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CHAPTER

1

Assessment of Phylogenetic Relationships among Crops and Their Genetic Resources for Successful Crop Improvement Programs

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CHAPTER 1

Crop genetic resources are invaluable sources of genes and gene complexes that are useful in breeding programs for crop improvement for salt tolerance, pest tolerance, flood tolerance, drought tolerance, frost resistance and others. Introductions of useful characters by breeders into crop cultivars from other species have tended to be most effective when these species are close relatives of the target crop or are even directly ancestral to it. Therefore, understanding phylogenetic relationships between crops and their genetic resources has been of considerable value as an important component of any successful crop improvement program. Traditionally, phylogenetic relationships among plants have been inferred based on agronomic and morphological characters. Because morphological characters are often functionally or developmentally correlated and converge when exposed to similar selective pressures, molecular markers are often preferable to morphological data for phylogenetic and systematic inference. Molecular markers can either detect changes in proteins and amino acids (biochemical markers, isozymes) or detect variation at the DNA level. These markers contributed immensely in the elucidation of genetic relationships within and among plant species. Examples of studies that used such markers for revealing phylogenetic relationships among crops, mainly those which are economically important, and their close genetic resources, mainly wild relatives that are most closely related to crops, are presented here without making detailed or critical analysis or evaluation of each of those examples.

1.1. Introduction

Biodiversity can most simply be defined as the variation that exists in the living world. Variability can also be found within a sequence of DNA which is the fundamental source of all biodiversity (Brinegar, 2009). Species (a Latin word meaning "kind" and refers to a taxonomic rank which is the basic unit of biological classification, Singh, 2012) of all living organisms have been regarded as a basic unit of biodiversity and it is the level at which most of the evolutionary studies have focused (Graybeal, 1995). Regardless of the importance of its rank, the species is probably the most controversial taxonomic rank in biological science, and there are over 22 concepts of species in use (Mayden, 1997; Wilkins, 2011; Singh, 2012).

The earliest concept of species was the Morphological (or Linnaean/Phenetic/ or Classical) Species Concept (Cronquist, 1978), which takes no direct account of evolutionary origin of organisms. Following Linneaus, naturalists became aware that ir-

3

respective of the levels of morphological similarities among species, they occur as reproductively isolated entities in the field. This led to the Biological Species Concept (BSC), in which species are recognized on the basis of being reproductively isolated and largely irrespective of any morphological differentiation. Ehrlich (1964) believes that reproductive isolation is important in evolution, but rejects basing the species concept primarily on reproductive criterion. Subsequently, Sokal and Crovello (1970) and Sokal (1973) supported this view.

The development of cladistic methods increased dissatisfaction with the biological concept of the species and led to the birth of the Evolutionary, Phylogenetic and Cladistic Species Concepts. The Evolutionary Species Concept was introduced by Simpson (1961), who believes that "a species consists of a group of populations that shares a common evolutionary fate through time". He emphasized that this concept would avoid the difficulties in determining actual or potential levels of interbreeding and gene flow, and it allows some degree of interspecific hybridization. All definitions of phylogenetic species proposed suggest that classifications should reflect the phylogenetic relationships (refer to the relative times in the past that species shared common ancestors) of the organisms. Wheeler (1999) stated that the phylogenetic concept is simple, broadly applicable, testable, and distinguishes the smallest groups of individuals that can meet the needs of the elements of nomenclature and phylogeny and biodiversity studies. Wheeler and Platnick (2000) defined the Phylogenetic Species Concept as "… the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states". However, van Regenmortel (1997) argued that species should not be regarded as classes or categories but as individuals since change via evolution is levied at the scale of the individual. There have been several phylogenetic species concepts proposed for plants over the past 30 years. The most popular of these is that of Cracraft (1983), who described the species as "the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent". Although species diversity in cultivated plants can be essentially similar to that of wild plants, infraspecific diversity is generally greater in the former due to human selection. Furthermore, breeders augment crop diversity through targeted introgression of genes from related species (Hawkes, 1997). Likewise, farmers and breeders have consciously or unconsciously altered the ploidy level of crops by polyploidy so that cultivated plants are far more commonly polyploid than wild species. For all of these reasons, the taxonomic status of crops is frequently far more complex than in wild plants. This also makes the species concept

4

more difficult to define and apply in crops. Hawkes (1997) argued that since both natural and artificial selections essentially evoke the same evolutionary pressures, systems of classification developed for wild plant groups should also be applied to cultivated taxa. Other less widely used species concepts include the Ecological Species Concept (Andersson, 1990) and the Cohesion Species Concept (Templeton, 1989).

1.2. Plant Genetic Resources—The Link between Biodiversity and Crop Breeding

Plant genetic resources for food and agriculture are the raw material**s** (traditional varieties, modern cultivars, crop wild relatives and other wild plant species) which are used by farmers and plant breeders to improve the productivity and quality of crops. They include all genetic materials of plant origin which have actual or potential value for food and agriculture such as tubers, seeds, and mature plants etc. (Department of Agriculture, Food and the Marine, online reference). They also include all our agricultural crops and even some of their wild relatives which often have valuable traits (Nordgen, online reference). It is worth noting here that only 30 of these crops provide 95% of human food energy needs, 60% of which are provided by four crops (rice, wheat, maize and potatoes) (Commission of Genetic Resources for Food and Agriculture, online reference).

Loss of genetic resources has resulted in major concerns about future food and nutrition security (Wageningen, online reference) in the context of climate change and greater ecosystem instability. Crop wild relatives could be conserved to secure future global food resources and produce varieties of grains, vegetables, fruits, legumes and tubers that are more adaptable to local climates (Espuig, 2014). They are species found growing in the wild that are genetically related to domesticated crops, forages, medicinal herbs, and other useful plants but are undomesticated themselves (The Crop Site, 2012). Most of these relatives grow as weeds in disturbed habitats, such as field margins, roadsides, orchards and traditionally managed agricultural land (Department of Agriculture, Food and the Marine, online reference).

Crop wild relatives are invaluable sources of genes and gene complexes that are useful in breeding programs for crop improvement for salt tolerance, pest tolerance, flood tolerance, drought tolerance, frost resistance and others (Fu and Allaby, 2010;

Das et al., 2013). They hold the key to successful crop improvement programs through introgression of desired genes from them to cultivated crop species. Scientists have released the most complete database of the wild relatives of common food crops (Espuig, 2014).

An example of crop wild relatives is presented by the genus *Aegilops* L., which is a close wild relative of wheat *Triticum* L. *Aegilops* represents the largest part of the secondary gene pool for wheat which is the most widely grown plant in the world. *Aegilops* species have useful characteristics that can be exploited for wheat improvement. Amphiploids from interspecific crosses between tetraploid wheat and *Aegilops* species are useful bridging germplasm for introduction of desirable alien characters to bread wheat *T. aestivum* (Friebe et al., 1996a). Several agronomically interesting characteristics such as resistance to biotic and abiotic stresses have been transferred from *Aegilops* species to wheat (Friebe et al., 1996b). Gulbitti-Onarici et al. (2009) referred to studies that have been carried out to elucidate the evolutionary relationships of the wild and domesticated species belonging to the genera *Triticum* and *Aegilops*. Wild relatives of cultivated rice also play a very important role in rice breeding (Ratnasekera, online reference). Another example is the genus *Salvia*, which includes species that are widely used horticulture crops. *Salvia* diversity represents a largely untapped resource for crop improvement which might be accessed by means of interspecific hybridization (Tychonievich and Warner, 2011). Carvalho and Renner (2012) believe that the discovery that *C. papaya* is closest to a clade of herbaceous or thin stemmed species has implications for plant breeders who have so far tried to cross papaya only with woody highland papayas (*Vasconcellea*).

Although many characters have been introduced to crop cultivars such as disease resistance, tolerance of stresses such as salinity and improved nutritional quality (Hodgkin, IPGRI), Sajib et al. (2012), however, believe that thousands of valuable allelic variations of traits of economic significance remain unutilized. Domestication and historical crop improvement have reduced the genetic diversity of our modern crops. These crops will need to be adapted to give higher yields to feed a growing population in order to accommodate increasing environmental pressure. This is addressed by crop genetic improvement using diversity collections to identify gene combinations and new genes that can be introduced into crops using the most modern tools for selection and analysis and conventional breeding techniques (without using genetic modification) (Vegetable Genetic Improvement Network, online reference). Holland (2004) added that incorporation of exotic germplasm, which refers to crop

Assessment of Phylogenetic Relationships among Crops and Their Genetic Resources for Successful Crop Improvement Programs

CHAPTER 1

varieties unadapted to a breeder's target environment and is an important resource for crop improvement, is the best means to enhance the genetic base of modern crops substantially, but it is neither rapid nor easy.

It has been reported that crop varieties with a narrow genetic base can be completely destroyed by diseases. Therefore, plant breeders attempt to go back to older varieties or closely related wild species in order to find resistance genes for the disease in question (Nordgen, online reference). For example, Ortiz et al. (2013) believe that the main constraint to the genetic improvement of peanut (*Arachis hypogaea* L.) is the narrow genetic base of the extant cultigen, and that the more diverse wild *Arachis* species constitute valuable resources for the genetic upgrading of peanut because they have the genetic variability and agronomically useful characters needed to improve the cultigen (Holbrook and Stalker, 2003).

Based on what stated above, a broad genetic base with a rich and diverse germplasm collection, which is the backbone of every successful crop improvement program, is required for progress in plant breeding (Sun et al., 2001). Tychonievich and Warner (2011) argued that the crossability of two species is often related to chromosome number and phylogenetic relationships because 1) crosses between closely related species with the same chromosome number are more likely to hybridize and produce fertile progeny, whereas sterile offspring is produced (resulting from genetic incongruity or meiotic errors) when distantly related species with different chromosome numbers are crossed or else they may not hybridize, and 2) successful crosses were mostly within close phylogenetic groupings. Therefore, information on the cytogenetics and phylogenetic relationships among wild species and between these species and crops is critical to complete utilization of the wild materials and the rational development of breeding programs (Ortiz et al., 2013).

It has also been revealed that introductions of useful characters by breeders into crop cultivars have tended to be most effective when the wild species are close relatives of the target crop species or are even directly ancestral to it (Oldfield, 1989). Therefore, knowledge of the phylogenetic diversity, which represents the heritable variation within and between the populations of plant species, within germplasm collection is an important foundation for crop improvement (Das et al., 2013). Understanding phylogenetic relationships between crop species and their wild relatives also provides significant information about crop evolution, the origins of our major crop plants (e.g. Petersen et al., 2006), and the potential of these relatives for breeding of

CHAPTER 1

Assessment of Phylogenetic Relationships among Crops and Their
Genetic Resources for Successful Crop Improvement Programs

crops, therefore, has been of considerable value for the use of plant genetic resources (Hodgkin, IPGRI). Hence, the assessment of phylogenetic relationships at the interspecific level and the identification of gene pools are considered important for any successful crop improvement program (Agrawal et al., 2014).

1.3. Phylogeny Construction in Plants

Phylogeny (the evolutionary history of a group of entities) is an important powerful tool for plant breeders because it points to a few close relatives as focal points for crop improvement. It also provides information on the wild relatives of crop species which should be the subject of conservation work as in the case of the Brassicaceae (Hodgkin, IPGRI). Soltis and Soltis (2003) believe that comparisons of plant species or gene sequences in a phylogenetic context can reveal the most meaningful insights into biology. They referred to the two reviews of Soltis and Soltis (2000) and Daly et al. (2001) that presented examples of the importance of a phylogenetic framework to diverse areas of plant research.

The main aim of phylogeny reconstruction is to describe evolutionary relationships in terms of relative recency of common ancestry. These relationships are represented as a branching diagram, or tree, with branches joined by nodes and leading to terminals at the tips of the tree (Harrison and Langdale, 2006). There are three main types of relationship distinguished. These are monophyly, paraphyly and polyphyly (Hennig, 1966). Monophyletic groups include all the descendants from a single ancestor, as well as that ancestor (Harrison and Langdale, 2006). Monophyletic and paraphyletic groups have a single evolutionary origin. A step by step guide to phylogeny reconstruction was presented by Harrison and Langdale (2006). Soltis and Soltis (2003) also described phylogeny reconstruction. These authors argued that because trees depicting organismal phylogenies have accumulated so rapidly, it is often difficult for the non-expert to know how to obtain a tree for a group of interest (Soltis and Soltis, 2003). Therefore, they encourage molecular biologists to contact systematics "experts" to obtain the best supported trees for a given clade of interest. In their review, they referred to the phylogenetic trees available for monocots and other angiosperms such as families of Solanaceae, Poaceae, Fabaceae, Brassicaceae, *Antirrhinum* spp., Brassicales, seed plants, Monilophytes (or Moniliforms), and Tracheophytes.

Tikader and Kamble (2008) stated that exploitation of wild relatives of crop plants to a large extent depends on the efficient use of germplasm resources available in

Assessment of Phylogenetic Relationships among Crops and Their
Genetic Resources for Successful Crop Improvement Programs

CHAPTER 1

natural habitat and the centre of diversity. This requires the identification and selection of the crop germplasm which will be used as a parent. In traditional plant breeding, selection is based on the appearance (phenotype) of the crop, where the best plants would be kept and used for subsequent crosses (Vegetable Genetic Improvement Network, online reference). Phenotypic characters, however, are either not variable enough among species or too plastic to be used for identification at the species level (Haider and Nabulsi, 2008), but nowadays plants are selected based on their DNA profile (genotype) using molecular markers (heritable differences in nucleotide sequences of DNA at the corresponding position on homologous chromosome of two different individuals, which follow a simple Mendelian pattern of inheritance, Kesawat and Das, 2009) that are more stable within species (See Haider, 2011, for review). For example, Haider and Nabulsi (2008) investigated polymorphism in the chloroplast DNA (cpDNA) among 21 *Aegilops* species (including *Ae. mutica* that is now known as *Amblyopyrum muticum*) and between the latter and *T. aestivum* to generate markers for the diagnosis of all targeted species. Such genetic markers can be more accurate for characteristics that show wide variation depending upon their growth environment. Therefore, they are also used for selection in which they reveal small differences in the DNA sequence between individuals (polymorphisms) and speed up the breeding process considerably (Vegetable Genetic Improvement Network, online reference).

Traditionally, germplasm has been characterized and phylogenetic relationships have been also inferred based on agronomic and morphological traits. For example, phylogenetic relationships among weedy, wild and cultivated species of Sri Lankan rice were established based on morphological traits (Ratnasekera, online reference) such as seed characteristics (grain length, presence of awn, awn color, awn length, pericarp color, and 100 seed weight) and plant characteristics (leaf length/width, plant height, number of tillers, number of panicles, panicles length, and filled/unfilled seed). Using phenetic analyses of morphological data, Castillo and Spooner (1997) examined boundaries and interrelationships of *Solanum* sect. *Petota* series *Conicibaccata*, a group of 40 wild potato species, composed of diploids, tetraploids, and hexaploids, which is distributed from central Mexico to central Bolivia. Phylogenetic relationships of 15 genotypes of the genus *Lens* and 7 of their interspecific hybrids were also determined by morphological (quantitative and qualitative) characters (Ahmad et al., 1997). In 2002, Forte et al. used traditional analysis of twenty major morphological traits (e.g. leaf size, flower color, and the presence of burs) for deter-