

## Polyploidy, evolutionary opportunity, and crop adaptation

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**Abbreviations:** LG – linkage group; QTL – quantitative trait locus; RFLP – restriction fragment length polymorphism; WUE – water use efficiency

### Abstract

The finding that even the smallest of plant genomes has incurred multiple genome-wide chromatin duplication events, some of which may predate the origins of the angiosperms and therefore shape all of flowering plant biology, adds new importance to the molecular analysis of polyploidization/diploidization cycles and their phenotypic consequences. Early clues as to the possible phenotypic consequences of polyploidy derive from recent QTL mapping efforts in a number of diverse crop plants of recent and well-defined polyploid origins. A small sampling examples of the role(s) of polyploidy in conferring crop adaptation from human needs include examples of (1) dosage effects of multiple alleles in autopolyploids, and (2) ‘intergenomic heterosis’ conferring novel traits or transgressive levels of existing traits, associated with merging divergent genomes in a common allopolyploid nucleus. A particularly interesting manifestation of #2 is the evolution of complementary alleles at corresponding (‘homoeologous’) loci in divergent polyploid taxa derived from a common ancestor. Burgeoning genomic data for both botanical models and major crops offer new avenues for investigation of the molecular and phenotypic consequences of polyploidy, promising new insights into the role of this important process in the evolution of botanical diversity.

### Background

Polyploidy permeates virtually all of angiosperm biology. While it has long been apparent that many angiosperm taxa had undergone one or more chromosomal duplication events in their evolutionary history, early hints (McGrath et al., 1993; Kowalski et al., 1994) of chromosomal duplication even in the smallest of angiosperm genomes were recently borne out (Blanc et al., 2000; Paterson et al., 2000; Arabidopsis Genome Initiative, 2000; Vision, et al. 2000) by analysis of the completed *Arabidopsis* sequence. The finding that one period of chromatin duplication (perhaps a single event) predates most the divergence of most dicots from a common ancestor, and another event may predate the monocot–dicot divergence

(Bowers et al. 2003), implies that most if not all angiosperm lineages may have been shaped by a few common ancient polyploidization events, then further modified by additional recent events.

While polyploidy as traditionally defined appears to be roughly equally prevalent in cultivated and non-cultivated plants (Hilu, 1993), analysis of crop plant genomes offers opportunities to study many phenotypic consequences of polyploidy in a manner that combines applications-oriented research with investigation of phenomena that may be fundamental to botanical evolution. Polyploidy is far less abundant in animals than plants, arguably due in part to the need in animals for monosomic sex-determining chromosomes. Consequences of polyploidy in plants may include a much higher rate of gene loss, and

more rapid apparent decay of synteny than in animals (Bowers et al., 2003). Several recent studies associate non-linear phenotypic effects with the additive or even less-than-additive (Eckhardt, 2001). merger of two or more genomes with divergent evolutionary histories in a common nucleus. In this chapter, a tiny sampling of cases that have been investigated in my lab are reviewed, then I suggest how emerging research opportunities may yield new insights into the phenotypic consequences of polyploidy.

### Case studies

*Non-linear dosage effects of corresponding ('homoeologous') alleles in sugarcane, an autopolyploid*

Autopolyploid genomes, containing many different homologous chromosomes that can pair and recombine in most or all possible combinations, have been under-explored at the molecular level due to their special problems in genetic and molecular analysis. The importance of autopolyploidy is highlighted by its prominence among cultivated crops, including sugarcane (8–18x), sugar beet (3x), ryegrass (4x), bermuda grass (3–4x), cassava (4x), potato (4x), alfalfa (4x), red clover (4x), Grande Naine banana (3x), apple cultivars (3x), and many ornamentals. It is noteworthy that many of these crops are cultivated for vegetative products and are vegetatively propagated, autopolyploidy often being associated with reduced seed production.

Sugarcane is a classical example of a complex autopolyploid genome. Cultivated sugarcane varieties have about 80–140 chromosomes, comprising 8–18 copies of a basic  $x = 8$  or  $x = 10$  (Irvine, 1999). Most chromosomes of cultivated sugarcane appear to be largely derived from *Saccharum officinarum*—however, *in situ* hybridization data suggest that about 10% may be derived from *S. spontaneum* (D'Hont et al., 1995).

Like other vegetatively propagated plant species, cultivated sugarcane (*Saccharum* spp. hybrids) and its wild relatives are highly heterozygous. Pure inbred lines do not exist due to the difficulty of self pollination and the random pairing of multiple homologous chromosomes. The segregating populations used in genetic studies are

first-generation progenies from crosses between two cultivated varieties, or cultivated varieties and wild species. Genetic mapping uses the subset of DNA polymorphisms that show simplex segregation ratios, and these 'single-dose' markers can also be employed to locate QTLs. However, the fundamental complexity of autopolyploid genetics resulting from heterozygosity and lack of preferential pairing is further complicated by the fact that economically important traits such as sugar content are complex industrial traits, influenced by variation in carbon fixation, photosynthate partitioning into sucrose, transportation and accumulation of sucrose in harvestable biomass, and extractability of sucrose from biomass.

We have used a detailed genetic map to analyze the inheritance of numerous traits in two interspecific  $F_1$  populations (Ming et al., 2001). For example, 36 significant associations between variation in sugar content and unlinked loci detected by 31 different probes were found. The 36 sugar content QTLs correspond to only eight non-overlapping regions of the sorghum genome, with single homologous genomic regions accounting for three QTLs in three cases, and two QTLs in five cases. In a subset of four of these cases, single DNA probes detected sugar content QTLs at each of two or more unlinked loci, making it possible to investigate whether the dosage (zero, one, or two 'copies') of the chromosomal region(s) containing the favorable allele(s) had non-additive (i.e. non-linear) effects on phenotype. Considering sugar content, all four cases showed non-linear tendencies suggesting less-than-additive effects, but in only one case (CSU0428b, dM) did the regression line have a significant non-linear (in this case, quadratic) component. Other traits for which significant effects were linked to larger numbers of loci detected by common probes provided a test of higher dosages. For example, two DNA probes each detected three loci associated with plant height, and another two DNA probes each detected four loci associated with plant height. In all four cases, the regression lines showed less-than-additive gene action, with significant ( $p < 0.05$ ) quadratic trends in three cases, and a significant quartic trend in one case.

Multiplex segregation at QTL loci may be partly responsible for the phenotypic buffering that is argued by many to be one factor in the