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REVIEW

Trends in genomics and molecular marker systems for the development of some underutilized crops

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Abstract
The term 'underutilized' is often used to characterize the range of plant species whose potential contribution to food security, health, income generation, and environmental services has not yet been fully exploited. To harness unexploited resources, the first step is to prevent them from extinction and to conserve them *in-* and/or *ex-situ*. To utilize plant species as crops, plants must be collected, conserved, evaluated, and then if necessary manipulated. In this context, significant international efforts have focused on impeding the erosion of genetic diversity. Thousands of new accessions are introduced into germplasm institutes each year. Assessment of their molecular diversity is necessary to eliminate redundant genotypes. Marker systems have been used not only for genotyping to reduce redundancy and develop a core set, but also for a wide variety of other purposes. The use of markers based on single nucleotide polymorphisms, copy number variation, and insertions/deletions, as well as genotyping by sequencing, is becoming popular for genetic mapping and analyses of quantitative trait loci. This review discusses current marker systems and genomic analyses of a number of underutilized crops.

Keywords GBS; Genotyping; Mapping; Molecular marker systems; Underutilized crops

Introduction

Terms such as 'underutilized', 'neglected', 'orphan', 'minor', 'promising', 'niche', and 'traditional' are often used interchangeably to characterize the range of plant species whose potential contribution to food security, health, income generation, and environmental services has not yet been fully exploited (http://www.underutilized-species.org/). Such crops are often strongly linked to the cultural heritage of their places of origin, and tend to be local, traditional crops (and their ecotypes and landraces) or wild species whose distribution, biology, cultivation, and use remain poorly documented. Furthermore, these species tend to be adapted to specific agro-ecological niches and marginal lands, and are underutilized. However, here we would like to extend the definition of 'underutilized crops' to those which, although currently used to meet human needs, require further research to extend their usefulness.

It is clear that the over-dependence of humanity on relatively few plant species represents a danger to the security of the human food supply. Broadening the range of plant species on which we depend will improve health and nutrition, as well as income generation and ecological sustainability. Constraints to the wider production and use of unexploited crops can often be overcome. Indeed, many formerly unused crops are becoming globally significant (e.g., oil palm, soybean, kiwi fruit). Many underutilized species have the potential to contribute to food security (Kunkel, 1984). It is important to put each potential crop to appropriate use. However, it can be difficult to define the best utilization of each crop. This is further complicated by the fact that numerous species disappear before they are documented and studied. In particular, modern agricultural practices, urban expansion, deforestation, and other human activities continue to drive the pace at which species are becoming endangered and going extinct. Hence, to exploit new potential resources, the first step is to prevent them from extinction and conserve them *in-situ* and/or *ex-situ*. Then they must be collected, conserved, evaluated, and if necessary manipulated to develop them into useful and healthful crops. In this context, significant international efforts have focused on impeding the erosion of genetic diversity. More than 600,000 plant samples are held by the Consultative Group on

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International Research (CGIAR) to preserve the biodiversity of crop species (http://ftp.fao.org/planttreaty/news/news-0003_2n.pdf), and hundreds of thousands of new samples are introduced into germplasm institutes each year (Park et al., 2009). In such newly introduced germplasms, it is necessary to assess redundancy. In an effort to maximize genetic variability and minimize repetitiveness, the concept of creating a 'core collection' was introduced to maintain the optimum size of samples in a population (Frankel, 1984; Yonezawa, 1985; Brown, 1989; Moe et al., 2011; Zhao et al., 2011). In this case, several efficient marker systems are needed to classify specimens more rapidly than possible using previous methods based on phenotypic traits.

Genetic diversity is influenced by selection, mutation, migration, population size, and genetic drift (Hedrick, 2005; Ouborg et al., 2006). Understanding how each of these factors influences the genetic diversity of a population is critical to the conservation of species (Park et al., 2009). In the past, morphological traits were commonly used to evaluate the genetic diversity of populations. However, morphological markers are often greatly influenced by the environment, which limits their utility for assessing real genetic diversity (Chen and Nelson, 2004). Significant advances in molecular biology have shifted the focus from assessing biodiversity based on morphological markers to using isozymes and DNA markers (Bretting and Widrlechner, 1995; Karp and Edwards, 1997). This review focuses on current knowledge of the genomic and molecular marker systems of some underutilized species.

Molecular and DNA marker systems

Variation between individuals in a population or between populations in a species can be easily evaluated through the use of a variety of markers. Morphological markers were used before the discovery of proteins and DNA. Sax (1923) demonstrated that differences in seed size, seed coat, and pigmentation patterns were genetically linked in the common bean (*Phaseolus vulgaris*) (Sax, 1923). However, morphological traits that exhibit continuous variation between individuals in a population often obscure the evaluation of genetic diversity. Moreover, pleiotropism and a multifactorial basis to morphological traits further disguise the characterization of plant populations (Park et al., 2009). The discovery that genes encoded proteins and enzymes led to the utilization of isozymes and other proteins as marker systems for analyzing populations (Scandalios, 1969; Hamrick et al., 1979). Although protein markers circumvent environmental effects, the number of detectable isozymes are limited and they are typically tissue- and developmental stage-specific (Park et al., 2009). For this reason, most researchers began to focus on the use of DNA marker systems for genetic and ecological analyses of plant populations. Such systems have many advantages over traditional morphological and protein marker systems.

Southern blot-based marker systems were the first generation of DNA marker employed. Shortly after the first demonstration of the usefulness of restriction fragment length polymorphisms (RFLPs) in human genetics for linkage analysis (Botstein et al., 1980), the technique was adopted by plant research communities (Chang et al., 1988; Tanksley et al., 1989). RFLPs result from point mutations at restriction enzyme (RE) recognition sites. Chromosomal mutations such as insertions, deletions, inversions, and translocations can also cause RFLPs (Park et al., 2009). The RFLP technique employs molecular hybridization of cDNA or genomic DNA probes with genomic DNA fragmented by REs. Another Southern blot-based marker system relies on mini-satellite probes for 'fingerprinting' (Jeffreys et al., 1985). However, the use of such systems for analyzing large populations is limited in some laboratories by the technical complexity and high cost.

Marker systems based on polymerase chain reaction (PCR) were the second generation of DNA marker for genetic analysis (Mullis et al., 1986). PCR revolutionized genetic and ecological analyses of populations because it requires only a small amount of DNA, is inexpensive, and is simple enough to perform on a large scale. Among the many PCR-based markers, random amplification of polymorphic DNA (RAPD), amplified fragment length polymorphisms (AFLPs), and microsatellite or simple sequence repeats (SSR) are the most commonly used, with other systems being variations of these three. Inter-SSR (ISSR) is a variation the RAPD technique with an SSR strategy, and its application was reviewed by Godwin et al. (Godwin et al., 1997). AFLP markers exhibit dominant inheritance, which can be converted into co-dominant STS markers to detect alleles of a given locus (Jones et al., 1997). The sequence-characterized amplified region (SCAR) marker system is introduced to increase the reproducibility. SCAR marker is designed from the sequence of formerly analyzed fragment such as AFLP. SSRs are also highly abundant in plant genomes (Morgante and Olivieri, 1993; Wang et al., 1994). SSR polymorphisms (SSRPs) were first detected Weber and May (1989), who used PCR with two flanking primers (Weber and May, 1989). Detailed information on these two marker systems is provided by Park et al. (Park et al., 2009). A new marker technique called the restriction site amplified polymorphism (RSAP) system was developed in 2010 in China (http://www.china-papers.com/?p=64910). This involves two primers of 18 nucleotides. Starting at the 5′ end of each primer are 12-14 bases of arbitrary sequence, followed by restriction site sequences (4-6 bases). The restriction sites of the two primers are different. RSAP is simpler than other DNA marker techniques based on restriction sites, and has moderate throughput ratio and reliability; in a previous study, it was well amplified in *Oryza sativa* L. and *Momordica charntia* L.2 (http://www.china-papers.com/?p=64910).

Third-generation marker systems are based on non-gel molecular markers, single nucleotide polymorphisms (SNPs), and microarrays (Lindroos et al., 2002; Choi et al., 2007). The

polymorphism of a single base can be assessed by through-put analysis, hybridization with allele-specific oligonucleotides (ASO) (Hashimoto et al., 2004), primer extension (Sybänen, 1999), invasive cleavage (Lyamichev et al., 1999), and oligonucleotide ligation assays (OLA) (Iannone et al., 2000). The theory behind each of these techniques is reviewed in Sobrino et al. (Sobrino et al., 2005) and Semagn et al. (Semagn et al., 2006). The BioMark Real-Time PCR System sets a new standard for high-throughput real-time qPCR assays to detect SNP polymorphisms, integrating thermal cycling and fluorescence detection on Digital Array™ integrated fluidic circuits (IFCs) and Dynamic Array™ IFCs (Fluidigm). The streamlined workflow for applications provides high sensitivity and a dynamic range, at extremely high-throughput levels. There are numerous SNPs in plant genomes. Although these new-generation marker systems are powerful tools for linkage disequilibrium analysis, germplasm assays by haplotyping, quantitative trait loci (QTL) analysis, and a few other methods (Gupta et al., 2001; Rafalski, 2002), their use is only feasible in those species for which extensive nucleotide sequence information is available. Insertions/deletions, indels (Bapteste and Philippe, 2002; Väli et al., 2008) and copy number variation, CNV (Illumina, 2007) are also used as DNA markers. However, both require sequencing and alignment in genotyping. Genotyping by sequencing (GBS) is the most precise of any marker system. The sequencing of the complete genomes of many plant species is now underway with the aid of technical advances in DNA sequencing. Consequently, crop improvement programs can be sped up using these new sequencing technologies.

Advances in next-generation technologies have driven the costs of DNA sequencing down to the point where GBS is now feasible for highly diverse species with large genomes. The strategy involves constructing GBS libraries based on reducing genome complexity with REs. This approach is simple, quick, extremely specific, and highly reproducible (Elshire et al., 2011). It is particularly useful for studying species that lack a complete genome sequence, because only a reference map around the restriction sites is required, and this can be done during the sample genotyping process. Future application of GBS to breeding, conservation, and global species and population surveys may allow plant breeders to select for novel germplasms or species without first having to develop new molecular tools, and/or may help conservation biologists to determine population structure without prior knowledge of the genome or species diversity (Elshire et al., 2011).

Genetic analysis of some underutilized crops

A summary of the information on marker development and genetic diversity of some underutilized crops is presented in Table 1 and the uses of markers in the flow from wild types to advanced cultivated crop plants are demonstrated in Figure 1.

Cereals

Being staple crops, cereal grains are grown in greater quantities and provide more food energy worldwide than any other type of crop. The global cereal production in 2009, 460.88 million metric tons (mmt), was a marked increase over that of the previous year, 381.75 mmt (FAOSTAT, http://faostat.fao.org/site/570/default.aspx#ancor; accessed 15 Nov. 2011). This increase is assumed to be a result of the development of crop-improvement strategies. Genetic manipulation is one of the most important strategies for making rapid improvements to crops. Genetic engineering has opened up new possibilities by allowing the transfer of individual genes, even from completely unrelated organisms such as fungi or bacteria, into plants. Genetic engineering thus provides a supplement to classical breeding approaches, and has focused mainly on conferring traits such as resistance to herbicides, pesticides, pests, disease, and stress; changing plant composition; increasing yields; and for pharmaceutical purposes. In this review, we omit the major cereals and discuss only one cereal crop, millet.

Millet; The most widely cultivated millet species are pearl millet (*Pennisetum glaucum*), foxtail millet (*Setaria italica*), proso millet, common millet, hog millet or white millet (*Panicum miliaceum*), and finger millet (*Eleusine coracana*) (Annex, 1996). *Setaria italica* is a small diploid C4 panicoid crop species, whose genome is being sequenced by the Joint Genome Institute (JGI) (Doust et al., 2009). It is closely related to grasses used as sources of bioenergy such as switchgrass (*Panicum virgatum*), napiergrass (*Pennisetum purpureum*), and *Pennisetum glaucum*, and is a tractable experimental model because of its small diploid genome (490 Mb) and tendency to inbreed (Doust et al., 2009). Li and Brutnel suggested 515 Mb genome size of *Setaria italic* (Li and Brutnell, 2011). However, The outbreeding species have much larger genomes: pearl millet (diploid, 2,352 Mb), napiergrass (tetraploid, 2,254 Mb), and switchgrass (tetraploid, 1,372-1,666 Mb; octaploid, 2,352-3,136 Mb; (Bennett et al., 2000). Some genetic resources such as genetic maps (Devos et al., 1998; Wang et al., 1998) and a small collection of expressed sequence tags (ESTs) (Zhang et al., 2007) are already available for foxtail millet, but most of the tools for development and genetic research of this species require sequencing. Two complete genetic maps were created using RFLP markers in the late 1990s (Devos et al., 1998; Wang et al., 1998). Comparison of the position of common markers in foxtail millet and rice genetic maps showed that the two genomes were highly colinear, with six foxtail millet chromosomes that were orthologous to single rice chromosomes and three foxtail millet chromosomes that were each orthologous to two rice chromosomes (Devos et al., 1998). Embryogenic callus cultures (Rao et al., 1988; Vishnoi and Kothari, 1996) have been established *in vitro* for foxtail millet. However, successful regeneration of only one

Table 1. Markers developed and Diversity analysis of some underutilized crops.

No	Scientific name	Common name	Identified Markers	Polymorphic Markers	Diversity	Alleles identified	Source
	Cereals						
1	*Secale cereal L.*	Rye	SSRs (3799), SNP (5234)	SSR (61 out of 115), SNP (4557)	59 inbred lines		(Haseneyer et al., 2011a)
				ISBP	64		(Bartoš et al., 2008)
2	*Panicum miliaceum* L.	broomcorn millet	SSR	16	98	78	(Hunt et al., 2011)
3	*Setaria italica*	foxtail Millet	RFLP				(Devos *et al.*, 1998)
			GBS	500-1500 bp fragments	50 cultivated, 34 wild	9 unlinked loci	(Wang et al., 2010)
			SSR	84	155	1356	(Vetriventhan, 2011)
			Morphological	25	155		(Vetriventhan, 2011)
4	*Hordeum vulgare*	Barley	SSR	15	136	130	(Struss and Plieske, 1998)
			SSR	12	116	128	(Chen et al., 2010)
			RAPD	250-3000 bp fragments	15 landraces	578 out of 698	(Abdellaoui et al., 2010)
	Beans						
5	*Glycine max*	Soybean	SNP	550	444 RILs		(Hyten *et al.*, 2010)
			SSR	99	303	2128	(Li et al., 2010)
			SNP	554	303		(Li *et al.*, 2010)
			SDS PAGE	Protein	92	26 bands	(Malik et al., 2009)
6	*Vigna angularis*	Red bean	SSR	40 transferability	6 species		(Srimathy and Jayamani, 2010)
			GBS	4 plastid DNA sequencing	18 species of genus *Vigna*		(Javadi *et al.*, 2011)
			SSR	36	178	431	(Banni et al. 2011, submitted)
7	*Phaseolus vulgaris*	Kidney bean	SSR	67	279	402	(Burle et al., 2010)
			Mineral	Iron, zinc contents	90	310,28 (Iron, Zinc)	(Tryphone and Msolla, 2010)
			SSR	30	96	117	(Wooju and Park, 2012, submitted)
8	*Vigna ratiata* (L.) Wilczek	Mungbean	SSR	15	692	66	(Gwag *et al.*, 2010)
			SSR	15	55	56	(Kabir and Park, 2011)
			SSR	15	705	66	(Moe *et al.*, 2011)
			AFLP	6 paired combination	705	695 total fragments	(Moe *et al.*, 2011)
			SSR/ SNP and indel	1630/ 2098			(Moe *et al.*, 2011)
	Vegetables and Fruits						
9	*Amaranthus* sp.	amaranths	isozyme	30 loci encoding 15 enzymes	23 cultivated and wild		(Chan and Sun, 1997)
			RAPD	239 out of 600 RAPD			
			Isozyme	3 out 5 enzymes	52		(Yudina et al., 2005)
			AFLP	826 out of 851 AFLP fragments	27		(Xu and Sun, 2001)
			ISSR	147 out of 203 ISSR			
			SSR	179 out of 353	35 acc. From different species 92 F2 for linkage mapping	731	(Mallory et al., 2008)
			SNP (27,658)	419 SNP	134 F2		(Maughan et al., 2011)
10	*Allium sativum* L.	garlic	isozymes	7 groups out of 72 possible (by four enzyme system)	110	17	(Pooler and Simon, 1993)
			RAPD	12 out of 13	8 mutants resistant to white rot disease (*Sclerotium cepivorum*).		(Nabulsi et al., 2001)
			RAPD	4 locus-specific markers	25 garlic clones	24 polymorphic bands	(Ipek *et al.*, 2003)
			AFLP				
			RAPD	15 out 120	75	128 polymorphic bands	(Choi et al., 2003)
			SSR	8	90	64	(Ma et al., 2009)
			SSR (8 novel)	8	613	113	(Zhao *et al.*, 2011)
			SSR	7	120	37	(Jo et al, 2011, submitted)
11	*Vitis vinifera* subsp. vinifera,	grape	RAPD	10	76	126	(Maia et al., 2009)
			SNP (5,387)	4951	950		(Myles et al., 2011)
	OThers						
12	*Jatropha curcas L.*	Physic Nut	SSR	100	12 lines from various parts of the world		(Sato et al., 2011)
13	*Phoenix dactylifera*	Date Palm	SNP (3.5 million)	SNP (1,605 that segregated with gender)	Sex identificaton		(Dous et al., 2011b)

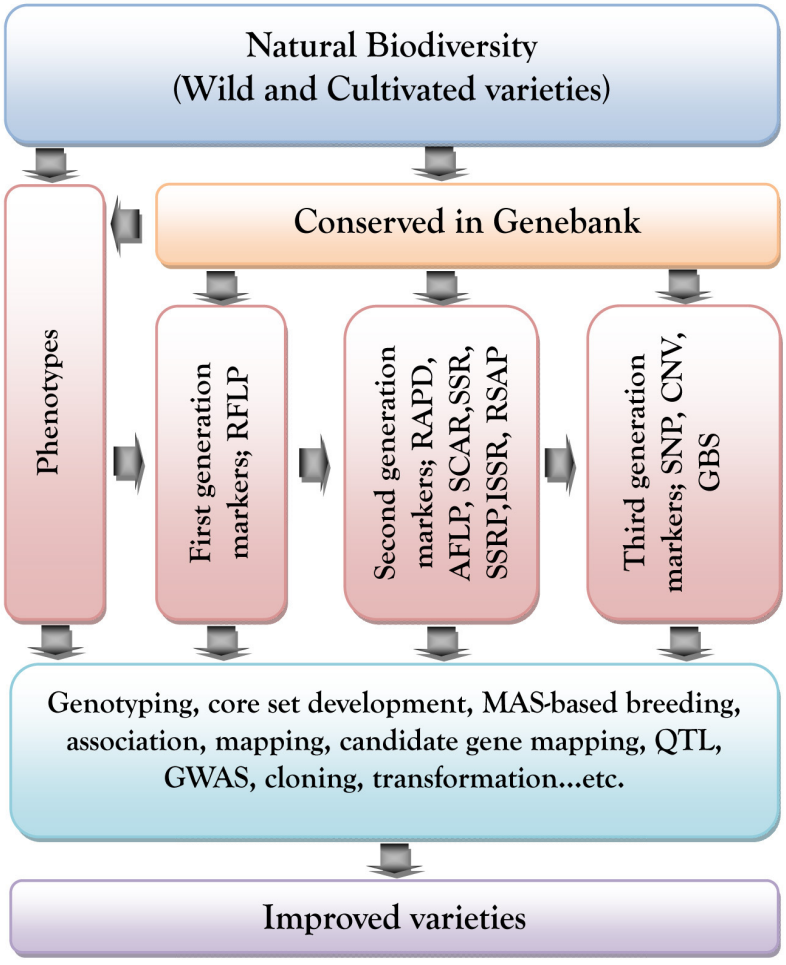

Figure 1. Contribution of Marker systems in the development of crop plants from natural wild types to improved varieties.

transgenic plant has been reported using *Agrobacterium* with an efficiency of 6.6% (Liu et al., 2005). Recently, model genetic systems of millet have been reviewed in detail by Li and Brutnell (Li and Brutnell, 2011).

Legumes

Legumes are members of the family Fabaceae (or Leguminosae). Soybean, munbean, redbean, cowpea, common bean, and many others are common legume crops on the market. The legume information system, a component of the model plant initiative (MPI), was developed by the National Center for Genome Resources in cooperation with the USDA Agricultural Research Service, under a specific cooperative agreement. Some plant genome and gene family tools are available at legume information system (LIS; http://www.comparative-legumes.org/pages/resources).

Soybean; Soybean (*Glycine max*) is one of the most important crop plants for seed protein and oil content, and for its capacity to fix atmospheric nitrogen through symbioses with soil-borne microorganisms. Schmutz et al. sequenced the 1.1 Gb genome using a whole-genome shotgun approach and integrated it with physical and high-density genetic maps to create a chromosome-scale draft sequence assembly (Schmutz et al., 2010b). A total of 46,430 protein-coding genes were predicted, 70% more than that of *Arabidopsis*. Hyten et al. performed high-throughput SNP discovery through deep re-sequencing of a reduced representation library to anchor and orient scaffolds in the soybean whole genome sequence (Hyten et al., 2010). They discovered a total of 7,108 to 25,047 SNPs in the 286 Mb sequence using a reduced representation library that was subsequently sequenced by the Illumina sequence-by-synthesis method on the clonal single molecule array platform. A total of 550 of the 565 SNPs from SoyOPA-3 and 1,240 of the 1,254 SNPs from SoyOPA-4 were mapped using 444 recurrent inbred lines (RILs) to create 20 linkage groups corresponding to the 20 chromosomes of soybean, and had an estimated total genetic length of 2,537 cM. Kim et al. focused on the re-sequencing of wild soybean *G. soja* (accession no. IT182932) and a subsequent comparative genomic analysis with reference

to the *G. max* genome (Kim et al., 2010; Schmutz et al., 2010b). They also identified a large degree of nucleotide and structural variation between the wild and domesticated soybean (Kim et al., 2010). Recently, a good review on diversity analysis and allele mining of soybean germplasm have been done by Sammour (Sammour, 2011).

Mungbean; Mungbean (*Vigna radiata* [L.] Wilczek) is one of the most widely cultivated species throughout the southern half of Asia. It is a self-pollinating diploid plant with $2n = 2x = 22$ chromosomes (Menancio et al., 1993) and a genome of 515 Mb/1C (Parida et al., 1990). Moe et al. classified the more than 20,000 valid unigenes in Sunhwa and more than 25,000 in Jangan with specific functions using the BLAST program based on nucleotide sequence similarity (Moe et al., 2010). They identified a higher number of SSR motifs in Jangan (1,630) than in Sunhwa (1,334), and 8,249 SNP variations, including 2,098 high-confidence candidates, between these two accessions. Gwag and colleagues (Gwag et al., 2006; Gwag, 2008; Gwag et al., 2010) developed seven polymorphic SSR markers and assessed genetic diversity among 692 mungbean accessions collected from 27 countries in 9 different geographic regions, using 15 SSR markers. Diversity analysis on 55 accessions with 15 SSR markers was performed by Kabir and Park (Kabir and Park, 2011). Recently, our group developed a core set from 705 accessions collected from different countries (Moe et al., 2011).

Red (or Azuki) bean; Red bean also known as azuki bean [*Vigna angularis* (Willd.) Ohwi & Ohashi], belongs to a group of legume family (Fabaceae). Several papers have analyzed the genetic diversity and domestication of red bean (Kaga et al., 2008; Xu et al., 2008). Kaga et al. constructed a linkage map of 592 red bean individuals using SSR, RFLP, and AFLP markers (Kaga et al., 2006). The consensus linkage map consisted of a total of 896 markers with an overall length of 854 cM and an average distance of 3.1 cM between SSR markers. Kaga et al. investigated a reciprocal translocation between cultivated and wild red bean on the basis of the linkage map having a pseudolinkage group and clustering of seed productivity-related QTL with a large effect near the presumed breakpoints (Kaga et al., 2008). In total, 162 QTL were identified for 46 domestication-related traits. Many researchers from China and Japan have performed genetic analyses of the red bean (Han et al., 2005; Kaga et al., 2005; Wang et al., 2009; Javadi et al., 2011; Wang et al., 2004). Srimathy and Jayamani used a set of 40 SSR primer pairs derived from red bean to assess transferability, and tested their ability to amplify microsatellite loci in seven species (*V. mungo* var silvestris, *V. mungo, V. umbellata, V. trilobata, V. aconitifolia, V. radiata* var sublobata, and *V. radiate*); all 40 pairs exhibited cross-species amplification (Srimathy and Jayamani, 2010). Recently, Banni et al., (2012) evaluated the genetic diversity and gene flow of 178 red bean accessions using 36 polymorphic SSR markers. We discovered that in one locus, CEDG029, one allele (144 bp) was shared by all three groups of varieties and species (var. *nipponensis*, var. *angularis*, and *V. nakashimae*) and three alleles (136, 144, and 188 bp) were shared between wild ancestors and cultivated varieties.

Garden or kidney beans; Garden or kidney beans, also known as common bean (*Phaseolus vulgaris*) are indigenous to America. They were probably domesticated by the Incas and were early used by the Amerindians of both South and North America. Today, the young pods (string or snap beans), unripe seeds (shell beans), and dried ripe seeds are all used for human consumption. Over 1,000 varieties are cultivated worldwide (http://www.faculty.ucr.edu/~legneref/botany/legunuts.htm). Variation analysis of phaseolin seed protein (Gepts and Bliss, 1986; Gepts et al., 1986) and allozymes (Koenig and Gepts, 1989; Singh et al., 1991) has revealed the existence of two major groups within the common bean germplasm, a Mesoamerican one and an Andean one. Recently, our group assessed the genetic diversity and population structure of 96 common bean accessions collected from 7 countries using 30 polymorphic SSR markers, and detected two distinct genotype groups (Wooju et al., 2012, our group submitted).

Two root-based cDNA libraries under high and low phosphorus conditions from the Mesoamerican genotype DOR364 have been constructed and ESTs sequenced to discover new SSRs. EST-SSRs are more common in cereals than in legumes (Choumane et al., 2004; Kumpatla and Mukhopadhyay, 2005). There are approximately 70,000 other EST sequences of the common bean, including collections from Ramirez et al., Melotto et al., and Thibivilliers et al. along with small groups of Genbank entries (Melotto et al., 2005; Ramírez et al., 2005; Thibivilliers et al., 2009). Melotto et al. created a library from anthracnose-infected common bean leaves, which contains approximately 4,000 unigenes; Hanai et al., screened this library for microsatellites, and identified a set of 140 EST-based SSRs (Melotto et al., 2005; Hanai et al., 2007, 2010). These SSRs have been used for genetic mapping, rather than germplasm characterization. Tryphone and Msolla (2010) assessed the diversity of common bean genotypes in terms of iron and zinc contents under screenhouse conditions (Tryphone and Msolla, 2010). Their data suggested that genetic factors for increasing iron co-segregate with those for increasing zinc, because of a significantly positive correlation (r=0.416; P<0.001) between iron and zinc. Blair et al. discovered SSRs of various di- and tri-nucleotide motifs, and developed microsatellites from the library of bean microsatellite cDNA (Blair et al., 2009, 2011).

Medicinal crops

Of the 250,000 higher plant species on Earth, more than 80,000 are medicinal. India is one of the world's 12 biodiversity centers, containing over 45,000 plant species (Joy

et al., 1998). According to the World Health Organization, around 21,000 plant species have medicinal potential, of which around 5,000 have been studied (Joy et al., 1998). Correct genotype identification of medicinal plant material remains an open area.

Ginseng; *Panax ginseng* is one of the most important plant resources in Korea (Suh et al., 2011). It is a medicinal herb that naturally exists in only three regions: Korea, Manchuria, and the Littoral province of Siberia (Woo et al., 2004). The value of Korean ginseng as an emergent medicine and tonic for long life is known worldwide, and it is actively searched for on the Korean peninsula. It is considered to have properties that strengthen the human body and ultimately prolong human life (Carlson, 1986). However, to date, little genetic manipulation of *P. ginseng* has been performed. The unigene database is a potential tool for the development of markers for medicinal plant genomes. Genome sequences are also available at the National Center for Biotechnology Information (NCBI) website at http://www.ncbi.nlm.nih.gov/genomes/static/gpstat.html.

Recently, new ginseng cultivars with superior agricultural traits have been developed in Korea. The six Korean ginseng cultivars can be distinguished from foreign ginsengs using 85 ISSR primers (Lee et al., 2011). The sequence-characterized amplified region (SCAR) marker system was introduced to increase the reproducibility of these polymorphisms. One SCAR marker, PgI821C650, was successfully converted from a randomly amplified polymorphism by UBC-821(Lee et al., 2011).

Onion; The triploid onion is a hybrid species with three sets of chromosomes, two from true onion (*Allium cepa*) and the third from an unknown parent (Fritsch and Friesen, 2002). Various clones of the triploid onion are grown in different regions. There are very small genetic differences between the clone Pran and the Croatian clone Ljutika, implying a monophyletic origin for this species (Friesen and Klaas, 1998). Several markers, including isozyme markers (Cramer and Havey, 1999), RFLPs (Bark and Havey, 1995), SSRs (Fischer

Table 2. List of currently available whole genome sequencing on some underutilized crops.

No.	Scientific name	Common name	Genome size Mbp	Sequenced Mbp/coverage	Protein coding gene	Sequencing Agency/ technology	Published
	Cereals						
1	*Sorghum bicolor*	Sorghum	730	625.7/ 89.7%	27,640	USA/ shotgun sequencing	(Paterson et al., 2009)
2	*Secale cereale*	Rye		2.03	36000	Czech Republic/ BAC end sequencing	(Bartoš *et al.*, 2008)
				87-166	49,294	Germany/ 454 GS FLX	(Haseneyer et al., 2011b)
	Beans						
3	*Vigna ratiata* (L.) Wilczek	Mungbean	515	6.16/ 7.76	8606/ 10,758	Korea/ 454	(Moe *et al.*, 2010)
4	*Glycine max*	Cultivated Soybean	1,100	969.6/ 88%	46,430	USA/ ABI, 3730XL	(Schmutz et al., 2010a)
5	*Glycine soja*	Soybean		286		USA/ Illumina	(Hyten *et al.*, 2010)
6	*Glycine soja*	Wild Soybean	915	915.4/ 97.65%	102	Korea/ Illumina GA and 454	(Kim *et al.*, 2010)
7	*Ricinus communis*	Castor Bean	350	350/ 100%	5,491	USA/ ABI AB3730xl	(Chan et al., 2010)
	Vegetables and Fruits						
8	*Cucumis sativus*	Cucumber	350	243.5/ 70%	26,682	BGI (China)/ Sanger and Illumina GA	(Huang et al., 2009)
9	*Solanum tuberosum*	Potato	850 M	725.8/ 86%	39,031	The Potato Genome Sequencing Consortium / 454, and Illumina	(Pgsc, 2011)
10	*Fragaria vesca*	Japan Raspberry / woodland strawberry	240	209.8/ 87%	34,809	USA/ Roche/454, Illumina/Solexa / SOLiD platforms	(Shulaev et al., 2011)
11	*Vitis vinifera*	Pinot Noir Grape	505	487/ 96.4%	30,434	The French-Italian Public Consortium	(Jaillon et al., 2007)
12	*Malus domestica Borkh.*	Domesticated Apple	743	603.9/ 81.3%	57,386	USA/ 454 GS FLX	(Velasco et al., 2010)
13	*Carica papaya*	Papaya	370	271/ 73.2%	21,784	USA/ shotgun sequencing	(Ming et al., 2008)
	Others						
14	*Populus trichocarpa*	Black Cottonwood Tree	485	410/ 84.5%	45,000	USA/ shotgun sequencing	(Tuskan et al., 2006)
15	*Selaginella moellendorffii*	Spikemoss	212.6	208.8/ 98%	22,285	USA/ Sotgun	(Banks et al., 2011)
16	*Physcomitrella patens*	Moss	480	480/ 100%	35,938	Germany/ Shotgun	(Rensing et al., 2008)
			500	480/ 98%	35,938	Germany/ shotgun sequencing	(Rensing *et al.*, 2008)
17	*Ectocarpus*	Brown Algae	196	214/ 109%	16,256	France/ cDNA, Illumina	(Cock et al., 2010)
18	*Jatropha curcas L.*	Physic Nut	410	285.8/ 69.7%	40,929	Japan/ cDNA, Illumina	(Sato *et al.*, 2011)
19	*Phoenix dactylifera*	Date Palm	658	380/ 90%	>25,000	Qatar, USA/ Illumina	(Dous et al., 2011a)
20	*Theobroma cacao*	Cacao	430	326.9/ 76%	38,737	France/ Roche/454, Illumina and Sanger	(Argout et al., 2011)

and Bachmann, 2000), and SSR- and SNP-ESTs (Kuhl et al., 2004; Martin et al., 2005), have been developed and have been proven to be reproducible for mapping (Mccallum et al., 2006) and cultivar discrimination (Jakse et al., 2005). Martin et al. (2005) added 100 genetic markers to the intraspecific map derived from the BYG15-23xAC43 segregating family, producing 14 linkage groups encompassing 1,907 cM at LOD [logarithm (base 10) of odds] score 4 (Martin et al., 2005). Mccallum and Havey (2006) used 96 short- and long-day onion populations including key open-pollinated varieties widely exploited by breeders and a wide selection of landrace accessions from the USDA-ARS (U.S. Department of Agriculture, Agricultural Research Service) collection to survey the allelic content of population samples by sizing fluorescent-labeled PCR products on standard capillary sequencers (Mccallum and Havey, 2006). The data showed good concordance of molecular data with known pedigrees. Mccallum et al., (2008) surveyed genetic variation in a cultivated onion germplasm using SSR markers and EST-SSRs to develop SNPs (Mccallum et al., 2008). At present, molecular identification and genetic diversity of *Fusarium* species associated with onion fields in Turkey (Bayraktar and Dolar, 2011) and their pathogenicity towards onion, and the genetic diversity of isolates of the pathogenic fungus *Colletotrichum gloeosporioides* (Phyllachoraceae) from the State of Pernambuco, Brazil (Nova et al., 2011) have been surveyed for onion related diseases.

Garlic; Garlic (*Allium sativum* L.) belongs to the family *Liliaceae*. The genus *Allium* contains more than 600 species (Osman et al., 2007). Garlic is a diploid obligate apomict that is primarily propagated asexually from cloves (Bradley et al., 1996). Clonal selection is the main breeding method for modern garlic, because plant sterility usually precludes crop improvement through cross-hybridization (Lampasona et al., 2003). As reported by Bozzini (Bozzini, 1991), garlic has a chromosome number of 2n = 16, although some plants in the Campania region of Italy are tetraploid (4n = 32) and some cultivars might be triploid. Molecular markers such as isozyme markers (Lallemand et al., 1997), random amplified polymorphic DNA (RAPD) , and AFLPs (Volk et al., 2004; Ipek et al., 2003, 2005, 2008) have been used to assess the genetic diversity of and relationships among garlic clones. Fernandez developed a garlic phylogeny of 48 diverse clones using five arbitrary RAPD primers (OPJ-12, OPC-13, OPE-17, OPAB-14, and OPC-5), which gave 24 polymorphic bands and 183 AFLP bands (Fernandez, 2001). The high level of genetic variation in garlic has been detected using different molecular markers (Volk et al., 2004; Ipek et al., 2008). However, little information on the genome of garlic is available, as is the case for other crop plants; thus, the use of GBS and whole genome sequencing (WGS) is rapidly expanding.

Solanaceae

The Solanaceae are a family of flowering plants that includes a number of important agricultural crops including the potato, pepper, tomato, eggplant, tobacco, and deadly nightshade. Solanaceae includes over 3,000 species of annual and perennial plants, vines, herbaceous plants, sub-shrubs, shrubs, and some trees (http://www.newworldencyclopedia.org/entry/Solanaceae).

Potato; There are now more than a thousand different types of potato, due largely to selective breeding. More than 99% of the potatoes cultivated worldwide can be found in the Chiloé Archipelago and it was recognized as a potato germplasm (Solano et al., 2007). Most potato cultivars are autotetraploid (2n = 4x = 48), and highly heterozygous (Pgsc, 2011). During the 1960s, genetic studies focused on morphological characteristics (Hijmans and Spooner, 2001), and the potato germplasm has been described using phenotypic characteristics (Ortiz and Huaman, 1994). The first protein and enzyme pattern analysis to identify potato cultivars was conducted by Stegemann and Loeschecke (Stegemann and Loeschecke, 1976). Since then, various technologies have been developed to facilitate direct detection of genetic polymorphism at the DNA level using molecular markers. Molecular markers have contributed to a greater knowledge of potato genetics (Ritter et al., 2004). These molecular markers and DNA marker systems have been used in the *Solanum* genus to analyze biodiversity and for phylogenetic studies (Ritter, 2000; Spooner et al., 2005). DNA markers such as RAPD (Isenegger et al., 2001; Sun et al., 2003), SSRs (Ashkenazi et al., 2001; Raker and Spooner, 2002), and ISSRs (Bornet et al., 2002) have also been used. AFLPs have been widely used in cultivated potatoes (Straadt and Rasmussen, 2003; Furini and Wunder, 2004) and their wild relatives (Karolus et al., 1998). Solano et al. defined 20 accessions of native potato collected on the island of Chiloe into four clusters using a single AFLP combination (Solano et al., 2007). The Potato Genome Sequencing Consortium (PGSC) is an international group of academic and industrial organizations committed to sequencing the complete potato genome to meet the world's food needs. A homozygous doubled-monoploid potato clone was used to sequence and assemble 86% of the 844 Mb genome (Pgsc, 2011). They predicted 39,031 protein-coding genes and presented evidence of at least 2 genome duplication events indicative of a palaeopolyploid origin. As the first genome sequence, the potato genome reveals 2,642 genes specific to this large angiosperm clade. They also sequenced a heterozygous diploid clone and showed that other potentially deleterious mutations that likely cause inbreeding depression frequently occur.

Pepper; Several studies have used molecular markers such as RFLPs, AFLPs, and RAPDs to assess the level of variation among *Capsicum* species (Rodriguez et al., 1999), construct molecular linkage maps (Lefebvre et al., 1995; Livingstone

et al., 1999), and clone or tag genes related to useful traits (Huh et al., 2001). Nagy et al. and Huang et al. reported the development of microsatellite markers from the pepper small-insert genomic library (Nagy et al., 1998; Huang et al., 2000). Kang et al. developed a pepper molecular linkage map containing 150 RFLP and 430 AFLP markers (Kang et al., 2001). Lee et al. developed polymorphic *Capsicum* microsatellite markers and integrated them into an existing molecular map of the pepper (Lee et al., 2004). Forty-six microsatellite loci were placed on the SNU-RFLP linkage map, which was derived from an interspecific cross between *Capsicum annuum* (TF68) and *Capsicum chinense* (Habanero). The current SNU2 pepper map with 333 markers in 15 linkage groups contains 46 SSR and 287 RFLP markers covering 1,761.5 cM, with an average distance of 5.3 cM between markers (Lee et al., 2004). RSAP and SRAP (Sequence-related amplified polymorphism) and SSR were adopted to analyze the genetic differences among 10 elite inbred lines. The results showed that RSAP had a higher number of total loci (51) and polymorphic bands (13) per assay ratio, being 1.5- and 1.3-fold higher than SRAP, and 17- and 6.5-fold higher than SSR, respectively (http://www.china-papers.com/?p=64910).

In terms of resistance genes, the Pvr4 gene confers complete resistance to the three pathotypes of potato virus Y (PVY) and pepper mottle virus (PepMoV). Caranta et al. (1999) mapped eight linked AFLP markers around this locus in an interval from 2.1 ± 0.8 to 13.8 ± 2.9 cM (Caranta et al., 1999).

Kim et al. (2007) developed molecular markers linked to the L4 locus conferring resistance to tobamovirus pathotypes in pepper plants, and performed AFLP with 512 primer combinations for susceptible (S pool) and resistant (R pool) DNA bulks against pathotype 1.2 of pepper mild mottle virus. They successfully converted L4-b into a simple 340-bp SCAR marker that mapped 1.8 cM of the L4 locus and 0.9 cM in another BC10F2 population. Romer et al. identified a DNA-based marker that is diagnostic for the *Capsicum annuum* bacterial spot resistance gene Bs3 (Römer et al., 2010).

In 2009, the Seed Biotechnology Center, University of California, genetically mapped more than 6,000 pepper genes. These are now being correlated with data regarding physiological and quality traits in hot peppers (http://sbc.ucdavis.edu/research/breeding_tools.html, accessed November 2011). Transcriptome sequencing was performed by Lu et al., who identified more than 10,000 unigenes using a functional annotation scheme. They reported a total of 1265 and 1436 SSR motifs for YCM334 and Taean, respectively, and a total of 3218 SNPs with high confidence (Lu et al., 2011).

Tomato; As a crop plant, the tomato is one of the best-characterized plant systems. It has a relatively small genome of 0.95 pg or 950 Mb per haploid nucleus, and features such as diploidy, self pollination, and a relatively short generation time make it amenable to genetic analysis (Arumuganathan and Earle, 1991). Lankhorst et al. adapted the 6-specific RAPD assay to the tomato (Lankhorst et al., 1991). RAPD markers could be directly identified among the set of amplified DNA fragments. Their chromosomal position on the classical genetic map of tomato was subsequently established by RFLP linkage analysis. One of the RAPD markers was found to be tightly linked to the nematode resistance gene Mi (Lankhorst et al., 1991). By 1988, the classical linkage map of the tomato genome comprised 233 morphological and isozyme loci. The tomato RFLP map was constructed using an F2 population of the interspecific cross *L. esculentum* x *L. pennellii*; it contained more than 1030 markers, which were distributed over 1276 cM (Tanksley et al., 1992). An integrated high-density RFLP-AFLP map of the tomato based on two independent (*L. esculentum* x *L. pennellii*) F2 populations was also constructed. The map spanned 1482 cM and contained 67 RFLP and 1175 AFLP markers (Haanstra et al., 1999). Shirasawa et al. developed EST-SSR markers, genome-derived SSR markers, and EST-derived intronic polymorphism markers, of which 2,047, 3,510, and 674, respectively, were established and used for polymorphic analysis of the cultivated tomato *Solanum lycopersicum* LA925 and its wild relative *Solanum pennellii* LA716 (Shirasawa et al., 2010). A high-density genetic linkage map composed of 1,433 new and 683 existing marker loci was constructed on 12 chromosomes, covering 1,503.1 cM. Information on these DNA markers is available at http://www.kazusa.or.jp/tomato/. Two linkage maps were developed, and six QTLs were identified on five chromosomes (1, 3, 4, 7, and 8) in the BC1 population by means of interval mapping and restricted multiple QTL mapping. These QTLs came from *S. pennellii*, with the exception of the minor QTL located on chromosome 8, which was provided by cv. Anl27. In the F2 population, they identified a QTL on chromosome 7 in a similar region to that detected in the BC1 population (Trujillo-Moya et al., 2011).

Cole crops

'Cole' refers to any of various plants belonging to the Cruciferae or mustard family (Brassicaceae). The mustard family includes cool-season crops such as cabbage, Brussels sprouts, cauliflower, collards, kale, kohlrabi, mustard, broccoli, turnips, and watercress.

Cabbage; The putative haploid genome size of *Brassica* is -600-660 Mb (O'Neill and Bancroft 2000; Paterson et al., 2001). A total of 595,321 cabbage (*Brassica oleracea;* 2n=18*)* shotgun reads were sequenced by The Institute for Genome Research (TIGR) in collaboration with Washington University and Cold Spring Harbor (Katari et al., 2005). The availability of WGS in cabbage provides an unprecedented opportunity for development of microsatellite or SSR markers for genome analysis and genetic improvement of *Brassica* species. A total

of 752 SSR markers among the six varieties showed polymorphisms. Of these, 266 markers that showed clear scorable polymorphisms between *B. napus* varieties were integrated into an existing *B. napus* genetic linkage map (Snowdon et al., 2006). Extensive efforts have been made to develop SSR markers in *B. napus* and its two diploid progenitors, *B. rapa* and *B. oleracea*, through genomic library screening using probes containing repeat motifs, followed by DNA sequencing (Varghese et al., 2000; Suwabe et al., 2002) . Information on *Brassica* microsatellites is available at http//www.brassica.info/ssrinfo.htm. Several *Brassica* genome sequencing projects have been conducted for various purposes (Katari et al., 2005; Lim et al., 2006). The availability of WGS sequences in *Brassica oleracea* provides an opportunity to develop microsatellite or SSR markers for genome analysis and genetic improvement of *Brassica* species. Li et al. developed 1,398 new SSR markers and used them to survey polymorphisms among a panel of six rapeseed varieties; 752 showed polymorphisms among the six varieties (Li et al., 2011). These new markers are preferentially distributed in the linkage groups in the C genome, and significantly increased the number of SSR markers therein.

Carrot; Carrots (*Daucus carota* subsp. sativus) belong to the Umbelliferae family. The heritability of nematode resistance (*Meloidogyne javanica*) was evaluated using the open-pollinated cultivars Brasília as resistant, and Kuronan as tolerant (Huang et al., 1986). Schulz et al. reported a linkage map using 10 isozyme loci, 14 RFLPs, 28 RAPD markers, and 6 isolated PCR fragments as RFLP probes; the results included eight linkage groups with an average distance of 13.1 cM (Schulz et al., 1993). Two molecular maps of carrots were then constructed (Westphal and Wricke, 1997; Vivek and Simon, 1999) of a locus controlling disease resistance. Another linkage map (approximately 200 marker loci) was constructed using isozyme, RFLP, RAPD, AFLP, RAMP, and microsatellite markers in a population segregating the *M. hapla* resistance locus derived from the wild species *D. carota* subsp. Azoricus (Ali, 2008). Santos and Simon (2002) reported that most AFLP products from two unrelated carrot populations had high identity and equal size, and they mapped to the same linkage group in both F_2 populations (Santos and Simon, 2002).

Inheritance studies on natural carotenoid mutants have identified factors conditioning root pigment accumulation (Simon, 2000), and both simply inherited pigment traits and QTL have been incorporated in the maps (Just et al., 2009). The addition of 22 genes from the carotenoid biosynthetic pathway (Just et al., 2007) as well as transposon-display markers (Grzebelus et al., 2007) into one of the maps has increased both marker informativeness and coverage. However, Cavagnaro et al. pointed out that direct comparisons between the reference and other carrot maps are currently difficult due to the lack of common markers across maps, likely due to insufficient availability of informative and robust PCR-based markers (Cavagnaro et al., 2011).

Microsatellite isolation and marker development in carrot genomic distribution, linkage mapping, genetic diversity analysis, and marker transferability across the Apiaceae was recently reported (Cavagnaro et al., 2011). A genetic map of 55 of 196 SSRs was successfully constructed on the carrot reference map. SSR loci were distributed throughout the nine carrot linkage groups with 2-9 SSRs/linkage group. Consequently, SSRs were successfully cross-amplified in carrot-related taxa across the Apiaceae (Cavagnaro et al., 2011).

Conclusion

The diversity of nature is continually being diminished due to increasing human intervention. Although it is difficult to conserve all natural diversity, its exploration should be accelerated to facilitate better use of natural resources. Several agencies and cooperatives worldwide have been collecting and conserving species to combat their extinction. To develop wild species as crops, it is necessary to collect, conserve, evaluate, and usually manipulate them. In this context, hundreds of thousands of new samples are being introduced into germplasm institutes each year. The concept of creating a core collection has been developed to reduce sample redundancy in a germplasm. However, morphological or genetic data at a minimum are necessary to develop a core set. Several marker systems have been used not only for genotyping and developing the core sets, but also for a number of genomic analyses. The various marker systems have different advantages in terms of complexity and the usefulness of results. Advanced sequencing technology has forever changed the methods by which genetic and genomic information of crop plants is obtained and analyzed. Crop-improvement programs can be accelerated using these advanced sequencing technologies. Currently, sequencing-based markers such as SNP, CNV, indels, and GBS for genetic mapping and QTL analysis are becoming popular. This review should help guide the use of updated marker systems and increase the available genomic information of a number of underutilized crops.

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