

Creating new interspecific hybrid and polyploid crops

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Agricultural selection of desirable traits in domesticated plant and animal species mimics natural evolutionary selection for ability of species to survive, thrive, and reproduce in the wild. However, one evolutionary process is currently underutilised for human agricultural purposes: speciation through interspecific hybridisation and polyploid formation. Despite promising successes in creation of new hybrid and or polyploid species in many genera, few geneticists and breeders deliberately take advantage of polyploidy and interspecific hybridisation for crop improvement. We outline the possible benefits as well as potential problems and criticisms with this approach, and address how modern advances in technology and knowledge can help to create new crop species for agriculture.

A technological toolbox opening up new avenues for agriculture

Understanding of the principles of inheritance and genetics and the successive development of new technologies [1] has carried agriculture forward to the point where an extraordinarily large number of people can be supported by a relatively small cultivated area. However, increasing population pressure, decreasing agricultural production area, and climate change are now threatening food security worldwide [2]. In order to increase crop productivity, innovative new plant breeding methods are needed [2].

Plant breeding traditionally comprised simple selection and growth of plants with desirable agricultural traits. Originally, this was entirely based on phenotype: only plants which had the desired observable traits were selected to give rise to the next generation. The incorporation of the principles of genetics and heredity into understanding of crop phenotypes allowed more complex selection to take place for crop improvement [1]. Molecular markers were developed, which allowed genotypes (see [Glossary](#)) to be inferred for some traits without relying purely on phenotypic information. This reduced the burden of phenotyping and improved the accuracy of selection, allowing breeders to more rapidly fix desirable traits in breeding pools [3]. Irradiation and related mutation-induction methodologies

were also discovered and used to produce novel variation [4]. Genetic modification technology, where single gene insertions or changes are made to confer particular traits not naturally found in the crop species, shows great potential for some applications, and has successfully been used to induce disease and insect resistance and herbicide tolerance [5]. However, this methodology currently has limited application for breeding of complex, quantitative traits [6], which unfortunately includes yield and many forms of abiotic stress tolerance. Further improvements in genetic screening with the increasing accessibility of next-

Glossary

Allele: a DNA sequence variant of a gene, generally encoding the same protein but with slight variations. Also refers to noncoding sequence differences between two homologous DNA sequences at a single genomic location.

Allopolyploid: containing a complete set of chromosomes (haploid or diploid) from at least two different species.

Autopolyploid: containing three or more haploid sets of chromosomes from the same species (e.g., $3\times$ = autotriploid; $4\times$ = autotetraploid).

Diploid: an organism or cell containing one set of homologous chromosome pairs (two sets of chromosomes, usually of maternal and paternal origin, respectively); often referred to as $2n = 2\times$.

Gamete: a germline/sex cell, usually with half of the parent chromosome complement; for example, an ovule, pollen, or sperm or egg cell.

Genomic introgressions: regions of a genome that result from recombination and integration of genetic material from one species into another species.

Genotype: genetic information or set of allelic variants of an individual.

Genotyping-by-sequencing: acquiring genotype information through DNA sequencing, generally via a high-throughput process.

Germplasm: a general term referring to genetic variants within a species or clade; for example, cultivars, accessions, and lines.

Haploid: a basic chromosome number set, one half of a homologous chromosome complement (often referred to as n or x ; the chromosome number most commonly found in gametes).

Heterosis: effect by which two different alleles at a single genetic locus confer a greater phenotypic advantage than two copies of the same allele.

Homologous: containing the same sequence of genes or DNA but with (usually) different allelic variants or minor sequence variation.

Homoeologous: sharing an ancestral homologous relationship; stretches of DNA with similarity between species or nonhomologous chromosomes.

Interspecific hybridisation: When two species come together to form a new species with genetic information from both parents.

Linkage disequilibrium: relationship between tracts of DNA within a genome resulting from historical chromosome recombination events and population structure (e.g., selection pressure).

Meiosis: cell division and segregation of parent chromosomes into new daughter cells to produce gametes.

Phenotype: expression of genetic information as mediated by the environment; for example, visible traits.

Polyploidy: presence of three or more sets of haploid chromosomes within a single cell or organism.

Quantitative trait loci: genetic locations that contribute to a quantitative phenotype.

Somatic: of the body; when referring to cells those cells that are not in the germline (i.e., gametes).

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generation sequencing are expected to allow more rigorous and rapid selection for desirable genotypes in segregating populations [6]. These advances in technology are predicted to facilitate improvement of quantitative traits like yield.

The rise of next-generation sequencing has been a powerful addition to the molecular breeding toolbox. The availability of reference genome sequences for many agriculturally important species has dramatically improved our ability to identify genes of interest underlying desirable traits. This in turn allows development of molecular markers and similar genetic resources with which to characterise individual breeding lines, screen germplasm, and undertake trait-related and genome-wide marker-assisted selection [6]. As sequencing technology becomes ever faster and more cost-effective, genotyping-by-sequencing approaches will gradually supersede traditional approaches relying on previously developed sets of molecular markers [6].

The availability of next-generation sequencing to rapidly genotype individual crop plants for selection offers a genuine breakthrough in technology. When coupled with fully annotated genomes, desirable allelic variation can be readily selected for [6]. However, fundamentally the allelic variation needs to be present in the first place before this technological leap forward can be implemented to full effect. Unfortunately, in many crop species there has been significant loss of genetic diversity, either due to intensive breeding for particular domestication traits or homogenisation of breeding varieties and loss of local, adapted genotypes [7]. This is a serious issue for many of our important, staple food crops, which not only may have much slower rates of improvement through traditional selection cycles [8], but may also have shared vulnerability to particular pests and diseases as a result of inbreeding [9]. Maintaining a genetically diverse germplasm base for crop cultivars is of critical importance: the Irish potato famine, caused by late blight, and the southern corn leaf blight in the 1970s in the USA are both examples of how serious disease outbreaks caused by over-homogenisation of crop cultivars can be [10].

Naturally, there is a solution. In the wild, plant diversity and speciation are often facilitated by interspecific hybridisation [11], and many of our important crop species are hybrids and polyploids (Box 1). Under natural evolutionary pressures, plant species often come together to form novel hybrid species. These species can benefit from increased vigour due to allelic heterosis [12], and often show transgressive segregation for phenotypic traits [13] and exploitation of different environmental niches than their progenitor species [11].

Success or failure of a novel crop species is related to meiotic behaviour

Previous attempts to produce hybrids and polyploid crops have resulted in both successes and failures. Notable small successes include triticale, a hybrid between wheat and rye produced in the late 19th century [14]; various *Citrus*, such as tangelo, blood lime, rangpur, and limequat [15]; *Prunus* hybrids, such as plumcot and pluot [16]; and *Vitis* (grapevine) hybrid varieties [17]. Many of these crops show novel phenotypes [18], as well as resistances to various

Box 1. Prevalence of hybrid species formation and polyploidy in crop species

Hybrid species formation is extraordinarily prevalent in plants, and is usually accompanied by genome doubling (polyploidy), facilitated by the involvement of 'unreduced gametes' (carrying a diploid rather than haploid progenitor genome) in hybridisation events [11]. Two conventional forms of polyploidy exist: allopolyploidy, which is the result of hybridisation between two different species; and autopolyploidy, which is the result of duplication of a single genome, or possibly hybridisation between two different genotypes within the same species. Auto- and allopolyploidy exist on a spectrum rather than being discrete from each other, as the relationship between the progenitors can vary from very distant (e.g., species from two different genera) to autopolyploids arising from a single plant [11]. However, allopolyploidy is perhaps of greater interest for breeding than autopolyploidy, as allopolyploidy generates more novel genetic diversity and hybrid vigour [13] and generally (although not always) results in less meiotic instability [11,51]. All angiosperm species have at least one historical polyploidy event [46], and many genera have undergone several rounds of hybridisation and genome doubling in recent history [41]. Many of our modern crop species are polyploid, such as potato (*Solanum*), sweet potato (*Ipomoea*), cassava (*Manihot*), taro (*Colocassia*) and yams (*Dioscorea*), wheat (*Triticum*), sugarcane (*Saccharum*), cotton (*Gossypium*), canola (*Brassica*), strawberry (*Fragaria*), and kiwifruit (*Actinidia*). Other crops are interspecific hybrids, such as most citrus cultivars [15] and domesticated apples, while other crops are triploids, such as banana and seedless watermelon.

pathogens [19]. However, most of our highly successful hybrid crop species (Box 1, e.g., wheat, cotton, canola, and sugarcane) were formed without targeted human intervention. The reason for this is simple: most new hybrid plants are not yet genomically stable [20]. In the range of successful human-produced hybrid species listed previously, almost all are vegetatively propagated clones. This means of reproduction allows hybrids to be created and utilised without needing to have normalised meiosis and chromosome segregation. However, many novel hybrids do not initially have stable meiosis and hence regular chromosome transmission to the next generation. Without stable meiosis, these hybrids can lose chromosomes and essential genetic information, losing fertility and viability and 'falling apart' within a few generations.

In some species, such as the natural allohexaploid bread wheat, a genetic locus is present that qualitatively prevents association of nonhomologous chromosomes, stabilising meiosis. In wheat, this locus is known as *Ph1*, for 'pairing homoeologous', which it prevents between the three wheat genomes A, B, and D [21]. This effect is postulated to occur by promotion of crossovers between homologues and suppression of crossovers between homeologues [22], putatively by effects on timing of chromosome condensation in chromosomes belonging to the different genomes [23]. Breeding efforts in wheat containing the *Ph1* locus have allowed thousands of stable synthetic wheat varieties to be produced, incorporating valuable genetic diversity from wild progenitors [24] by utilising this natural meiotic stabilisation effect. Similarly, the effect of this locus on preventing pairing between wheat and rye chromosomes in interspecific hybrids presumably helped stabilise the novel synthetic crop triticale, a wheat-rye hybrid ($2n = AABBRR$ or $2n = AABBDDRR$) [25].

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