Chapter 13

Unavailability of Wild Relatives

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Introduction

The unavailability of crop wild relatives (CWRs) may come in many forms, namely, limited possibilities of gene flow with related species because of clonality, differing ploidy levels, or other crossing barriers between species. Alternatively, it may simply mean that we lack information about the wild relatives, but in the future, unavailability of wild relatives may also involve extinction of species. In this chapter we first discuss clonally propagated crops, which may or may not have limited fertility in general or in interspecific crosses. Three genera of important clonal crops are discussed in detail: *Dioscorea*, *Musa*, and *Saccharum*. We also analyze polyploid crops (which, of course, may also be clonally propagated, so this category is not separate from the previous one), and detail the genetic consequences of polyploidy depending on the different kinds of formation of 2*n* gametes. The concept of endosperm balance number (EBN) is explained and its consequences for potential hybridization among different ploidy levels are summarized. Other crossing barriers besides different ploidy levels also exist between crops and some of their wild relatives; we describe a few examples of these, as well as some recent cases of success

at overcoming these barriers. In other cases, the "unavailability" of CWRs really means a lack of information about the wild relatives, so a few examples of recent advances in studies of the origins of crops and their evolutionary relationships with their wild relatives are described, namely, in the genera *Zea* and *Manihot*. Finally, we describe studies that aim to predict the levels of extinction of species or extirpation of populations, namely, that of CWRs, as the global climate changes in coming decades, and the factors that make such predictions challenging.

Clonal crops

Some crops that are propagated asexually (clonally) have little or no ability to reproduce sexually, whereas others retain the ability to form sexual seed. In cases in which the crop, or certain cultivars, is sterile or nearly so, there are obvious challenges in the use of wild relatives for crop improvement. Examples of crops with low fertility are yams (*Dioscorea* spp.), taro (*Colocasia esculenta* (L.) Schott) and other aroids, banana/plantain (*Musa* spp.), and some breadfruit cultivars (*Artocarpus altilis* (Parkinson) Fosberg) (Simmonds, 1962; Zerega *et al.,* 2004; Lebot *et al.,* 2005). Many *Citrus*

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species and cultivars are not only propagated clonally, but even their seeds are often formed by apomixis, so they too are clones of the parent plant (Roose *et al*., 1995). On the contrary, many crops that are primarily propagated asexually are still capable of sexual reproduction, and in some of these cases are interfertile with wild relatives. Some crops that were assumed to be propagated only asexually are not always so; in potato (*Solanum* sect. *Petota* Dumort.) and cassava (*Manihot esculenta* Crantz) there is direct evidence that Indigenous farmers bring sexual progeny into cultivation (Boster, 1985; Franquemont *et al*., 1990; Malagamba and Monares, 1992; Salick *et al*., 1997; Elias and McKey, 2000; Elias *et al*., 2001; Pujol *et al.,* 2002). Taro is propagated "almost exclusively asexually" (Hancock, 2012), but it is found in both diploid and triploid forms, and the diploids in Melanesia, both wild and cultivated, are known to flower and set viable seed (Lebot, 1999). Ulluco (*Ullucus tuberosus* Caldas), which was thought to be a sterile apomict, turned out to be fertile (Pietilä *et al.,* 1990). Even some triploid and pentaploid bitter potatoes, usually considered sterile, have been observed forming viable seed that produce fertile offspring (Alejandro Bonifacio, PROINPA, personal communication). Indeed, the importance of sexual reproduction in the evolution of clonally propagated crops is generally underestimated; most supposedly clonal crops are really in "mixed clonal/sexual systems" (McKey *et al*., 2010).

However, even when clonal crops are not sterile, they can face other challenges for introducing genes from wild relatives. Favored clones have combinations of genes that would be broken up by interbreeding with other individuals of the same species. This is in addition to the ordinary challenges of introducing alleles to a crop from undomesticated members of the same or different species. In some clonally propagated crops, such as grapevines, the problem is not so much unavailability of wild relatives but rather the strong preference for certain clones in global or local markets and unacceptance of hybrids by consumers. Grapevines were traditionally propagated by cuttings in Europe, but in the mid-1800s vineyards in many areas of Europe were devastated by grape phylloxera (*Daktulosphaira vitifoliae*), pest insects introduced from North America (Alleweldt and Possingham, 1988). Initial attempts to breed resistant grape varieties by crossing European grapes (*Vitis vinifera* L.) with several American wild species gave rise to varieties producing unacceptable wine flavors, so as an alternative to hybridization, grafting of European grape varieties on rootstocks of phylloxera-resistant or tolerant American grapes was developed. More recently, interspecific hybrids between more carefully selected *V. vinifera* parents and different American *Vitis* species (*Vitis aestivalis lincecumii*, *Vitis rupestris*, and *Vitis riparia* instead of strong-tasting *V. labrusca*) have produced hybrids with better flavor qualities than the initial interspecific hybrids of the nineteenth century (Reisch *et al.* n/d).

The following sections discuss the globally important clonally propagated crops yam (*Dioscorea* spp.), banana (*Musa* spp.), and sugarcane (*Saccharum* spp.) in more detail.

True yam, *Dioscorea* spp.

Taxonomy and geographic distribution

Yams are members of the genus *Dioscorea* L. (family Dioscoreaceae), a genus that comprises approximately 450 species (Govaerts et al., 2007) of which 10 are cultivated as staple yams (Lebot, 2009). The species are herbaceous climbing monocots that are mostly dioecious, although some species have individuals with bisexual flowers. Yams grow throughout the tropical and subtropical regions of the world.

Origin and domestication

The following three centers of origin are generally agreed upon for the most important cultivated edible yams: Southeast Asia for *Dioscorea alata* L.*, Dioscorea esculenta*

(Lour.) Burkill, *Dioscorea opposita* Thunb., and *Dioscorea bulbifera* L. (Alexander and Coursey, 1969; Burkill, 1951), West Africa for *Dioscorea rotundata* Poir., *Dioscorea cayenensis* Lam., and *Dioscorea dumetorum* (Kunth) Pax (Coursey, 1967), and Tropical South America for *Dioscorea trifida* L.f. (Alexander and Coursey, 1969). Onwueme (1978) considered *D. bulbifera* as a species appearing at the same time in Asia and in Africa, and it is worth noting that *D. bulbifera* is the only yam species with wild populations known from both Africa and Asia (Ramser *et al.*, 1996).

Yam domestication has occurred independently within each of the three centers. *D. alata,* considered the most diverse species (Mignouna *et al.*, 2002), is believed to have originated from spontaneous hybrids between *Dioscorea hamiltonii* Hook. f. and *Dioscorea persimilis* Prain & Burkill in Southeast Asia (Coursey, 1967). During the domestication process, there was an East to West movement of *D. alata* and *D. esculenta*, another Asiatic species now growing widely in Africa and the Americas (Ng *et al.*, 2007). *D. rotundata* and *D. cayenensis* are the two most important species in West Africa, although there has been controversy whether they are same or different species, and they have both been described as resulting from a process of domestication of wild yams of the section *Enantiophyllum* (Mignouna and Dansi, 2003). Indeed, the process of yam domestication by farmers is still ongoing in Benin (Mignouna and Dansi, 2003; Zannou *et al.*, 2004). These West African species were taken to the tropical and subtropical Americas and became an important crop in that region, particularly in the Caribbean (Ng *et al.*, 2007).

In some cases the cultivated and wild forms are not very distinct morphologically but they nonetheless have chemical differences. Wild species often produce secondary metabolites that protect them from predators, such as those in the toxic species *Dioscorea hispida* Dennst., which occurs in Southeast Asia. It is used in times of famine because its large tubers are easily dug and detoxicated by prolonged soaking (Lebot, 2009). This is a common practice in West Africa where farmers collect wild yam tubers and perform different practices that result in change in shape and taste and consider it as edible after two to three consecutive cycles of planting and harvest, although whether the basis of these changes is a form of phenotypic plasticity is unknown (Zannou *et al.*, 2006).

Uses

The cultivated *Dioscorea* species are an economically important staple source of starch in the diet while many of the wild yams are also important plants in times of food scarcity (Bahuchet *et al.*, 1991; Sato, 2001). The genus is also a favored source of medicinal plants used to extract precursors of cortisone and other steroid hormones (Kaimal and Kemper, 1999; Martin, 1969; Omoruyi, 2008; Vendl *et al.*, 2006). In West Africa yam is cultivated not only for consumption and as a source of income but it has also sociocultural values (Zannou *et al.*, 2004), being used for traditional religious observances, social gift exchange, and cultural festivals. Mignouna *et al.* (2009) suggested yam as a potential model organism as it represents an important biological link between the eudicots and grasses and has the potential to fill gaps in our knowledge of plant biology and evolution. As such, yams would also offer the possibility to gain new insights into processes such as tuberization and sex determination, which cannot be studied in current model organisms (Mignouna *et al.*, 2009).

Utilization of wild relatives in yam improvement

Yam is primarily a clonally propagated crop. Hence, its production is restricted to underground tubers, the reason being poor botanic seed production and germination. Regardless of inconsistent flowering and poor crossing success, intraspecific hybridization in cultivated species is relatively less challenging. Traits, namely, tolerance and adaptability to moisture

stress and low soil fertility and disease and pest resistance (Yam mosaic virus, anthracnose, fungi, and nematodes) are the most important in yam improvement programs. Interspecific hybridizations have also been made, with the aim of transferring some of these traits from wild relatives. *D. rotundata* has been crossed with wild *Dioscorea praehensilis* and cultivated *D. cayenensis* (Akoroda, 1985), and there have also been successful interspecific hybridizations between *D. rotundata* and wild relatives (*Dioscorea abyssinica* Hochst. & Kunth, *Dioscorea togoensis* R. Knuth, and *D. praehensilis*) made at International Institute of Tropical Agriculture (Robert Asiedu, personal communication). However, none of the wild relatives so far is used in yam variety development. The lack of better success in both intraspecific and interspecific hybridization in yams could be because of the ploidy variation within and between species, low pollen viability and genetic distance between the species.

Climate

Yams grow in warm, sunny climates with temperatures between 25 and 30°C and require ample moisture. They require deep, loose, textured loamy soil that is rich in organic matter, but they do not tolerate waterlogged conditions (Mignouna *et al.*, 2009). Worldwide, yam is the third most important tropical root crop after cassava and sweet potato (*Ipomoea batatas* L. Lam.) (Srivastava *et al.*, 2012). Regardless of its importance as a preferred staple food in West Africa, yam is considered as one of the neglected and underutilized crops on a global scale. Mignouna *et al.* (2009) indicate its likely increase in importance as climate change leads to necessary changes in global food systems. On the contrary, reports indicate that some species of *Dioscorea* are at risk of extinction, before we have made use of them (e.g., Wilkin *et al.*, 2008). Hence, both *in situ* and *ex situ* conservation measures that give priority to species at risk of extinction are vital.

Musa wild relatives and climate change

Banana (including plantain) is a monocotyledon with four known genomes, designated A, B, S, and T, which correspond to the diploid species *Musa acuminata* Colla, *Musa balbisiana* Colla, *Musa schizocarpa* N.W. Simmonds. and *Musa textilis* Née, respectively. No hybridization between B, T, or S genomes has been observed, but *M. acuminata* can hybridize with any of the three other species. Cultivated bananas composed of S and T genomes are very few. The two main progenitor species of the domesticated forms of banana/plantain are thus *M. acuminata* and *M. balbisiana,* both of which still exist in the wild. These two species have combined to generate a wide diversity of diploid and triploid cultivars with diverse genetic makeups varying from AA, AB, AAA, AAB, and ABB. Parthenocarpy, the basis for seedless fruit production, is an A genome contribution to cultivated bananas, whereas resistance to biotic and abiotic stress is generally attributed to the B genome (Simmonds, 1962). No subdivision exists within *M. balbisiana* taxonomy, whereas *M. acuminata* is divided into seven subspecies with different geographical distributions (Simmonds and Shepherd, 1955; Shepherd, 1999). The most frequently cultivated cultivars of banana are seedless triploids, especially, the commercially important Cavendish dessert banana (AAA), the East African Highland banana (AAA), and the staple African and Pacific cooking plantains (AAB), both of which have importance for food security. The origin of these triploid cultivars is a multistepped process. In each of the areas of distribution of the different subspecies of *M. acuminata*, multiple origins of parthenocarpy resulted in edible diploids. However, to explain the current pattern of diversity of cultivated *Musa*, De Langue and colleagues (2009) suggested that the first cultivated clones exhibited intermediate levels of parthenocarpy, occasionally producing seeds. The edible diploids that originated from each of the subspecies then likely diffused through exchanges between human communities and/or following human migrations. Once

the various cultivated diploids were brought into contact within cultivated plots, they are thought to have hybridized. Because of chromosomal rearrangements and unbalanced meiosis in these hybrids, diploid gametes are sometimes formed, so that in some cases the occurrence of sexual reproduction between them led to the emergence of triploid cultivars (reviewed in Perrier *et al.,* 2011). The most striking example is the likely resolution of the direct ancestry of the Cavendish and Gros Michel AAA subgroups: codominant nuclear simple sequence repeat (SSR) markers have revealed that two AA landraces named Akondro Mainty and Khai Nai On were the most likely providers of their AA and A parental genomes, respectively (Perrier *et al.,* 2009).

Many factors contribute to difficulties with breeding bananas. In addition to seedlessness, which is among the most important domestication traits in this crop, unbalanced meiosis because of hybridization limits the production of viable pollen and thus decreases fertility. Although triploid improved cultivars have qualities, such as higher yields, that make them desirable, they are especially challenging to improve through conventional breeding. To get around these difficulties, a common strategy for banana improvement consists of taking advantage of the seeds produced by wild species (e.g., Rowe and Rosales, 1996), which are thus of crucial importance for banana genetic improvement (Simmonds, 1987).

Another interest in using *Musa* wild relatives for breeding is the widening of the genetic basis of edible triploids, which diversified slowly through the accumulation of mutations (e.g., Noyer *et al.*, 2005 for plantain). Despite the occurrence of hybridization between subspecies and/or species, the multistepped origin of edible triploids induced an especially narrow bottleneck that resulted in a very low level of genetic diversity. One consequence of these low levels of genetic variability is cultivated banana's vulnerability to many pests and diseases. The wild *Musa* gene pool, including the two closest relatives, is an important potential source of new traits, in particular with regard to its wide geographical range and multiple environmental conditions.

Given the importance of banana wild relatives for breeding and their low presence in *ex situ* collections (unpublished results of a survey of *ex situ* collections in 2012 in the framework of MusaNet [Global *Musa* Genetic Resources Network] facilitated by Bioversity International), the conservation *in situ* of *Musa* wild relatives growing in the wild is of high priority. Such efforts have only just begun, because wild *Musa* relatives are often found in disturbed areas of standing forests of low priority for conservation. Even given successful *in situ* efforts, there is concern that climate change may also alter the suitability of such sites and result in the loss of diversity.

To examine in greater detail the implications of climate change for *Musa* wild relatives, the climate change scenarios of four collection sites (Table 13.1) were calculated. For these sites temperatures are projected to increase progressively 2°C by the year 2030 and another degree by 2050 (Figure 13.1). These temperatures appear to be well within the range for normal plant growth for *Musa*, even in 2050.

Projections of annual averages only provide a general picture of the conditions for plant growth, but unfortunately general climate change models do not yet predict quantitative variability. Past variability can be explored to understand what sort of events have occurred and could have threatened wild *Musa* relatives. On the basis of the data for 1950–2009 for the same four collection sites of *Musa* wild relatives, anomalies were calculated. Anomalies are the annual difference in temperature and precipitation from the "normal" level, in this case the long-term average for each site over 1960–1990, and can be graphed to show how far years diverge in terms of temperature and rainfall from the long-term average. Sites for *Musa balbisiana* (Guangdong and Fujian provinces of China) have a higher likelihood of facing major weather extreme events showing

Table 13.1 Sampling locations of wild *Musa*.

| Genus	Species	Subspecies	Ploidy	Country	Province/island	Precipitation*	Temperature†
Musa	*acuminata*	*banksii*	$2x$	Papua New Guinea	New Guinea‡	3289	26.5
Musa	*acuminata*	*microcarpa*	$2x$	Indonesia	Halmahera§	2334	25
Musa	*balbisiana*	NA	$2x$	China	Guangdong¶	1872	21
Musa	*balbisiana*	NA	$2x$	China	Fujian¶	1592	18

Abbreviation: NA, not applicable.
*Average precipitation in millimeters from 1960 to 1990.
†Average temperature in degree centigrade from 1960 to 1990.
‡*Source*: The Second IBPGR/QDPI Banana Germplasm Mission to Papua New Guinea, 1989.
§*Source*: Bioversity International, ITFRI Triangle Banana Exploration Report, Indonesia, 2012–2013.
¶*Source*: Wang *et al.* (2007).
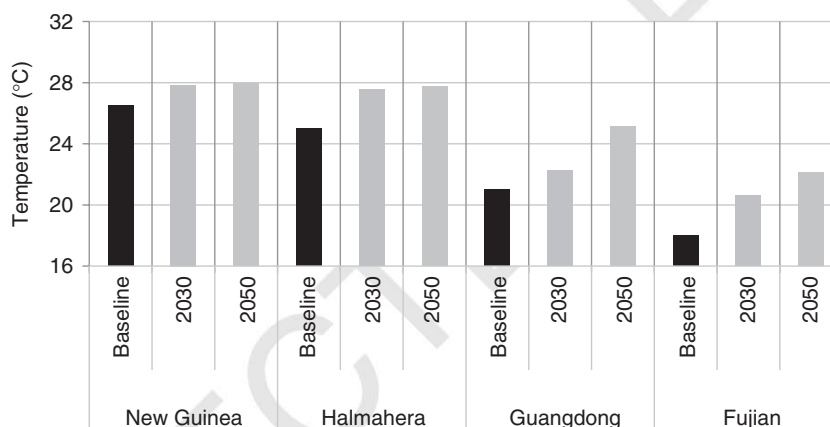
Fig. 13.1 Temperature projections for the years 2030 and 2050: average values of 20 GCMs, scenario A2. *Source*: Ramirez and Jarvis (2008).

a wider temperature range than sites where *M. acuminata* were collected (Figure 13.2). New Guinea and Halmahera, the areas where *M. acuminata* subspecies are found, have more points toward the center of the graph indicating less variability in temperature and precipitation.

These results suggest that such threats as increased deforestation may be a greater threat to *Musa* wild relatives than climate change. Climate change might have an indirect negative impact on the wild habitat of *Musa* relatives by increasing climate suitability for other crops and thereby accelerating deforestation and changes in land use.

Sugarcane *Saccharum* spp.

Sugarcane is a clonally propagated crop that retains the capability for sexual reproduction and even for interspecific hybridization, despite its complex interspecific relationships not only because of multiple ploidy levels in both wild and domesticated plants, but also because of different base chromosome numbers among the wild species. Sugarcane comprises species in the genus *Saccharum*, and the crop is usually considered to include two wild species (*Saccharum spontaneum* L. and *Saccharum robustum* Brandes & Jeswiet ex Grassl.) and
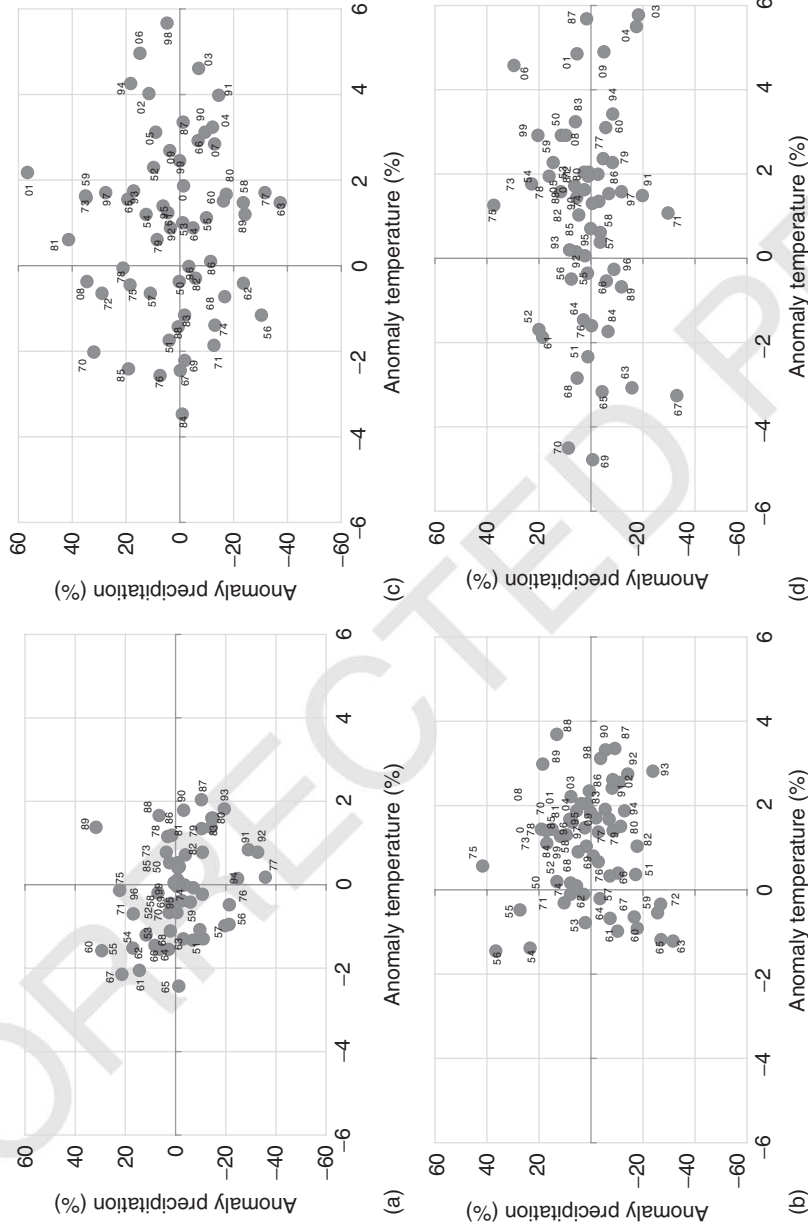
Fig. 13.2 Annual temperature and precipitation variability from 1950 to 2009; numbers indicate years (e.g., 67 = 1967). (a) New Guinea, (b) Halmahera, (c) Guangdong, and (d) Fujian. *Source:* Harris *et al.* (2013).

several domesticated ones (traditional cultivars are classified as *Saccharum officinarum* L., *Saccharum barberi* Jew., *Saccharum sinense* Roxb., and *Saccharum edule* Hassk.) (Roach, 1995), although some taxonomists reduce many of these to synonymy (see discussion in Brown *et al.*, 2007).

The two wild species currently have overlapping distributions, and molecular data indicate that there has been genetic exchange on New Guinea, but it seems likely that earlier in the Quaternary they were allopatric, being separated at Wallace's Line before humans modified environments and dispersed the species (Grivet *et al.,* 2004, 2006). *S. robustum* grows wild on the Melanesian islands and is cultivated as medicinal on New Guinea, whereas *S. spontaneum* spans a greater range of latitude and elevation, having a widespread distribution in diverse habitats around tropical and subtropical mainland Asia and near islands (Inman-Bamber *et al.,* 2011). *S. robustum* has thicker and taller stalks than *S. spontaneum*, whereas the latter is more variable not only in height and diameter, but also have resistances to both abiotic stresses and some pests and diseases; neither of the wild species has as high sugar content as in the cultivars (Roach, 1995). That the wild species have different base chromosome numbers was suspected at first on the basis of their chromosome numbers, which is multiples of 8 in the case of *S. spontaneum* ($2n = 40–128$) and multiples of 10 in the case of *S. robustum* ($2n = 60–110$), and these different monoploid numbers have been confirmed by FISH (fluorescent *in situ* hybridization) and by the data of ribosomal 45S and 5S (Grivet *et al.,* 2006). With a monoploid number of $x = 8$, *S. spontaneum* ploidy levels are interpreted as $5x$ to $16x$, whereas *S. robustum* has $x = 10$, meaning that its ploidy levels are $6x$ to $11x$, the most common being $8x$ and $10x$ (Roach, 1995).

S. officinarum L. ($2n = 80$) is cultivated throughout Melanesia, with its highest diversity in western New Guinea (Grivet *et al.*, 2006). The canes are large and colorful, and were called Noble when they were encountered by early

Dutch explorers (Grivet *et al.*, 2006). These traditional cultivars were previously hypothesized to have originated from interspecific or even intergeneric hybridization, but recent molecular data suggest that these were originally domesticated directly from *S. robustum*, most likely on New Guinea (Grivet *et al.*, 2006). Evidence for this hypothesis includes that it shares with *S. robustum* a monoploid number of $x = 10$, with most clones having $2n = 8x = 80$ (Inman-Bamber *et al.,* 2011) and also that its mitochondrial haplotype, restriction fragment length polymorphisms (RFLPs) of nuclear single copy DNA, and leaf flavonoids are more similar to *S. robustum* than to *S. officinarum* (Grivet *et al.*, 2004, 2006).

S. barberi Jeswiet and *S. sinense* Roxb. ($2n = 81–124$) were historical cultivars in India and China, respectively, which are now found primarily in germplasm collections (Grivet *et al.,* 2006). Compared to *S. officinarum* the plants are smaller, the canes are thinner with duller colors and a lower sugar content (Grivet *et al.,* 2006, Inman-Bamber *et al.,* 2011). On the contrary, they are better adapted to subtropical conditions (Grivet *et al.,* 2006). These species were probably the earliest ones to be dispersed westward and around the world, being replaced by the "Noble" *S. officinarum* clones later, when larger-scale plantations were developed (Roach, 1995). There remains some conflicting evidence about the origins of these species. On the one hand, Grivet *et al.* (2004, 2006) summarize evidence from low-copy nuclear data, GISH (genomic *in situ* hybridization), and hybridization of satellite and *Alu*-like repeated elements from *Erianthus* and *Miscanthus*, all of which indicated that *S. barberi* and *S. sinense* are probably simply hybrids between *S. officinarum* and *S. spontaneum*. On the contrary, Brown *et al.* (2007) found that SSRs indicated that *S. barberi* and *S. sinense* had contributions from other genera as well.

The only nonsweet traditional cultigen is *S. edule* Hassk., which is cultivated from New

Guinea to Fiji for its edible aborted inflorescence, used as a nonsweet vegetable (Grivet *et al.,* 2006). This species has $2n = 60$–122, mostly in multiples of 10 (Grivet *et al.,* 2006; Inman-Bamber *et al.,* 2011), and although more data are needed to confirm this idea, it is thought to be selected from *S. robustum*.

Despite the different monoploid numbers of the species, interspecific hybridization has been very important in the breeding of modern sugarcane cultivars. Many of the original crosses between cultivated *S. officinarum* and wild *S. spontaneum* were introduced in the early twentieth century, with continued backcrosses to *S. officinarum* since then (Roach, 1995). This eventually led to a narrowing of the genetic base because of inbreeding and also because of the fact that when *S. officinarum* is the female parent, the offspring usually have a somatic chromosome number of $2x + x$; in the 1960s, efforts were made to widen the genetic base (Roach, 1995).

Potential for intergeneric hybridization:

Other genera were previously thought to be involved in the ancestry of domesticated sugarcane, specifically the closely related genera *Miscanthus*, *Erianthus*, *Sclerostachya*, and *Narenga* (Grivet *et al.,* 2006; Inman-Bamber *et al.,* 2011). However, recent molecular studies using data from isozymes, nuclear and cytoplasmic RFLPs, satellite DNA, and low-copy nuclear RFLP did not find any evidence of contributions from these other genera to domesticated sugarcane (reviewed in Grivet *et al.,* 2006). *Miscanthus* was confirmed as being the most closely related genus to *Saccharum*. Although intergeneric hybridization does not appear to have played a role in the origin of domesticated sugarcane, the potential for successful crosses is shown by the confirmation that at least one clone of *Saccharum maximum* (Brongn.) Trin. is a hybrid between *Saccharum* and *Miscanthus*, although other clones did not show any contribution from *Miscanthus* (Grivet *et al.,* 2006). Despite some successful crosses

with other genera, they have not yet reached the level of being commercially valuable. However, given that the needs for biofuels are different from those for sugar production, the contributions from other genera are likely to be pursued further.

Ploidy differences between crops and relatives

As discussed above, sugarcane is clearly an example of both a clonally propagated crop and one with multiple ploidy levels, and even different base chromosome numbers in the crop and in related wild species, yet interspecific hybridization has been very important in the breeding of sugarcane. In other crops, hybridization among different ploidy levels has not been as successful. For instance, until very recently, no other species had been successfully hybridized with tetraploid *Coffea arabica* L., the most commonly grown commercial coffee species (and highest quality; i.e., mountain grown "arabica" coffee), as all other *Coffea* species are diploid, including cultivated *Coffea canephora* Pierre, commonly known as "robusta" coffee. Artificial hybrids between the two cultivated species are under study to understand coffee genetics (Lashermes *et al.*, 2000), and a natural interspecific hybrid between tetraploid *C. arabica* and diploid *Coffea liberica* is raising hopes that disease resistance from diploid *Coffea* species might eventually be introduced into $4x$ *C. arabica* through this hybrid (Prakash *et al.*, 2002). In some crops in which the crop and its known relatives are of different ploidy levels, the ploidy levels in either the crop or the wild species are still being discovered. An example is the Andean tuber crop oca, *Oxalis tuberosa* Molina, primarily an octoploid crop (reviewed in Emshwiller, 2002b) in which tetraploid local cultivars have recently been confirmed (Bradbury, 2013), which could potentially mean that these cultivated tetraploids could be hybridized with wild, tuber-bearing tetraploid populations (Emshwiller *et al.*, 2009). However, in many crops in which wild relatives

do not share the same ploidy level as the crop, attempts are made to overcome the ploidy barrier through various manipulations.

Ploidy manipulations

The union of numerically unreduced ($2n$) gametes is believed to be the predominant mechanism for spontaneous polyploidization in wild plant populations (Harlan and de Wet, 1975; Veilleux, 1985; Bretagnolle and Thompson, 1995). $2n$ gametes are produced by plants carrying meiotic mutations that interrupt meiosis so that gametes contain the parental (sporophytic, $2n$) chromosome number rather than half that number (the gametophytic number, n). Meiotic mutations occur naturally in cultivated and wild forms of polyploid crop plants, which usually belong to a polyploid series of species (Iwanaga and Peloquin, 1982; Pfeiffer and Bingham, 1983; Barcaccia *et al*., 2003; Jauhar, 2003; Lyrene and Vorsa, 2003; Carputo *et al*., 2003). Some meiotic mutations lead to the production of $2n$ eggs (Esen *et al*., 1979; Pfeiffer and Bingham, 1983; Werner and Peloquin, 1990), while others produce $2n$ pollen (Mok and Peloquin, 1972; Barba-Gonzalez *et al*., 2004; Camadro *et al*., 2008). In some crops, such as potato and blueberry, a cross between a tetraploid and a $2n$ gamete-producing diploid will yield almost exclusively tetraploid offspring; triploid seeds are inviable because of endosperm failure (Maine, 1994; Lyrene and Vorsa, 2003).

Significant genetic consequences result from the cytological change produced by a meiotic mutation (Mendiburu *et al*., 1974; Mendiburu and Peloquin, 1977; Peloquin *et al*., 2008). Normally, in anthers, the four products of meiosis are separated so that their poles define a tetrahedron. Cytokinesis then produces four haploid microspores. In contrast, one type of meiotic mutant, called parallel spindles, produces two microspores, each with an unreduced (sporophytic) chromosome number (Conicella *et al*., 2003; Camadro *et al*., 2008). The first division

is normal, but in the second division, the meiotic spindle fibers are parallel. When cytokinesis follows, two diploid microspores are produced. The genetic consequence of parallel spindles is equivalent to first division restitution (FDR) of meiosis because gametes contain nonsister chromatids in regions spanning from the centromere to the first crossover event. The parallel spindles genotype exhibits variable expressivity and incomplete penetrance (Ortiz and Peloquin, 1992). Consequently, a mutant plant typically produces both n and $2n$ gametes, and not all plants homozygous for the meiotic mutation produce $2n$ gametes. Because cytokinesis occurs after the first meiotic division in megasporogenesis, $2n$ egg formation is typically a second division restitution (SDR) mechanism (Stelly and Peloquin, 1986; Werner and Peloquin, 1990). SDR gametes contain sister chromatids from the centromere to the first crossover.

The genetic consequences of FDR $2n$ gametes are very different from those of SDR $2n$ gametes. In an FDR $2n$ gamete, all loci from the centromere to the first crossover on each chromosome have the same genetic constitution as the parent of that gamete. That is, loci that were heterozygous in the parent remain heterozygous in the gametes (Peloquin *et al*., 2008). Even in the chromosomal region beyond the first crossover, half of the loci that were heterozygous in the parent will remain so in $2n$ gametes. There is typically only one crossover per chromosome in potato (Yeh *et al*., 1964). Consequently, FDR $2n$ gametes transmit blocks of advantageous dominance (intralocus) and epistatic (interlocus) interactions to polyploid offspring following meiosis. In diploid plants, these interactions are lost during meiosis and fertilization. SDR $2n$ gametes contain nonsister chromatids from the centromere to the first crossover, so they are less effective at carrying heterozygous loci across generations. While FDR $2n$ gametes transmit 80% of the diploid parent heterozygosity to tetraploid offspring, SDR $2n$ gametes transmit less than 40% (Peloquin, 1983).

In angiosperms, viable seeds contain the double factors: embryo and endosperm. Diploid plants produce diploid embryos and triploid endosperm tissue. The endosperm contains two genomes of the maternal parent and one genome of the paternal parent. Intraspecific, intraploidy crosses in potato typically produce viable seeds containing well-developed endosperm. Conversely, in most interploidy crosses, the endosperm fails to develop properly, and seeds are inviable (Brink and Cooper, 1947). However, endosperm may also fail to develop adequately in some intraploidy, interspecific crosses, while some interploidy crosses succeed. A 2 maternal : 1 paternal ratio of endosperm balance factors, rather than genomes, is necessary for normal endosperm development in potato (Johnston *et al*., 1980). The endosperm balance factors presumably have a genetic basis, and genetic models have been proposed (Ehlenfeldt and Hanneman, 1988a; Camadro and Masuelli, 1995). The genes responsible for normal endosperm development have yet to be identified. However, knowledge of the presence of endosperm balance factors can be valuable even without the knowledge of the responsible genes. *Solanum* species have been assigned EBN on the basis of their ability to hybridize with each other (Hanneman, 1994). Barring other crossing barriers, viable seeds will be produced from crosses between plants with matching EBN values. This will result in a 2 maternal : 1 paternal ratio of endosperm balance factors after fertilization of the central cell to produce endosperm. The most common ploidy, EBN combinations in potato, are $6x$ (4EBN), $4x$ (4EBN), $4x$ (2EBN), $2x$ (2EBN), and $2x$ (1EBN). EBN can be increased through somatic doubling (Ross *et al*., 1967; Sonnino *et al.,* 1988) or the production of $2n$ gametes described above. EBN can be reduced through anther culture or parthenogenesis.

Breeders use EBN values to predict interspecific hybridization success and to design strategies to access wild germplasm by manipulating EBN (Ehlenfeldt and Hanneman, 1988b; Singsit and Hanneman, 1990; Menke *et al*.,

1996; Janssen *et al*., 1997; Carputo and Barone, 2005). However, it is important to note that EBN is only one component of a complex system of pre- and postzygotic interspecific crossing barriers in wild *Solanum* species (Masuelli and Camadro, 1997; Chen *et al*., 2004a). Consequently, crossing success is not guaranteed by matching EBN values.

The EBN concept also appears to function in other polyploid crops (e.g., oats, rice, and some other grasses; *Medicago*, *Trifolium,* and other legumes; blueberry; squashes; Ortiz and Ehlenfeldt, 1992; Carputo *et al.,* 2003), but most other polyploid crops have not yet been studied in this regard. A strategy for overcoming crossing barriers in other crops would be to try chromosome doubling and make crosses in both directions. The EBN concept does not overcome all crossing barriers, as even in potato there are other barriers (e.g., stylar barriers), but reciprocal crosses can often overcome these barriers.

Other crossing barriers that impede interspecific hybridizations

In addition to differences in chromosome numbers, whether ploidy differences or differences in monoploid number, other pre- and postzygotic reproductive barriers may make hybridizations with wild relatives difficult or impossible. In this case, wild relatives truly are "unavailable," yet sometimes these barriers can be overcome with modern methods. Buckwheat (*Fagopyrum*) is an example of a crop in which recent progress has been made in interspecific crosses using embryo rescue. The genus includes both diploids and polyploids, and most of the species have a distylous breeding system. In addition to these complicating factors, other reproductive barriers have meant inviable seeds were produced from most, but not all, previous attempts to generate interspecific crosses (Chen *et al.,* 2004b), but embryo rescue techniques have now had some success in hybridizations between *Fagopyrum esculentum* and *Fagopyrum tataricum* (both

diploid domesticates) and with *Fagopyrum cymosum* (a wild tetraploid) (Niroula *et al.,* 2006).

Crops that still have no fertility with wild relatives include faba bean and melon (although its relative cucumber has recent breakthroughs), described in more detail below.

Interspecific hybrids in cucumber

Another example of a case in which until recently no wild species were known that could be successfully hybridized with the domesticates is the genus *Cucumis* (Cucurbitaceae), which includes both the cucumber, *Cucumis sativus* L., and the muskmelon, *Cucumis melo* L. Some spontaneous (presumed to be feral) populations of *C. sativus* are known, specifically *C. sativus* var. *hardwickii* (Royle) Gabaev of northeastern India, Nepal, southern China, Myanmar (Burma), and Thailand (De Wilde and Duyfjes, 2007). These wild populations have been used to introduce into domesticated cucumber traits such as multiple lateral branching (MLB, which increases yield because more fruits forming on the side branches) and resistance to root-knot nematodes (Staub *et al.*, 2008). However, prior to the mid-1990s, attempts to broaden the genetic base of cucumber further by making interspecific crosses with other *Cucumis* species either failed or were unrepeatable (Delannay *et al.,* 2010). Most *Cucumis* wild species are found in Africa, are more closely related to each other than any of them are to cucumber, have a basic chromosome number of $x = 12$, and are classified in subgenus *Melo*. Cucumber, by contrast, is based on $x = 7$, is classified in subgenus *Cucumis*, and originated in Asia. In the early 1990s, Chen and colleagues rediscovered *Cucumis hystrix* Chakrav. in Yunnan province of southwest China (reviewed in Chen *et al.,* 2008). This species is also found in India, Bangladesh, Myanmar (Burma), and Thailand (Kirkbride, 1993, cited in Chen *et al.,* 1997; Uddin *et al.*, 2012). Although *C. hystrix* has $x = 12$ like the African wild species, random amplified polymorphic DNA (RAPD) data showed that it is more closely related to cucumber than to other $x = 12$ species, supporting its classification in subgenus *Cucumis* (Zhuang *et al.,* 2006). Despite their different chromosome numbers, *C. sativa* and *C. hystrix* were successfully crossed using embryo rescue techniques, which yielded a hybrid with $2n = 19$ (Chen *et al.,* 1997), which was then doubled to form the stable hybrid *C.* × *hytivus*, with $2n = 4x = 38$ (Chen and Kirkbride, 2000). This tetraploid hybrid was used to form introgression lines by backcrossing with cucumber. Although SSR and AFLP data showed that relatively little of the *C. hystrix* genome was introgressed into *C. sativus* in these lines, they nonetheless had gained resistance to fusarium and downy mildew (Zhou *et al.,* 2009). Further breeding efforts led to a diverse range of introgressed breeding lines of cucumber that have traits derived from *C.* × *hytivus,* including MBL lines that have sequential fruiting without the poor interior fruit quality associated with the lateral branching trait in lines derived from *C. sativus* var. *hardwickii* (Delannay *et al.,* 2010). Despite these advances in broadening the genetic base of cucumber with the synthetic hybrid *C.* × *hytivus*, there are as yet no other species that have been able to be crossed with muskmelons.

Unavailability of wild relatives of faba bean

The faba bean (*Vicia faba* L.) is a crop of intermediate importance on the world scale, covering about 2.5 M ha in 2010 and 2011 with an average yield of 1.6–1.7 t/ha (FAOstat, 2013). Its area is likely to increase, as it is widely adapted to cool temperate conditions, and many countries, particularly those of Europe, aim for independence from imported soybean (*Glycine max* (L.) Merr.). It is grown as an autumn-sown crop in Mediterranean and oceanic climates, and as a spring-sown crop in continental and boreal climates, thus succeeding from 42°S in Tasmania to 62°N in Finland. The young beans

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are a highly valued vegetable in many countries, and the dry beans a staple in some others, while the main use of the crop is as feed for livestock.

No wild progenitor of faba bean has ever been identified, and this makes it hard to identify its center of origin. The oldest material, from the seventh millennium BC, is not indisputably faba bean, as the seed size and some aspects of shape are equally consistent with other *Vicia* species such as *Vicia narbonensis* L. (Zohary and Hopf, 2000). Clear examples of faba bean have been found from more or less simultaneous sites, dated to the third millennium BC, around the Mediterranean basin and into central Europe. The most primitive existing germplasm is classified into the subspecific taxon (ssp. or var., depending on the taxonomist) *paucijuga*.

Several wild species of *Vicia* have clear affinities to faba bean. Nevertheless, their haploid chromosome number is 7, in contrast to the 6 of faba bean, the morphology of their chromosomes is different (Ladizinsky, 1975), and their DNA content is less than the massive 13 Gbp of faba bean. Chloroplast DNA sequences showed that all six of these species (*V. narbonensis*, *Vicia serratifolia* Jacq., *Vicia galilaea* Plitm. & Zoh., *Vicia johannis* Tamam., *Vicia kalakhensis* Kh., Max. & Bis., and *Vicia hyaeniscyamus* Mout.) are far more closely related to one another than any of them is to *V. faba* (Raina and Ogihara, 1994).

In the 1980s, there were several attempts to develop interspecific hybrids of faba bean with some of these wild relatives, with observations on pollen tube growth and attempts at embryo rescue. The embryos aborted less than 10 days after pollination, and cytological anomalies in the embryo and endosperm were often noted even earlier (Ramsay and Pickersgill, 1986; Roupakias, 1986; Lazaridou *et al.,* 1989; Zenkteler *et al.,* 1998). Differences in endosperm cell cycle time (Lazaridou and Roupakias, 1993) along with the general difficulty of culturing faba bean tissue (Abdelwahd *et al.,* 2008) contribute to the failure of interspecific hybridization in faba bean.

Nevertheless, there is considerable genetic variation within *V. faba*. Seed size ranges more than 10-fold, and it is grown in a greater variety of habitats than any other grain legume with the possible exception of pea (*Pisum sativum* L.). More detailed investigation of the greater than 20,000 accessions in world germplasm banks, perhaps using targeted methods such as the Focused Identification of Germplasm Strategy (FIGS), can help to identify germplasm with useful traits such as greater resistance to drought or disease (Khazaei *et al.,* 2013a, 2013b).

Lack of information about CWR and recent progress in several crops

Since the emergence of molecular systematics, many crops whose origins were mysterious have had their origins revealed, or at least tremendous advances have been made. These could be counted among crops for which wild relatives were unavailable when information about their origins was unknown, but which now have "available" wild relatives. In addition to maize and cassava, described in more detail below, many crops have had recent studies elucidating their origins or dispersal that were included in compilations (Motley *et al*., 2006; Zeder *et al*., 2006).

Maize

An example is maize (*Zea mays* L. subsp. *mays*), which was the center of fierce debate about its origins for many years. This was largely because it looks so unlike its progenitor, teosinte, that at first teosinte was classified as a different genus (*Euchlaena*) and only later was transferred to *Zea*, with some of the teosintes being classified as subspecies or varieties of the same species as cultivated maize (reviewed in Doebley, 1990, 2001). Debates between different camps of maize researchers, represented by George Beadle and Paul Mangelsdorf, were finally won when overwhelming evidence was presented

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by Beadle that teosinte was the progenitor of maize (reviewed in Doebley, 2001). Work of John Doebley and colleagues, beginning with isozymes in the 1980s and continuing to the present, has established that the teosintes that are most similar to cultivated maize in their molecular data are populations of *Z. mays* subsp. *parviglumis* Iltis & Doebley found in the valley of the Río Balsas in southwestern Mexico, and that that area is the probable area of origin for a single domestication of maize (Doebley, 1990, 2001; Matsuoka *et al.,* 2002). Establishment of the progenitor of maize has since allowed research on the genetics of domestication in maize (e.g., Dorweiler and Doebley, 1997).

Cassava

M. esculenta Crantz subsp. *esculenta* (cassava, manioc, yuca) is one of the crops for which the introduction of molecular methods has allowed new insights into questions of origins of domesticated crops that had previously been nearly impossible to solve. Before molecular data, the question of the origin of cassava was very challenging because *Manihot* has 98 species in the Neotropics, most of them difficult to define on the basis of morphological characters. Because of this morphological complexity, researchers had thought that there was much hybridization between the species, and indeed, it was thought that cultivated cassava arose through hybridization among several species, leading to a "compilospecies" with multiple origins (Rogers and Appan, 1973, cited by Olsen and Schaal, 2006).

After the introduction of molecular techniques in the 1980s, data from RFLPs, AFLPs, and DNA sequences all indicated that cassava is more closely related to wild *Manihot* species from South America than those from Central America, and in addition, populations of *Manihot* were found in South America that were so similar to domesticated cassava that they were named as a subspecies of the same species, that

is, *M. esculenta* subsp. *flabellifolia* (Pohl.) Cif. (reviewed by Olsen and Schaal, 2006).

M. esculenta subsp. *flabellifolia* occurs in the transition zone between the Amazonian rainforests and *Cerrado* vegetation, and the species was sampled by Olsen and Schaal (2006) from throughout the Brazilian parts of its range, along with samples of domesticated cassava from the core collection of CIAT and of *Manihot pruinosa*, one of the species that had been proposed as one of the progenitors in hypotheses of hybrid origins of the crop. Olsen and Schaal (2006) used DNA sequences of three low-copy nuclear genes: *G3pdh* (glyceraldehyde 3-phosphate dehydrogenase), *BglA* (beta-glucosidase), and *Hnl* (alpha-hydroxynitrile lyase) and five microsatellite (SSR) loci (Olsen and Schaal, 1999, 2001). For haplotypes of all three nuclear loci, as well as almost all of the SSR data, domesticated cassava showed a subset of the variation in *M. esculenta* subsp. *flabellifolia*, specifically those of the populations in the western end of the species range, not those of the eastern populations. The sequences of *M. pruinosa* were not well separated from those of wild *M. esculenta*, suggesting the possibility that hybridization had indeed occurred between these species. However, the data of *M. pruinosa* were nonetheless not very similar to cultivated cassava. Olsen and Schaal (2006) concluded that *M. esculenta* subsp. *flabellifolia* is the sole progenitor of domesticated cassava and thus that crop did not originate through hybridization. Their molecular data also pointed to the transition zone at the southwestern border of the Amazonian rainforest as cassava's area of origin, as the molecular data of cassava was a subset of the samples from the Brazilian states of Mato Grosso, Rondônia, and Acre. Although this area is close to the international border of Brazil, their sampling did not extend across the border into eastern Peru, Bolivia, or Paraguay. Future studies should at least include samples from lowland Bolivia, where *M. esculenta* subsp. *flabellifolia* is likely to occur. Olsen and Schaal (2006) point out that their results suggest

that cassava seems to have originated in the same archeologically important area as has been proposed by Piperno and Pearsall (1998) for domestication of *Arachis hypogaea* L. (peanut), *Capsicum baccatum* L. (chili pepper), and *Canavalia plagiosperma* Piper (jack bean).

Climate change and extinction of crop wild relatives

Many attempts have been made to predict how many species will be driven to extinction by climate change. Different researchers have proposed different ways of modeling future distributions, on the basis of different assumptions, to make these predictions. In addition to the debate about these models and assumptions, different researchers compare their predictions to empirical data in differing ways, such as comparing the predictions to the effects of past climate change as shown in the fossil record, herbarium specimens, or historical records. Most of the modeling studies include models both with and without migration, which represent the two extremes to set the outer bounds for dispersal, because the actual extent of migration is not possible to predict (e.g., Thomas *et al.,* 2004; Jarvis *et al.,* 2008). It is important to compare both scenarios because of the difficulty of predicting whether a species will be able to migrate; regardless of the innate dispersal ability, actual migration will be affected by habitat fragmentation in many cases and will be highly dependent on the habitat needs of the particular species. Idiosyncrasies of each species are difficult to predict. Despite the differences of opinion on the models, the one thing that most researchers agree on is that we need more information to be able to improve these predictions. For instance, it is clear that more information is needed about the extent to which species will be resilient to climate change, whether they will face tipping points, and about how changing climates will affect species interactions (Moritz and Agudo, 2013).

Some studies predict high levels of extinction, or at least extreme loss of geographic distribution of species because of climate change in the next decades. Although some of these studies are primarily based on animal taxa, those that include plants are also dire. For instance, Thomas *et al.* (2004) are often cited for their overall predictions of 15–37% of species endangered or extinct by 2050, but the details of their predictions about plant taxa in four regions are more nuanced and even more worrisome. The plant datasets they examined included 9 plant species of Amazonia, 192 species of Europe, 163 of the Cerrado, and 243 South African Proteaceae. Their models included a range of scenarios with and without dispersal, and greater or lesser climate change, to encompass both minimum and maximum predictions. These models led to predictions that the species that will have been "committed to extinction" by 2050 would be 36–100% of 9 plant species in Amazonia, 3–29% of 192 species in Europe, 38–75% of 163 plant species of the Cerrado, and 21–52% of 243 Proteaceae species in South Africa (Thomas *et al*., 2004). Their measure of the "number of species committed to extinction" by 2050 does not necessarily imply that those species will become extinct by 2050, because it is not possible to predict the lag time from when suitable habitat area is reduced to too little to sustain species and when the species actually becomes extinct (Thomas *et al*., 2004). In addition, they also discuss other uncertainties, such as the possibilities of interactions between global warming and other factors, namely, invasive species and habitat destruction, that make exact predictions impossible.

Other predictions are equally worrisome. Using different datasets, Warren *et al.* (2013) predicted that over 57% of widespread species of plants would lose 50% of their climatic range by 2080, but that these losses could be reduced by 40–60% if mitigation results in leveling off of emissions by 2016 or 2030, respectively.

Other studies question whether the levels of extinction will be so severe (Botkin *et al*., 2007; Moritz and Agudo, 2013). For example, Moritz

and Agudo (2013) assert that the levels of extinction in the fossil record during times of past climate change are not are great as many models predict. However, the resiliency they cite seems to be mostly at the genus level among mammals, which might not reveal much about the level of species-level extinction among plants.

Beyond outright extinction, however, the contraction of species ranges because of climate change, especially among montane species, can result in reduced gene flow and loss of allelic diversity. This reduction of geographic range, increased population subdivision, and loss of diversity has already been seen among small mammals (alpine chipmunks, *Tamias alpinus*) in Yosemite National Park in the Sierra Nevada range of California, USA, in an innovative comparison of diversity across 90 years through use of museum specimens (Rubidge *et al.,* 2012). It should be possible to conduct similar studies for CWR on the basis of herbarium collections of montane species, at least for species that have been frequently collected.

Predictions for extinction of crop wild relatives

In one of the few studies to use these methods specifically to make predictions for CWRs, Jarvis *et al.* (2008) modeled future climate for 2055 and used a "climate envelope species distribution model" to predict changes in geographic ranges of CWR species in three genera: 48 *Vigna* species (cowpea relatives), 108 *Solanum* species (potato relatives), and 51 *Arachis* species (peanut relatives). Not surprisingly, they found that the predicted impact of future climate change was greater when modeled without migration of the species than when the model permitted migration to new areas. These models represent the outer bounds in the (unpredictable) amount of migration to new areas that might actually occur. Not surprisingly, the projected loss of suitable areas reached extinction of more species when no dispersal was modeled (3 *Vigna*, 13 *Solanum*, and 31 *Arachis* species) than

when dispersal to newly climatically suitable areas was permitted in the model (no extinction of *Vigna* species, but extinction of 7 *Solanum* and 24 *Arachis* species; Jarvis *et al.,* 2008). All three genera showed smaller habitat patches under the modeled scenarios, but *Vigna* species were least affected, *Solanum* was intermediate, whereas *Arachis* was the most severely affected. These differences were attributed to *Arachis* species being more narrowly adapted, as well as their current ranges being in flat landscapes in which tracking climate would mean dispersing long distances; potato wild relatives, on the contrary, are highly endemic, but may be able to migrate relatively short distances to newly suitable areas as climate bands move up the Andes mountains as the climate changes (Jarvis *et al.,* 2008). In general, species that occur in areas with more complex topography may be able to find refuges, whereas global warming may have more severe effects on those in areas of low relief, because they must be able to migrate long distances to find newly suitable habitats (Jarvis *et al*., 2008; Moritz and Agudo, 2013). Jarvis *et al.* (2008) also point out the importance of differences in the degree to which different species may tolerate or even flourish in disturbed environments (such as some *Vigna* and *Solanum*) versus those that cannot tolerate disturbance. Habitat fragmentation particularly affects the latter species, which could also be a factor in the differences between the impacts of climate change on different plant taxa.

Jarvis *et al.* (2008) also compared their modeling results to the peanut germplasm lines and new cultivars that had been registered in the journal *Crop Science* between 2000 and 2005, and found that nearly half of these species that had already been useful in crop improvement were among those that their models predicted could become extinct. They recommend evaluating potential protected areas as possible climate change refugia.

Some habitats that are particularly rich in CWRs, such as montane cloud forests (Debouck and Libreros Ferla, 1995), may be particularly

vulnerable. Many species in these habitats are highly endemic, being found in ribbon-like distributions with very narrow elevational ranges (e.g., Emshwiller, 2002a, 2002b; Fjeldså, 1995). On the one hand, species in habitats of complex topography are thought to have an advantage when their climate changes because they can reach newly appropriate habitats or find refuge without traversing long distances, in comparison with species occupying low-relief areas (Jarvis *et al*., 2008; Moritz and Agudo, 2013). On the other hand, however, highly endemic tropical montane species may lose range area as elevation increases, and they may be especially vulnerable if the cloud base lifts, as has been shown for endemic vertebrates of tropical montane forests in Monteverde National Park in Costa Rica by Pounds *et al.* (1999).

Complicating factors for predictions of extinction

Predictions of whether species will be resilient or will become extinct are difficult for many reasons. Some of these are because of factors related to the idiosyncrasies of individual taxa, about which research is still lacking. In addition to the fact that some species cannot tolerate disturbance whereas other flourish in disturbed habitats, other differences in response to climate change are being discovered in recent research. For instance, recent research shows that some hybrids react differently to changes in precipitation than their parental species (Campbell and Wendlandt, 2013), or that some taxonomic families of plants that flower earlier in spring are more sensitive to temperature than later flowering taxa (Mazer *et al*., 2013).

Most modeling studies make assumptions that species distributions are at equilibrium with the climates in the areas where they are found. However, several recent studies discuss the finding that most species are actually in disequilibrium with their environment, and that distributions usually lag behind their ideal climate niche. Ordonez (2013) studied pollen profiles of 20 plant taxa in eastern North America following the Last Glacial Maximum, most of them trees but also include weedy herbaceous Asteraceae such as *Iva* and *Artemisia*, and he compared their distributions to modeled variables of temperature (mean, minimum, maximum, mean seasonal, etc.) and precipitation (total and seasonal) during the end of the Pleistocene. He found that the realized climate niche of these taxa lagged behind the modeled climate changes during the end of the last glaciations, so that the species occupied only a subset of the conditions in which they could have persisted (Ordonez, 2013). Svenning and Sandel (2013) discuss the theory of disequilibrium dynamics, which can occur at both the leading and trailing edges of a species range. On the one hand, the leading edge may lag because migration does not keep up to move the species into newly appropriate ranges; there may be a lag in population buildup, or there may even be lags in ecosystem development; on the other hand, the trailing edge of a species' range may also lag, because either clonality or longevity might delay extinction (Svenning and Sandel, 2013). In theory, there may even be the possibility of evolutionary adaptation or of delayed losses of ecosystem structure, although there are as yet few empirical data on these particular scenarios (Svenning and Sandel, 2013). Svenning and Sandel (2013) also point out that disequilibrium dynamics have been better studied in Europe and North America, especially regarding changes after the Pleistocene glaciations, and that these areas obviously do not represent the situation in other vegetation types, so much more research is needed to understand the potential situation in these other habitats.

Individual species abilities to buffer the effects of climate change are unknown and idiosyncratic, and there is also a dearth of information about how climate change will interact with habitat loss and fragmentation, potential biological invasions of pests, pathogens, and competitors, the effects of nitrogen deposition or other pollution, and changing disturbance

regimes, and whether there will be tipping points or whether species may prove to be resilient to climate change (Moritz and Agudo, 2013; Svenning and Sandel, 2013).

In contrast with the relatively slow movement of some taxa after the retreat of continental glaciations in North America, in which forest communities gradually changed over the course of thousands of years, invasive exotic species are examples of the highest potential abilities for species dispersal and population establishment in new environments (Svenning and Sandel, 2013). Invasive species also provide examples of cases in which the climate can limit their spread, and in which changing climates may allow them to have even greater impact. An example is the hemlock woolly adelgid (*Adelges tsugae*), an insect introduced to North America from Asia in the early twentieth century, that has caused extensive mortality in eastern hemlock (*Tsuga canadensis* (L.) Carrière) in the United States, but which cannot survive in areas where winter temperatures reach −-25 to −30°C. Although minimum temperatures have so far limited the spread of these aphid-like insects, temperature predictions suggest that hemlock will likely be extirpated in many states, and this important forest tree will persist only in the United States in a few areas of northern states (Dukes *et al*., 2009). Some other pests, diseases, and invasive or native species have also been documented to be influenced by climate change, but others do not show clear effects, and predicting how biotic interactions will be affected by climate change is very difficult in general (Dukes *et al*., 2009), so the potential effect on likelihood of extinction of CWRs is unknown.

Changing interactions among species can not only affect invasive exotic species, but can also drastically change the dynamics among native species, such as in recent cases of eruptions of native insects. For example, eruptions of native bark beetles in the conifer forests in western North America in recent years are well beyond the levels recorded in the past 125 years (Raffa *et al.,* 2008). The mountain pine beetle,

Dendroctonus ponderosae Hopkins, that was endemic on lodgepole pine (*Pinus contorta* Douglas ex Louden var. *latifolia* Engelm. ex S. Watson) is now attacking another species of pine (whitebark pine, *Pinus albicaulis* Engelm.) that was formerly protected by growing at higher elevations; previously, the colder temperatures in whitebark pine habitat kept the beetles at bay, but as temperatures are increasing, this tree species is now attacked, and it does not have the same level of coevolved defenses as lodgepole pine (Raffa *et al.,* 2013). The possibility of increased frequency of drought and high temperatures with changes in global climate may bring increased insect outbreaks followed by extensive tree die-offs as was seen in the pinyon ips beetle (*Ips confusus*) eruption in southwestern North America in the hot drought years of 2002 and 2003 in the pinyon pine–juniper woodlands (Breshears *et al.,* 2005). There are very complex interactions that affect whether the populations of conifer bark beetles will erupt, including the population density and genetic structure of both tree and beetle species (as well as their natural enemies and their symbiotic microbes and fungi), host defenses (terpenes, phenolics, etc.), and both threshold and feedback processes, including some cases of long-term delayed feedback (Raffa *et al.,* 2008). Recent years have seen an increase in the frequency and extent of eruptions as thresholds are passed, and ranges of the beetles have expanded to higher elevations and latitudes that were previously limited by colder temperatures. Consequently, mountain pine beetles have not only shifted to tree species with little or no coevolved defenses, but there is now even the frightening possibility that ranges of the beetles will cross the boreal forests of Canada to travel from western to eastern North America and expand throughout eastern conifer forests as well (Raffa *et al.,* 2008; Safranyik *et al.,* 2010). These are well-studied examples of complex interactions among multiple species and climate factors, which serve to illustrate the possibilities that may be occurring with less attention in other species, including CWRs.

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Models to predict extinction are based on predictions of changes in temperature and precipitation, but extreme weather events will also increase as a result of global climate change. The phenomenon of Arctic amplification means that because of relatively greater warming in the Arctic region than in other parts of the Northern Hemisphere, the curves of the Jet Stream are becoming more pronounced (greater amplitude of the waves) and are progressing eastward more slowly; this in turn means that weather conditions persist for longer in the north temperate region, so that extreme weather events such as both hot and cold spells and both drought and flooding are becoming more frequent and more severe (Francis and Vavru, 2012). Tropical cyclones will also increase in frequency and strength (Emanuel, 2013), so destruction in populated areas, such as those that occurred during Super storm Sandy in 2012 (Greene *et al.,* 2013) and Typhoon Haiyan in 2013 will increase. These storms could certainly threaten CWRs in coastal or island habitats, just as increasing occurrence of heat and drought could threaten species in other areas. The exact occurrence of particular extreme weather events cannot be predicted; only that they will become more frequent and more severe in coming decades as global climate changes can be foretold.

Even without the threat of climate change, habitat destruction is a serious threat to CWRs, especially those that have populations with small numbers of individuals in areas that are frequently disturbed by human activities. Such extirpation of populations has been observed in small wild populations of Lima beans, *Phaseolus lunatus* L., many of which have disappeared in the Central Valley of Costa Rica, and of which only a fraction of the populations have repopulated from the soil seed bank (Rocha *et al.,* 1997; Baudoin *et al.,* 2004). Although these studies leave uncertainty about the future levels of extinction, they leave no doubt that there will be extinction of at least some species of CWRs as global climate changes, interactions among species change, and habitats continue to be destroyed.

Conclusion

Clonal propagation, differences in ploidy levels, and other crossing barriers can impede use of CWRs in plant breeding, but progress in generating interspecific hybrids is being made, thanks to improvements in understanding EBN and in various techniques such as embryo rescue. In some crops clonality limits their ability to adapt to climate change, but those that are capable of sexual reproduction may face other challenges, as in the case of the preference for certain grape clones. In some tropical clonal crops, such as yams and bananas, although they tolerate high temperatures, their wild relatives may be more threatened by habitat loss than by climate change alone.

Recent decades have seen enormous progress in clearing up mysteries of crop origins, as we have seen for maize and cassava. Such research to clarify the origins of crops, and thus their evolutionary relationships with close wild relatives, will continue to benefit from advances in molecular methods, so that fewer and fewer crops will remain for which knowledge of crop progenitors will be lacking. However, we still lack much information about many CWRs, such as their crossability cultigens, their distributions, and climate niches, or, in some cases, even their existence. Some of these unknown, or at least understudied, species are already endangered, as in some recently described *Dioscorea* species.

Global climate change will undoubtedly lead to extirpation and even extinction of CWRs, but the causal relationship is not simple. Predictions are inexact because changes in temperature and precipitation are not the only factors involved. Interactions with other biotic and abiotic factors; nonequilibrium between climate, ecosystems, and species; and idiosyncrasies of species resilience or vulnerability are all unpredictable, as are individual extreme weather events. Despite the differences in the models used to

predict future levels of extinction of species, the point on which all researchers agree is the need for more information. Nonetheless, it is clear that climate change, in concert with other human-induced factors such as invasive species and habitat destruction, will lead to loss of populations and whole species of CWRs. We cannot afford complacency.

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