

EPISTATIC AND CYTONUCLEAR INTERACTIONS GOVERN OUTBREEDING DEPRESSION IN THE AUTOTETRAPLOID *CAMPANULASTRUM AMERICANUM*

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The consequences of combining divergent genomes among populations of a diploid species often involve F1 hybrid vigor followed by hybrid breakdown in later recombinant generations. As many as 70% of plant species are thought to have polyploid origins, yet little is known about the genetic architecture of divergence in polyploids and how it may differ from diploid species. We investigated the genetic architecture of population divergence using controlled crosses among five populations of the autotetraploid herb, *Campulastrum americanum*. Plants were reciprocally hybridized to produce F1, F2, and F1-backcross generations that were grown with parental types in a greenhouse and measured for performance. In contrast to diploid expectations, most F1 hybrids lacked heterosis and instead showed strong outbreeding depression for early life traits. Recombinant hybrid generations often showed a recovery of performance to levels approximating, or at times even exceeding, the parental values. This pattern was also evident for an index of cumulative fitness. Analyses of line means indicated nonadditive gene action, especially forms of digenic epistasis, often influenced hybrid performance. However, standard diploid genetic models were not adequate for describing the underlying genetic architecture in a number of cases. Differences between reciprocal hybrids indicated that cytoplasmic and/or cytonuclear interactions also contributed to divergence. An enhanced role of epistasis in population differentiation may be the norm in polyploids, which have more gene copies. This study, the first of its kind on a natural autotetraploid, suggests that gene duplication may cause polyploid populations to diverge in a fundamentally different way than diploids.

KEY WORDS: Intraspecific hybridization, line-cross analysis, outbreeding depression, polyploid, population differentiation.

Populations of a species with limited gene exchange will diverge genetically over time due to natural selection and genetic drift (Wright 1931). This basic premise of population genetics forms the foundation for our understanding of population divergence and ultimately the process of speciation (Coyne and Orr 1998; Turelli and Orr 2000). However as many as 70% of plant species are thought to have polyploid origins (Masterson 1994), and doubling the chromosome set, either within species (autopolyploid)

or in interspecific hybrids (allopolyploid), may influence the patterns and process of future population divergence. For example, a larger number of allele copies per locus exist in polyploids relative to diploids, increasing the potential for allelic diversity, allelic interactions, and redundancy. Additionally, multiple polyploid lineages may arise independently within a species, creating a mosaic of populations with different diploid ancestry (Seagraves et al. 1999; Soltis and Soltis 2003). Although polyploidy is common

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