Origins of genomes in polyploid potato species

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Why have some wild potatoes become polyploid? Whole groups of species (in series *Longipedicellata, Demissa, Acaulia* for example) have four or six sets of chromosomes, compared to two in normal diploids, and indeed most of our cultivated potatoes are also polyploid. Wild potato polyploids which are hybrid in origin (allopolyploids) have profoundly changed their strategy for persisting and evolving in their environment. They are largely isolated from their diploid progenitors and so cannot readily exchange genes with them. Along with the fixed heterozygosity comes a degree of hybrid vigour and metabolic diversity, but also a shift from outbreeding, characteristic of most diploid species, to the ability to self-pollinate. This loss of self-incompatibility probably arises from the inability of SI systems to work properly in polyploids, and fundamentally alters the genetics of populations of the species. The shift to self-fertility has advantages where individuals are widely-scattered, or where insect pollinators are infrequent or unreliable. In fact, competition in high altitude *Solanum* and other alpine plants for the few, generally large insect pollinators found at these altitudes appears to lead to either large, showy flowers or a switch to smaller, less conspicuous self-pollinating flowers. One additional effect of the change towards homozygosity is the increased ability to exploit recessive alleles whose effects could be lost in interbreeding and genetically diverse populations. It is possible that this change in breeding strategy can permit different approaches to survival when wild populations are under threat from virulent pathogens.

Why does the origin of the genomes in these polyploid wild species matter? These polyploids are often sources of valuable genes for potato breeding. *Solanum demissum*, for example, has been the main source of many key blight resistance genes. Are there better sources of these genes in the diploid species which gave rise to hexaploid *S. demissum*, and indeed do they still survive? In some cases, polyploid species may be acting as reservoirs of the genomes of extinct diploid ancestors, raising the intriguing possibility that if it was possible to cause polyploids to lose one or more genomes, extinct precursor species may be regenerated. Such flights of fancy may be unrealistic, but it is the case that both polyploid and diploid wild species from the Commonwealth Potato Collection (CPC) are increasingly important for the development of new cultivated potatoes with enhanced ability to fight pests and diseases. For exploitation strategies to proceed efficiently, it is important to understand the origins and relationships of the available genomes.

Use of molecular marker and DNA sequence data offers an approach for studying genome origins and relationships in tuber-bearing *Solanum*. We have used the highly multiplex Amplified Fragment Length Polymorphism (AFLP) method to ‘fingerprint’ CPC material, comprising representatives of the major diploid series and all of the main polyploid groups. These data suggest strong taxonomic affinities between species of differing ploidy, suggesting that they share genomes ultimately derived from diploid progenitors. For example, members of the hexaploid series *Demissa* and the largely tetraploid *Acaulia* cluster together. It appears that the two groups have two genomes in common, with series *Demissa* possessing an additional genome from a further hybridisation event. This is particularly interesting as these two polyploid series have very distinct geographic origins with *Acaulia* only being found in S. America and series *Demissa* being of Mexican origin. It has been suggested that the Mexican diploid and, almost uniquely, self-fertile species *S. verrucosum* provided the additional genome found in *S. demissum.* Our evidence appears to confirm this, and indicates that perhaps the allotetraploid stock similar to *S. acaule* was only able to survive the high selection pressure presented by late blight populations in Mexico by forming secondary hybrids with *S. verrucosum*, a species well-adapted to the pathogen. We also see an association of these species with members of the tetraploid Mexican series *Longipedicellata*, suggesting that these series share genomes of common origin. However, AFLP marker-based profiles are not ideally suited to this purpose, lacking the resolution required to identify individual genomes. A more appropriate strategy is the use of PCR to amplify single-copy gene segments from the different genomes contained in diploid and polyploid taxa. PCR primers were designed to conserved regions of genes such that the derived products span more rapidly-evolving intronic regions. DNA sequence was obtained for three nuclear and four chloroplast gene fragments from ~25 species representing the majority of diploid and polyploid groups of *Solanum*. Rates of chloroplast gene sequence polymorphism are extremely low (~1% nucleotide polymorphism). Nonetheless phylogenetic analysis of our data suggests close relationships between polyploid series *Acaulia*, *Longipedicellata*, and *Demissa* and with Mexican diploid *S. verrucosum*, strengthening the hypothesis that these groups share common origins and suggesting that the Mexican diploid may be the maternal parent of these polyploids. The nuclear gene data are more variable (11-28% nucleotides polymorphic). Analysis of a ~450bp fragment of a sucrose synthase gene reveals intriguing relationships between the sequences from polyploid series *Acaulia*, *Longipedicellata*, and *Demissa* with those from diploid series *Tuberosa, Piurana, Pinnatisecta* and *Megistacroloba* (see Fig. 1). It is likely that series *Longipedicellata* may have evolved from series *Pinnatisecta* and *S. verrucosum* and series *Acaulia* from *Piurana* and an unknown diploid. The hexaploids appear to be derived from *Acaulia* plus the genome of *S. verrucosum*. With a clearer view of the origins of the genomes in these polyploids, we are now in a better position to decide where, for example, novel resistance genes are likely to be found.

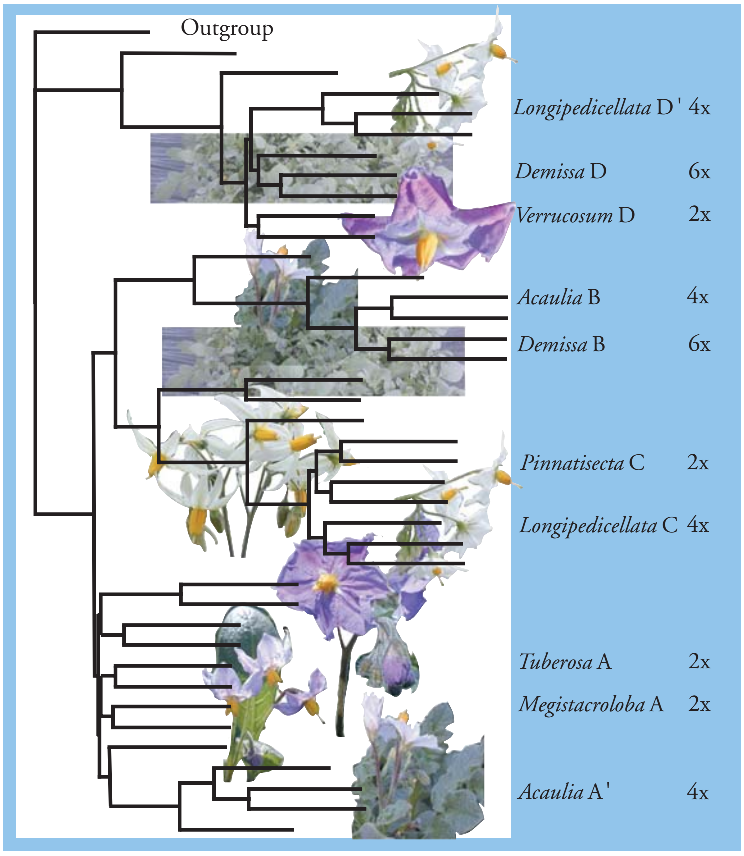

Figure 1 Relationships between the genomes in polyploid groups and their diploid ancestors in wild potatoes, determined from the DNA sequence of sucrose synthase gene fragments.