

Notes on R. W. Allard's Paper: History of Plant Population Genetics.

Annu. Rev. Genet. 1999. Volume 33:1-27

This paper was published in 1999, 53 years after Allard's Ph.D thesis at the University of Wisconsin, titled: A cytogenetic study of the effect of backcrossing to common wheat in a hybrid between *Triticum vulgare* Vill. and *Triticum timopheevi* Zhuk. 1946. I had the privilege of using the 1999 paper the last two times that I taught Advanced Plant Breeding, Agron./Hort. 850. The paper should be read in its entirety to appreciate Allard's dedication to plant genetics, and his understanding of the role of history in plant population genetics. He gives great credit to people in the Fertile Crescent, 13,000 years ago, who set the stage by selecting and perpetuating the most reliable, productive, and nutritious food plants. In the main these have been inbreeding plants, as well as outbreeding, vegetatively-propagated species. In the abstract, he has a sentence that was very sobering to someone steeped in traditional alfalfa breeding. Allard writes: "It is noteworthy that maize joined wheat, rice and barley as a truly major crops worldwide only after its conversion to self-pollination combined with hybridization between favorably interacting inbred lines increased yield of maize several-fold in the twentieth century." It is apparent to me that there is an important message here.

Part one of Notes reviews statements about self- and cross-pollinated plants. The goal is to explore the genetic foundations of inbreeding and outbreeding set down by Allard, as they relate to self-pollinated annual *Medicago* species on the one hand, and to cross-pollinated perennials on the other. After reading the paper several times, and teaching from it, I am comfortable with the reproductive systems of all of the *Medicago* species, and believe that there is one unified genetic theory for all of them. Selfers and crossers must operate under the same set of genetic rules. They have different genetic loads, and different levels of inbreeding depression, but the rest is standard genetic theory for diploids and polyploids.

On page 3, Allard champions the wild plants on which the mobile gatherers depended. These were almost entirely large-seeded grasses and legumes that produced good yields of nutritious seeds in nature. Much of the reason for dependable seed production of these species is that their small flowers are cleistogamous, i.e. their flowers normally pollinate in an unopened state. This protects them against many environmental hazards, and leads to self-pollination that if continued 4 or 5 generations within any lineage causes each lineage to approach homozygosity so that all individuals soon become virtually identical. Then, when outcrosses occur between genetically different plants, subsequent selfing is likely to lead to segregation of new lines superior to those originally present. As Allard points out, within-line crosses, as well as among-line crosses

often lead to segregation that culminates in homozygous lines superior to any that were originally present in the population.

Allard points out on page 3, that species with chasmogamous flowers that open before pollination like our perennial *Medicago* species, usually outcross indiscriminately. Such undisciplined crosses are likely to lead to variable progeny, very few of which are likely to be equal or superior to their parents. I believe this is a disadvantage of synthetic cultivars, especially those involving unimproved materials. We will come back to outcrossers again.

Returning to the merits of cleistogamy, Allard discusses how even cleistogamous flowers sometimes are open, thus permitting occasional outcrossing, particularly among neighboring plants. Now he brings in the **concept of epistasis** by stating: ...”the selfing that occurs during the first few generations following outcrosses between genetically superior individuals with the same family leads to segregation that may result in **superior epistatic combinations of favorable interacting alleles of different loci.**” An important thing to keep in mind about selfing while reading Allard's paper is that effective recombination under selfing takes place in the first few generations, and rapidly decreases with the approach to homozygosity. Now consider what happens to the superior epistatic combinations of favorable interacting alleles just established above, when they are involved in wider crosses outside the family. In this case, Allard points out that **selfing promotes** the survival of the superior genotypes in each lineage of the wider cross **by reducing the likelihood that such genotypes will be dismantled by the segregation** that results from wider crosses. In other words, blocks of favorable alleles that stay in tact through the first one or two generations of selfing, have a good chance of staying in tact. I believe that Allard is explaining how coupling-phase linkages are protected by selfing. He goes on to state: “This continuing population genetic process of occasional crossing (as little as 1%), followed by self-fertilizations with progeny lines, almost certainly played an important role in the evolution and continuing improvement in performance of wild, predominantly selfing lineages in the Fertile Crescent, a process that predisposed many self-pollinators to success when they were domesticated. I believe that the same principles apply to wild species in nature, in our case the self-pollinated annual species of *Medicago*.”

On pages 4, 5, and 6, Allard presents examples of important self-pollinated crops, and reviews the advantages of vegetative propagation, by tubers, grafts, etc., whereby superior genotypes can be cultivated, and then he returns to selfers on page 7. Here he asks a question that sounded counterintuitive to me the first time that I read it. Allard asks: “Why should selfing species adapt to changed circumstances more rapidly than outcrossers?” In the early part of my career, I thought that heterozygous outcrossers could adapt more rapidly. By the middle part of my career, I was receptive to Allard's thinking, and started inbreeding myself, and now in the sunset years, I believe that Allard is right. Hence, quoting Allard on page 7: “All individuals in an outbreeding population are

highly heterozygous at many loci and all **outbreeding populations carry high segregational loads because of chance hybridizations between genetically different genotypes**. However, although outbreeding populations gain on the whole from their high recombination rates, which presumably lead to evolutionary flexibility and enhanced opportunities to exploit favorable recombinants, random **outcrossing** also has a downside. Intercrossing between favorably interacting multiallelic complexes and unfavorable multiallelic complexes **usually leads to disassembly of existing favorable complexes** present in the plants before still more favorable complexes can be formed by segregation and the frequency of favorable multilocus combinations can be increased by selection. Thus, when outcrossing is commonplace, adaptedness is likely to decrease, at least in the short term, due to unrestricted segregation.” Allard concludes that this is much less likely to happen in inbreeders.

The above description of outbreeding populations summarizes the early and middle part of my career. We would produce a new synthetic by intercrossing superior parents, and the product would not be as good as the parents. We would usually blame it on pollination problems leading to unbalanced contributions of parents, and/or that the parents were not as unrelated as had been assumed. Sometimes these factors probably were involved; however, Allard really “nails it”, by pointing out that the process that we were using usually leads to disassembly of existing favorable complexes present in the parents. Then, our whole process ended before the frequency of favorable multilocus combinations could be increased by selection.

Allard’s paper came out when we were summarizing the first 35 years of our work, and after several students on my project had been inbreeding alfalfa at both diploid and tetraploid levels, including doubled diploids that are equivalent to single crosses of completely inbred plants. Allard’s paper covers everything that we learned the hard way, so to speak, i.e. our data agree with every point that he makes, and, he states things so beautifully. Allard’s paper, and our data and experience, support inbreeding in the improvement process. This does not require inbreeding to homozygosity. A statement about inbreeding in alfalfa that my students have cited in their papers comes from Demarly, who indicated that the purpose of inbreeding in alfalfa was not to reach homozygosity, but to fix favorable alleles (see the last paragraph of Crop Sci. 23:633-636).

To be continued. Part two of Notes will review inbreeding research in alfalfa as related to Allard’s paper, including the accumulation of favorable alleles in advanced populations of doubled diploids, perhaps the most precise tool available in alfalfa for such research.

Part three of Notes will focus on Heterosis, which begins on page 20 of Allard’s paper. Best wishes, Edwin T. Bingham, ebingham@wisc.edu