BOOK REVIEW

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Hybrids abounding



Dangerous Liaisons? When Cultivated Plants Mate with Their Wild Relatives

by Norman C. Ellstrand

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Reviewed by Steven H Strauss and Stephen P DiFazio

Crops are far from fully domesticated. Gene flow and genetic pollution are everywhere, varying only by degree. Crop alleles are ubiquitous, infiltrating native ecosystems with unknown consequences. This is the state of the world according to Norman Ellstrand. In *Dangerous Liaisons? When Cultivated Plants Mate with Their Wild Relatives*, Ellstrand, a professor of genetics at the University of California at Riverside and a widely respected contributor to scientific assessments of gene flow from transgenic crops, methodically describes the small but growing literature on gene exchange between common crops and their mostly obscure wild relatives. He concludes that the time has come for society to take stock of this long-standing and understudied problem.

Ellstrand begins with a highly accessible discussion of the theoretical consequences of gene flow, and then spends most of the book cataloging what is known about its extent and consequences. He ends with a discussion of the effects and management of gene flow, including for the "special" case (his quotes) of genetically modified (GM) crops. Ellstrand states in several places that similar risks are presented by gene flow from GM and conventional crops. The controversies over regulation of GM crops, the technical ease of tracking, and the availability of grant funds has made transgene flow much easier to study, so it has achieved a higher profile. However, Ellstrand correctly highlights one characteristic that differentiates today's transgenes from most conventional domestication alleles: dominance. Traditional domestication genes are largely recessive, whereas commercialized transgenes have been universally dominant. Dominance will cause the effects of transgenes to be manifest even when heterozygous, as in progeny of first generation crosses between crops and wild plants. This can enable much more rapid spread of advantageous genes (e.g., herbicide- or pest-resistance genes in some environments), but should equally likely slow

the spread of genes for domestication traits that lower fitness within wild populations. Conventionally bred traits are also more commonly part of multigenic systems (several unlinked genes, not one, give the new trait). This makes it more difficult for natural selection to operate on the new alleles. Ellstrand shows that cavalier statements that genetic pollution is the same in conventional and transgenic agriculture are wrong. Gene action matters, and transgenic traits as a class, at least so far, differ from many conventionally bred traits in their genetic basis. In some cases this increases risk, and in others it reduces it.

Ellstrand pays a great deal more attention to the effects of hybridization between conventionally bred crops and wild relatives, which can result in the generation of new weeds, making old weeds harder to control, and the swamping of native gene pools. He provides enough data to make a convincing case that hybridization happens in virtually every major crop and has had, at least in a few well-studied cases, large impacts. However, the data by no means demonstrate that hybridization is a ubiquitous or even an important problem in most crops in most areas of the world. He weaves the example of weedy sugar beet throughout the book, but this is primarily a case where gene flow from a wild relative (weed beets) to the crop has caused localized agronomic impacts. Ellstrand presents no evidence that gene flow from cultivated sugar beet to weed beets has resulted in adverse effects on native ecosystems, or even that the weed beet problem itself is significant outside of beet fields. He also spends little time differentiating those cases where crops hybridize with exotic, weedy relatives versus native species. It appears that the former is most common, which may be a problem for farmers but is of little concern when it comes to preservation of natural biodiversity. Finally, Ellstrand virtually ignores the many crops and regions where genes from wild populations, rather than from crops, dominate gene flow. This is unfortunate because it is in some of these cases, including for major crops like grasses and trees, where 'genetic pollution' of wild species by domestication transgenes may both be highly likely to occur and highly unlikely to be of ecological significance.

This book is written from the perspective of a population geneticist, such that impacts are often described in terms of allele frequencies rather than trait physiologies and crop ecosystems. As a result it does not offer many insights into the relative risk of various traits and genetic architectures with respect to invasiveness due to hybridization, which Ellstrand refers to as a "mystery" (p. 189). He also does not consider gene flow within the larger context of the environmental effects of agriculture. Although there is a discussion of management of gene flow in the final chapter, Ellstrand dodges the key question of how society is to make decisions about what kinds of breeding it should continue to promote and what kinds to carefully scrutinize. In stark contrast to GM crops, breeding is essentially unregulated throughout the world. Should regulations be imposed so that every crop and new variety is scrutinized by federal governments for their gene flow consequences prior to commercial release? When will GM crops likely reduce the environmental impacts of gene flow, and when will they likely exac-

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erbate them? The decision about how to regulate new varieties will cost society greatly both if is too stringent and if it is too lax. Testing the environmental safety of new varieties in a rigorous way requires that many genotypes and backcrosses be ecologically monitored in a large number of environments for many years. The requirement for such elaborate tests would likely make the majority of conventional breeding programs economically unprofitable, as it appears to have done for most kinds of potential GM crops. Such a system would thereby forego vast numbers of new varieties whose yield, quality or pest resistance traits could greatly reduce the broader environmental effects of agriculture. So is worry about gene flow pennywise and pound-foolish? Unfortunately, Ellstrand retreats from this challenge-which would require serious consideration of traits and ecosystems in addition to genes and hybrids. Such an analysis would have greatly enhanced the practical utility of this book for regulators, policy makers and nongovernmental organizations.

Ellstrand makes the case that gene flow is so complex, so commonplace, and its consequences so unpredictable that the only reliable mitigation strategy will often be at the front end, during crop design. It is therefore fitting that he ends the book with a discussion of methods for minimizing its extent. He discusses the potential for sterility traits like the much maligned 'terminator,' and 'transgene mitigation' genes that reduce fitness, and points out that there does not appear to be a single publication that documents the effectiveness of such traits under field conditions. Though industry clearly is interested in genetic use restriction technologies (GURTs) for proprietary reasons, they have not seen fit to study, or perhaps to publish on, their environmental aspects. Industry is unlikely to take the lead in this area in the future because genetic confinement technologies usually do not provide much added financial value, they are biologically complex (*i.e.*, expensive to develop), they will require customization to highly diverse crop biologies and production systems (reducing profitability), and environmental performance data must be generated by public sector scientists for credibility. There is, however, precious little public sector funding for development of crop biosafety technology. Politicians and research agencies should take heed, or may face the prospect that the main fruits from billions of dollars of public funding in plant genomics may be publications rather than crops engineered for higher yield, stress tolerance and environmental safety.

In spite of the acrimony surrounding gene escape from GM crops, Dangerous Liaisons? presents a rigorous and even-handed look at the science and technology surrounding crop gene flow. Denial worked fine for 10,000 years, but will not cut it in the era of GM, globalization and rapidly expanding human populations. Breeders, agronomists and agribusiness need to stop thinking as though the impacts of gene flow in agriculture are restricted to seed production fields. Activists need to start being honest with the public; genetic pollution is not new, nor unique to GM crops. Much as Rachel Carson did for pesticides four decades earlier, Ellstrand's book serves notice that society will need to come to terms with the genetic promiscuity of agriculture. We may someday look back and find that it was GM that shined light on the gene flow problem such that we could no longer ignore it, but that it also gave us the knowledge and tools to manage it. h