What drives polyploidization in plants?

Organisms with more than two full sets of chromosomes occur throughout many different taxonomic groups, but they are especially prevalent among ferns and flowering plants. The ferns are known to have very high ploidy levels, including the highest known 2n = 1440 in Ophioglossum reticulatum (Khandelwal, 1990). The flowering plants reflect a broad range of chromosome numbers (Weiss-Schneeweiss & Schneeweiss, 2013) from 2n = 4 to 2n = 640. More importantly, surveys of levels of polyploidy among flowering plants have estimated that at least 35% of present species within genera are recent polyploids (Wood et al., 2009). Because of the high level of occurrence of polyploidy in vascular plants, it must be the case that polyploidy has been associated with speciation and is, therefore, of substantial evolutionary significance. Despite considerable investigations on the mechanisms and consequences of polyploidy, both taxonomic and evolutionary, much less is known about the causes of polyploidy (Soltis et al., 2010). Why the phenomenon has been so common in certain groups and not in others is poorly understood. The formation of polyploids does correlate with some environmental factors, such as latitude and elevation (i.e. lower temperatures), a correlation known for decades (e.g. Ehrendorfer, 1980), and this has recently been confirmed with more precise data (e.g. Ranunculus, Ranunculaceae; Schinkel et al., 2016). In this issue of *New Phytologist*, Wagner et al. (pp. 2039–2053), however, looks at the reasons for propensity for polyploidization from an interesting genetic perspective.

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In any discussion of polyploidy, it is necessary to clarify the different types of mechanisms that result in chromosome set multiplication. The two general mechanisms are autopolyploidy and allopolyploidy (Fig. 1). The former is the simplest way for a chromosomal set to be multiplied, and this occurs within the same individual plant (through somatic doubling by failure of chromosomes to separate during mitosis) or, more frequently, by crosses within the same population (or individual) involving unreduced gametes, yielding polyploid offspring. Autopolyploids are known to be common within plant species, and numerous examples of polyploid cytological races exist (e.g. in *Melampodium*, Asteraceae; Stuessy et al., 2004). Although it was initially thought that autopolyploids would have little chance of leading to speciation because they are so genetically similar to the parents and with meiotic problems leading to reduced fertility, it is now acknowledged that polyploidization may be more common than realized previously (Parisod et al., 2010). The more frequent mode of polyploid formation, allopolyploidy, is via hybridization between two parents that have different adaptive norms, i.e. often different species, accompanied by chromosome doubling. This mechanism produces polyploid offspring that have genetic compositions different from either parent, and often different from the sum of the parents, which allows them to establish successfully and colonize new ecological niches. Numerous studies have revealed that allopolyploid species may have different ecological tolerances from their diploid progenitors (Ramsey, 2011). Furthermore, the multiplication of chromosome sets provides each chromosome with a homolog for often successful instantaneous bivalent pairing in meiosis, which has a better chance of resulting in fertile offspring.

To determine factors that influence propensity toward polyploidization, Wagner et al. have taken the approach of examining two...
closely related genera, one consisting of all diploid species and the other containing both diploid and polyploid species. The idea was to determine the degree of genetic diversity among diploid species of both genera as well as their proclivity for interspecific hybridization. Wagner et al. selected diploid species of two closely related genera of the sunflower family (tribe Anthemideae, subtribe Leucanthemi-nae): Leucanthemum from Europe and Rhodanthemum from North Africa. The species of Rhodanthemum are all diploid, whereas those in Leucanthemum are both diploids and polyploids (more than 25 species; 4x to 22x). The authors are testing the hypothesis that hybridization is more common between species that are sufficiently genetically similar so that they can cross, but also genetically distinct enough to prevent homoeologous chromosome pairing and multivalent formation during meiosis in offspring, which can lead to sterility or reduced fertility in the gametes (Buggs et al., 2011).

To assess genomic divergence and traces of hybridization, Wagner et al. used several molecular markers and analytical approaches. For evaluation of phylogenetic Bray–Curtis genetic distance (Göker & Grimm, 2008) between diploid species of both genera, nucleotide sequences from eight nuclear single-copy markers plus internal transcribed spacer (ITS) and also five cpDNA intergenic spacer regions were examined. JML and gene-tree gsi (genealogical sorting index) were employed for detection of hybridization. To provide a time frame for the evolutionary events, a molecular clock was calibrated using *BEAST* (Heled & Drummond, 2010) for the phylogenies within both genera. The evaluations of molecular clock assessments relied on previous phylogenetic estimates of molecular divergence within Anthemideae along with fossil pollen data from *Artemisia*.

The data revealed that the diploid species of *Leucanthemum* are clearly more divergent among each other than those in *Rhodanthemum*. The data also showed that the diploid species of *Leucanthemum* carried more genomic signatures of past interspecific hybridization events than did those of *Rhodanthemum*. The importance of genetic divergence as a stimulus for hybridization had been proposed by Darlington (1937), and it has since been regarded as controversial (Paun et al., 2009; Buggs et al., 2011). The results of the current study provide arguments supporting the early hypothesis, suggesting an important role of genetic distances in promoting allopolyploidization.

The remaining question was why did the species of *Leucanthemum* hybridize so frequently? A map of present distribution of the genus reveals localization in many of the previous refugial areas in Europe during the Pleistocene. As Wagner et al. suggest, the changing climate during the Pleistocene may have led to secondary contacts between species, which in view of the genetic distances previously discussed, might have led to allopolyploidization. The species of *Rhodanthemum* southward in the Atlas mountains of Morocco would have been much less affected by Pleistocene climatic changes, and this, plus the lower genetic divergence among species, may explain the absence of polyploids in this lineage.

The important conclusion by Wagner et al. is that we now have a specific hypothesis for the formation of allopolyploids within particular groups of flowering plants, which can be tested in other genera. The challenge will be to select systems in which closely related sister genera differ in amounts of diploid and polyploid species, so that genetic divergence and tendencies for hybridization can be examined in each and compared. The tendency for allopolyploidization is clearly influenced by various environmental and genetic factors that are often acting in synergy and hence difficult to disentangle. The article by Wagner et al. provides clear evidence that genetic divergence among diploid species is indeed one of these significant stimuli and should always be considered when analyzing causes of allopolyploidization in other groups of species.

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