

Polyploidy and ecological transfiguration in *Achillea*

Donald Levin¹

Section of Integrative Biology, University of Texas, Austin, TX 78713

Polyploidy is a prominent chromosomal/genetical feature in most flowering plant groups (1, 2).

Change in the number of chromosome sets (and thus gene dosage) is an important factor in the genesis of new species, in part because plants with higher ploidal levels often have ecological tolerances that differ from those of their progenitors. Plant evolutionists have been very interested in the origin of such differences, which may arise in two distinctive ways (3, 4). In the absence of hybridization, ecological divergence may be a simple by-product of change in ploidal level. Ecological divergence also may arise from natural selection acting on polyploid populations. It is impossible to distinguish between these alternatives from studies of two established entities that may have diverged in ploidal level thousands of years ago. In PNAS, Ramsey (5) demonstrates that a ploidal increase alone indeed may allow the invasion of a habitat that was previously unassailable by a long-established species. This study also demonstrates that long-standing polyploids are better adapted to this new habitat than are newly emergent ones.

Polyploid Preadaptation

Ramsey (5) focuses on ecological differences between tetraploid ($2n = 4x = 36$ chromosomes) and hexaploid ($2n = 6x = 54$ chromosomes) populations of *Achillea borealis* (Asteraceae). This study system is well chosen for the issue under consideration because unlike most ploidal shifts, the shift in *A. borealis* is not associated with interspecific hybridization; if it had been, it probably would have been impossible to ascertain the role of chromosomal change per se in ecological divergence, because the interaction of two disparate genomes also could generate new habitat tolerances (6). Hexaploid *A. borealis* has a common genetic background with its tetraploid progenitors.

The tetraploid and hexaploid *Achillea* cytotypes do not coexist. Hexaploid populations prefer more xeric habitats than their tetraploid compatriots. Whereas many studies comparing the habitats of alternate cytotypes do not provide specific habitat differentials, Ramsey (5) analyzes soil texture and resident species. Soils in tetraploid sites have significantly more organic matter and gravel, but less sand, than soils in hexaploid sites. Hexaploid *Achillea* is allied with sand dune specialists, whereas tetraploid *Achillea*

is associated with grassland and forest edge species.

To determine whether an increase in ploidal level contributed to this difference, Ramsey (5) introduces tetraploids and hexaploids produced by tetraploids (hereafter referred to as neohexaploids) into dune sites populated by the long-existent hexaploids. During a 3-y trial, the neohexaploids had a 70% survival advantage over their tetraploid progenitors, thus demonstrating that a ploidal change alone could foster a niche shift. Although no information was provided, we may surmise that the former had a substantial reproductive advantage as well. We are told that both tetraploids and hexaploids flowered in the dune site.

Greenhouse and garden trials in many species have shown that neopolyploids

A ploidal increase alone indeed may allow the invasion of a habitat that was previously unassailable.

differ from their progenitors in a spectrum of attributes, including flowering time, flower size, photosynthetic rate, production of secondary products, herbivore resistance, and tolerance to a range of soil conditions (3). Are such differences adaptive or just meaningless in the real world? The *Achillea* study shows that a shift in ecological tolerance may be biologically relevant, because a habitat where such a shift is adaptive was within seed dispersal range. If neopolyploids were preadapted to habitats that were not available locally or did not exist anywhere, then the neopolyploids would be evolutionary novelties without a future.

Ramsey (5) demonstrates that resident hexaploid introductions have a 500% survival advantage over the tetraploid introductions in dune sites, which means that they are better adapted to these sites than either the tetraploids or neohexaploids. This greater acumen must have developed during the evolutionary history of the hexaploid, much as novel ecological tolerances may evolve following the colonization of novel habitats without a change in ploidal level (7). The time when hexaploids began diverging from neohexa-

ploid colonists is unknown. The earlier the presence of self-sustaining hexaploid populations, the more time would have been available to reach contemporary levels of adaptation.

The Establishment of Polyploids

The rate of neohexaploid formation by tetraploid *A. borealis* is very low (about 0.4%) (8). Neohexaploids have not been found in tetraploid sites, but only during the screening of tetraploid progeny. As Ramsey (5) notes, the absence of neohexaploids may be due to minority disadvantage, because most of their offspring will be sired by tetraploids and thus result in sterile pentaploids. This absence may also be due to maladaptedness to tetraploid habitats; to the extent that neohexaploids did grow and reproduce in tetraploid sites, their populations would persist only through the continued input of "immigrants" from the tetraploid subpopulation.

Dispersal of neohexaploid seeds from tetraploid populations to potentially hospitable sites does not ensure the establishment of hexaploid populations. The genesis of polyploid populations is somewhat analogous to the arrival of an invasive species from a distant source. In both cases, the greater the number of seeds reaching a suitable site per unit time, the greater the probability of establishment. The probability of reaching suitable sites is a function of the distance between the seed source and such sites, because most seeds tend to move short distances. Propagule pressure is the paramount variable in dictating the success or failure of colonization attempts (9).

The establishment of populations does not mean that they will persist for long time periods. Recently formed populations may not be well adapted to new surroundings, making them especially prone to extinction as a result of environmental and demographic stochasticity (10), and inverse density-dependent processes (11).

Recently established hexaploid populations face another obstacle to long-term survival: If they are within pollination range of tetraploids, as they are apt to be because colonization is most likely

Author contributions: D.L. wrote the paper.

The author declares no conflict of interest.

See companion article on page 7096.

¹E-mail: dlevin@uts.cc.utexas.edu.

to be successful near tetraploid populations, hexaploid reproductive success will be reduced by the production of some sterile pentaploid progeny. If tetraploid pollen sources are large, more pollen reaching hexaploid stigmas may be from tetraploids than from other hexaploids. However, Ramsey notes (5), the potential for pentaploid seed production is muted by the neohexaploids initiating flowering somewhat earlier than the tetraploids. Given the various factors opposing successful establishment of hexaploid populations, their long-term persistence and subsequent evolution probably was achieved only after large numbers of colonization episodes.

Ramsey (5) reports that established hexaploids flowered about 3 wk later than neohexaploids. The phenological shift could be the result of selection for enhanced local adaptedness. However, the later flowering of the native also could be

the result of selection to minimize the production pentaploid seeds, which would have been very detrimental in the early history of this cytotype.

As with polyploids in general (1, 3, 6), established hexaploid populations must have passed through severe genetic bottlenecks in their evolutionary history. Newly founded hexaploid populations ostensibly carried only a small sample of the tetraploid gene pool. This being the case, where did the genetic variation allowing hexaploids to evolve greater tolerance to xeric habitats originate? Mutation is one likely source (12, 13). Existing populations may have been a source of greater importance. The tetraploid population(s) from which a hexaploid population was derived presumably had a history of recurrent neohexaploid seed formation and export, so that over time, neohexaploid seeds would transport different samples of tetraploid gene pool(s) to the hexaploid

population. The tetraploid gene pool per se also may change over time via gene flow from other tetraploid populations or via mutation. In addition to immigration from nearby tetraploid populations, established hexaploid populations may obtain novel variation from other such populations, especially if the hexaploids had multiple independent origins in genetically differentiated tetraploid populations. The recurrent origin of polyploids is the rule rather than the exception (14).

Ramsey's (5) *A. borealis* paper offers insights into not only a critical stage of polyploid evolution within the species, but also the role of ploidal change in fostering rapid, adaptive divergence, as exemplified by the numerous ecological races of *Achillea millefolium* (15). Ramsey's work also provokes thought about demographic aspects of ploidal transitions that have not been widely considered.

- Otto SP, Whitton J (2000) Polyploid incidence and evolution. *Annu Rev Genet* 34:401–437.
- Wood TE, et al. (2009) The frequency of polyploid speciation in vascular plants. *Proc Natl Acad Sci USA* 106:13875–13879.
- Levin DA (2002) *The Role of Chromosomal Change in Plant Evolution* (Oxford Univ Press, New York).
- Parisod C, Holderegger R, Brochmann C (2010) Evolutionary consequences of autopolyploidy. *New Phytol* 186:5–17.
- Ramsey J (2011) Polyploidy and ecological adaptation in wild yarrow. *Proc Natl Acad Sci USA* 108:7096–7101.
- Otto SP (2007) The evolutionary consequences of polyploidy. *Cell* 131:452–462.
- Levin DA (2000) *The Origin, Expansion, and Demise of Plant Species* (Oxford Univ Press, New York).
- Ramsey J (2007) Unreduced gametes and neopolyploids in natural populations of *Achillea borealis* (Asteraceae). *Heredity* 98:143–150.
- Simberloff D (2009) The role of propagule pressure in biological invasions. *Annu Rev Ecol Syst Evol* 40:81–102.
- Lande R (1988) Genetics and demography in biological conservation. *Science* 241:1455–1460.
- Taylor CM, Hastings A (2005) Allee effects in biological invasions. *Ecol Lett* 8:895–908.
- Behrman KD, Kirkpatrick M (2011) Species range expansion by beneficial mutations. *J Evol Biol* 24:665–675.
- Lynch M, Abegg A (2010) The rate of establishment of complex adaptations. *Mol Biol Evol* 27:1404–1414.
- Soltis DE, Soltis PS, Tate JA (2004) Advances in the study of polyploidy since *Plant speciation*. *New Phytol* 161:173–191.
- Ramsey J, Robertson A, Husband B (2008) Rapid adaptive divergence in new world *achillea*, an autopolyploid complex of ecological races. *Evolution* 62:639–653.