approximately 69% of the world's available water supply to mitigate this deficiency. Even in the US, where agriculture uses only about 46% of water, drought is the most significant factor causing losses of maize [40]. China and India are already classified as physically and/or economically "water scarce" [149]. Greater conservation and management of water resources appears necessary to sustain food production in the world's developing countries by 2025 [143]. By 2050, 54 countries are predicted to face "water scarce" conditions, challenging the food supply for 4 billion people, about 40% of the world's projected total [170].

Water loss from a plant is an un-avoidable consequence of photosynthesis [34], whereby the energy of solar radiation is used to fix carbon from atmospheric carbon

dioxide diffusing into the plant's leaves through stomata (epidermal pores). Increased stomatal conductance usually permits increased carbon assimilation, but simultaneously allows increased water loss by transpiration. This tradeoff has contributed to the evolution of numerous morphological and physiological features that modify plant water relations. Greater knowledge of these adaptations, and the genes and biochemical pathways that underlie them, is of high value toward development of plant genotypes that can provide the food, feed, fiber, feedstock and other products needed by humans with less water.

A Facile Taxon Members of the Cactaceae have evolved adaptations to many semi-arid areas of the planet, being found from the tropics to subarctic regions, and up to 7,000 feet elevation (Fig. 4). However commercial types of the leading fruit cacti, *Opuntia*, will not tolerate continued 40°C plus temperatures such as exist in tropical deserts of Sahelian Africa, the Middle East or the deserts of the Indian subcontinent (the Mimosoid legumes, discussed below, are eminently suited to such climates). Already an important food and feed in some countries, its combination of drought tolerance, heat acclimation, and compatibility with increasing carbon dioxide levels make cactus an ideal plant for cultivation in arid areas with rising carbon dioxide [37]. Understanding these adaptations at the molecular and biochemical levels will offer insights into botanical diversity, particular regarding plant response to environmental stress; and may identify genes, promoters, pathways, and strategies of value for improving adaptability of other plants to the approximately one-third of the earth's surface that is semi-arid or arid. Finally, remarkable variation in stem morphology, spine properties, and often spectacular flowers, has stimulated collection and cultivation of specimens as a hobby passionately followed by many.

Opuntia cacti are threefold more efficient in converting water to dry matter than traditional dryland crops, in large part due to a photosynthetic pathway called Crassulacean Acid Metabolism (CAM). CAM and other adaptations make cacti adaptable to high carbon dioxide levels [116, 119], increasing CO₂ uptake and water use efficiency without a decrease in photosynthesis [38, 177]. Under rainfed conditions, some cacti produce 15 Mg ha⁻¹ year⁻¹ of dry matter [120] while well-irrigated and fertilized *Opuntia ficus-indica* growing in Mexico can produce 46 Mg ha⁻¹ year⁻¹, among the highest productivities reported for any plant species [117]. A cold-tolerant relative, *Opuntia ellisiana*, after 3 years of plantation establishment, yielded 17.7 Mg ha⁻¹ year⁻¹ dry matter productivity with 662 mm rainfall and 285 mm water transpired, for a transpiration water use efficiency of 162 kg water/kg dry matter [68], to our knowledge the highest water use efficiency that has been measured by direct harvest in

Fig. 4 Forage *Opuntia* plantation established by Paulo Suassuna in 350 mm rainfall zone of northeastern Brazil that produced 460 tons fresh weight in 13 months, sufficient for 220 goats ha⁻¹ with 600 kg ha⁻¹ urea and 1,200 kg ha⁻¹ superphosphate. Photo by Remulo Carvalho



replicated field trials. Another CAM plant, pineapple, shows similarly high biomass accumulation with minimal water use [106].

Under drought stress, cacti preferentially maintain water in photosynthetically active chlorenchyma [61, 62, 114], also altering root meristem development [46] and decreasing water loss from roots [105, 115, 121, 122]. Lateral roots play an essential role in water uptake when droughted plants are rewetted [78].

Cacti also have the ability to acclimate to high temperatures that often co-occur with drought. The electron transport machinery of succulent plants are resistant to disruption at high temperatures [26]. Although CO₂ uptake and acid accumulation, indicators of photosynthetic activity, decrease rapidly with increasing temperatures, the ability of cactus to acclimate gradually to high temperatures can partially counter these affects [44, 118].

Current Knowledge of the Taxon The Cactaceae family, in the order Caryophyllales, is native to the New World and includes approximately 1,600 species. Particularly well-studied (and emphasized in this article) are members of the genus *Opuntia*, the ‘prickly-pear’ cactus. A staple in Hispanic and Native American cultures, annual consumption in Mexico of “nopalito”, the young tender stems of spineless *Opuntia* varieties, roughly equals annual cauliflower consumption in the USA [59]. Tunas, cactus fruits, popular in several Mediterranean and Caribbean countries, are 100–200 g in mass, and >13% in sugar content. Three main groups of fruit cultivars can be recognized according to the color of the peel and pulp; light green or ‘white’, yellow, and red (which includes an array of colors ranging from light red to the deep purple preferred by US consumers). Yields of 17,000 lb/ha and wholesale prices of

US\$1.10/kg afford potential returns of US\$18,700/ha. Both traditional and modern medicine associate cactus consumption with amelioration of diabetes [142]. An insect parasite of cactus, the cochineal (*Dactylopius coccus*), produces carminic acid, the first color-fast red dye used in Europe. Recent resurgence of interest in natural dyes has driven cochineal prices to \$50–80/kg, with the world’s limited supplies coming largely from Chile, Peru, and Bolivia. Cacti are a valuable animal fodder during drought, and an important ongoing food and water source for wildlife [56]. The stored water in *Opuntia ellisiana* plants after 3 years of plantation establishment was estimated at 170,000 kg/ha, a significant source of water in the dry season [68].

Our knowledge of cactus genetics (again exemplified by *Opuntia*) is only elementary. The base number of chromosomes for *Opuntia* is $n=11$ [134]. Wild *Opuntias* can be diploid, triploid, tetraploid and octaploid ($n=11$) [136, 181], with variable levels of polyploidy up to $2n=19$ times=209 reported, particularly in fruit cultivars [109]. While the showy flowers of *Opuntia* are insect-pollinated and lead to a high level of outcrossing, clonal propagation by apomixis is also found in several *Opuntia* species [165].

Several germplasm collections exist. The USDA has recently established an *Opuntia* collection at Parlier, California. Mexico accounts for three reliable germplasm banks, with the number of accessions varying from 50 to 150. South Africa, Italy, and Israel have small additional collections. Due to the perennial habit of this plant, maintenance of germplasm banks in situ is difficult and costly. Despite these limitations, basic descriptions of the most important cultivars and outstanding accessions are available [133]. Using 13 isozyme systems in four tissues, 32 Italian accessions could be separated into groups consistent with species, biotypes, and geographic origin [25]. A similar study carried out with

Turkish entries was unable to find differences among ecotypes and cultivated accessions [172]. Random Amplified Polymorphic DNA (RAPD) analysis has suggested some discrepancies between DNA-based estimates of relationships between *Opuntia* species and traditionally derived morphological estimates [179]. More work is needed to characterize these differences.

Flow cytometry of nuclei from *Opuntia cochellinifera* accession TAM 1308, a diploid, shows a DNA content of 878 Mbp/C, roughly twice the size of the rice genome and about three times the papaya genome. Other members of the family appear to have generally larger genomes, as this is about half of the next-smallest estimate in the Kew database (www.kew.org/cvalues). We are not aware of any genetic maps, although one BAC library of about 10 genome-equivalent coverage with approximately 85 kb inserts has been produced for TAM 1308 (A. H. Paterson, S. Thompson, R. Bunch, P. Felker, in preparation). The entire Cactaceae family has only 1,266 entries (sequences) in GenBank as of this writing. A system for genetic transformation of an elite prickly pear cactus by *Agrobacterium tumefaciens* has recently been reported [152].

Prosopis and Mimosoid Tree Legumes with Heat and Salt Tolerance

The Nature of the Opportunity Among the most problematic arid regions of the world in terms of cyclical droughts and famine are those of the hot tropical arid region that stretches from Dakar, Senegal across sub Sahelian Africa, the Middle East, Pakistan and the Rajasthan desert to Delhi, India. These regions typically have at least one month with mean daily maximum temperatures exceeding 40°C (<http://www.worldweather.org/085/c00249.htm>; <http://www.worldweather.org/074/c00327.htm>; <http://www.worldweather.org/066/c00531.htm>) that makes cultivation of most leading food crops very problematic. Plant productivity in such regions is limited not only by water, but also by extreme heat, soil C and N contents that are approximately one-tenth those of temperate agricultural soils [48, 144, 150, 164, 176] due to high soil respiration [85], and the extreme salinity resulting from high evaporation rates combined with run off to low-lying or special relief areas.

A Facile Taxon While the majority of commercial legumes (Leguminosae) belong to the Papilionoideae subfamily that have evolved in temperate climates such as China (*Glycine max*), mesic warm climates of the New World (*Phaseolus* spp.) or the Caucasian region (*Medicago sativa*), subfamily Mimosoideae has two genera—*Acacia* and *Prosopis* (Fig. 5)—that are prominent components of the hot dry

tropical and subtropical forests estimated to cover 31 million square km, an area three times larger than the USA [63]. *Acacia* has species native to five continents (N. and S. America, Africa, Asia and Australia) and *Prosopis* has species native to four continents (N. and S. America, Africa, Asia) [22, 63]. The major distinguishing feature, in economic terms, between *Prosopis* and *Acacia*

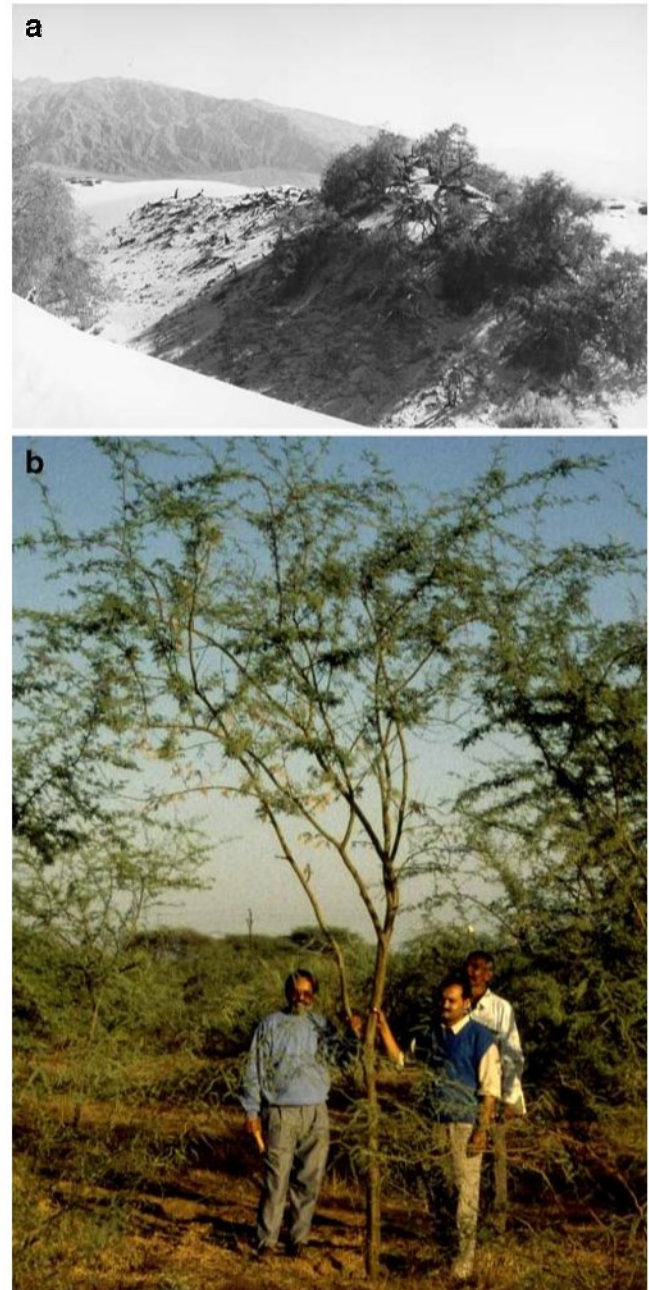


Fig. 5 **a** *Prosopis glandulosa* var. *torreyana* in Death Valley, California, the hottest location in the western hemisphere with a mean daily July maximum temperature of 46.6°C (115.8°F) (47 years of record). Note man to lower right. **b** Three-year-old erect thornless *Prosopis pallida* with sweet pods suitable for human food, in the Rajasthan Desert, Jodhpur, India. Photos from P. Felker

are the *Prosopis* pods of 10–40% sucrose [123] that were a major food source for people in the Indian subcontinent in Sanskrit times [101] and both North America [50, 55] and South America [41] in pre-Columbian times.

Evolution of perennials in arid regions (as opposed to short-lived annuals adapted to brief periods of moisture availability) has resulted in important ecological and physiological features [51] that are inadequately studied. *Acacias* have been reported to have 100% survival in salinities of 95 dS m⁻¹—twice the level of seawater [35] and *Prosopis* clones can grow in salinities of full seawater of 45 dS m⁻¹ [175]. In contrast, the papilionoid legume with the greatest known salinity tolerance is alfalfa which has a 50% reduction in growth at 9.6 dS m⁻¹ [141, 9]. Felker and Clark [52] measured *Prosopis* nitrogen fixation rates of 68 μmol/h in 3 m long soil columns whose tops were in air temperatures ranging from 43°C to 47°C and with leaf water potential from 2.9–3.8 MPa. In contrast, for cowpeas (*Vigna unguiculata*, probably the most drought tolerant of annual legumes) grown in a greenhouse with 27°C minimum–35°C maximum temperatures, nitrogenase activity declined from 10 to 1 μmol per plant/h when the leaf water potential reached 1.1 MPa [58]. Evolution under fluctuating moisture regimes probably has contributed to the exceptional stability of the stem conductive tissue (wood of *Prosopis*) with changing moisture, and as a result *Prosopis* wood is revered for fine furniture in Argentina and the USA [53].

Due to the high respiration requirement for nitrogen fixation, high photosynthesis rates under heat and drought stress are a prerequisite for nitrogen fixation under drought stress. Perhaps the most extreme measurements of *Prosopis* photosynthesis were conducted in Death Valley National Monument in California [110], to which *Prosopis* is native. The Greenland Ranch meteorological station in Death Valley has a mean daily July maximum temperature of 46.6°C (115.8°F) (47 years of record) and an absolute maximum temperature of 56.7°C (134°F) [171]. At air temperatures of 45°C and leaf water potentials of –4.5 MPa, the workers measured a maximum light saturated photosynthesis rate of 30 mg CO₂/dm²/hr (18 μmol s⁻¹ m⁻²) that was asserted to be among the highest photosynthetic rates for woody plants [110].

Current Knowledge of the Taxon Burkart [22] described 44 species of *Prosopis* native to four continents (North and South America, Africa and Asia). All of the species have 2n=28 except for some *P. juliflora* which are 4n [70]. Ramirez et al. [139] examined RAPD profiles of species native to all four continents and were able to distinguish the species native to the individual continents. Analyses of nuclear ribosomal internal transcribed spacers among various series of *Prosopis* suggested that some species were monophyletic as a result of independent speciation

that widely occurred in the New World [12]. RAPD and isozyme data for various populations of *Prosopis* showed the greatest source of variation to be within populations [57]. With the exception of the atypical shrubby *P. strombulifera*, with low gene heterozygosity and which spreads by rhizomes [80], all the species studied to date are self-incompatible [87, 154]. Bessega et al. [12] using isozyme data estimated an average 15% selfing rate within economically important North and South American species.

In its native Argentina the major factors limiting growth of *Prosopis alba* (in addition to being unsustainably harvested for use in manufacture of fine furniture—[53] are a suite of co-evolved insect predators and fungal pathogens. Some clones have been found to be resistant but crosses or heritability studies examining these characters have not been conducted (Ewens, personal communication).

One important asset that sets *Prosopis* apart from many potential economic plants of arid regions, is the presence of a rich interbreeding gene pool. The most advanced *P. alba* genetic improvement works are the replicated field trials evaluating 12 multipurpose *P. alba* clones (for fast growth, high pod production and palatable pods) [54] and 20 clones that grew in full seawater [175] at the Universidad Catolica de Santiago del Estero, Argentina by M. Ewens. This research station has ranked these clones for fungal and insect resistance and has made full sib crosses between resistant and susceptible clones. Techniques for rooting elite trees in some species [55], inter species graft compatibility among most important economic species [184] and mini-grafting techniques [49], makes it possible to clonally propagate superior hybrids.

Objections to cultivation of *Prosopis* on the basis of weediness appear to be based in part on lack of information. In the harsh arid region from Dakar to Delhi, informal introductions of *P. juliflora* were made about 100 years ago and have spread throughout this region. Unfortunately this introduction was not tested in its country of origin or destination and has bad form, large spines and unlike many of the New World *Prosopis*, pods that are not palatable to humans (P. Felker, unpublished). This species is considered a serious weed in Sudan, Kenya, Somalia and parts of Ethiopia, and some development agencies are strongly opposed to testing of any *Prosopis*.

While previous introductions of untested *P. juliflora* genetic materials either in the country of origin or domestication was a serious error, a wealth of data points to alternatives that appear unable to spread beyond cultivation. Replicated field trials comparing *P. juliflora* to *P. pallida* in Haiti [185], Cape Verde [69] and in the Rajasthan desert [71] have all found erect, thornless individuals of *P. pallida* with more rapid height growth than *P. juliflora*. A small population of erect thornless *P. pallida* with very sweet pods was observed in Kenya in 2004 where it was

erroneously known as *P. chilensis*. Local leaders noted that it did not spread due to low pod productivity and the fact that children and monkeys collected all the pods to eat (P. Felker, unpublished). Thus there is at least one example of erect, thornless, fast growing *Prosopis* with highly palatable pods being adapted to Sahelian Africa. In the center of biodiversity for *Prosopis* in northwestern Argentina there are large differences in weediness. For example, in the highly saline, high pH extensive salt flats near the Rio Saladillo in the Province of Santiago del Estero, weedy *P. ruscifolia* with its 15 cm long spines, poor quality pods and lumber has extensive distribution in grazed areas [175]. In contrast, in the same area, the highly revered *P. alba* with very palatable leaves and small thorns is only found near homes where emerging seedlings are protected by 2 m tall barricades (P. Felker, unpublished). Thus, like many crop genera [77, 126, 128], *Prosopis* includes both weedy forms and desirable, productive forms that appear to be partly if not largely dependent on humans for persistence.

Knowledge of *Prosopis* genome organization and linkage relationships is lacking, although the relatively small size of the *Prosopis* genome (392 to 490 Mbp) [45] make it an attractive potential functional genomics system. No genomic libraries have been reported for *Prosopis* but an EST library of 1,400 sequences has been compiled for *P. juliflora* by the M.S. Swaminathan Research Institute in Tamil Nadu, India.

Synthesis

These examples, a sample strongly biased by the personal knowledge of the authors, illustrate in microcosm the diverse opportunities that exist to advance knowledge of fundamental questions in agriculture, ecology, evolution, and medicine through invigorated research into tropical plant biology. Some of these species are entering the post-genomic era while others remain virtually ‘unscathed’ by DNA sequencers, and initially such invigorated research into these and other taxa will accordingly range from basic tool development to integrative systems biology. We look forward, with enthusiasm, to a time when technological progress reduces the barriers to study of non-model organisms that are crucial to filling gaps in fundamental knowledge of botanical diversity and its evolution, with a wide range of practical benefits.

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