Evolution, 58(7), 2004, pp. 1637–1638

WHEN GOOD PLANTS GO BAD. . .

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Received May 1, 2004.

Plants hybridize. It's what they do. But how frequently do domesticated plants hybridize with their wild relatives? And what difference does it make if they do? These questions, the focus of Norman C. Ellstrand's recent book, *Dangerous Liaisons? When Cultivated Plants Mate with Their Wild Relatives,* form the basis of an intense international debate over the environmental safety of genetically modified (GM) crop plants. Defenders of GM crops cite the possible environmental benefits of such technology, including a decrease in the application of chemicals to agricultural systems, a transition to less toxic chemical treatments, and a reduction in topsoil loss due to the facilitation of zero-till agriculture (e.g., McGaughey et al. 1998; Trewavas and Leaver 2001; Dale et al. 2002). Opponents of genetic modification, in contrast, are quick to point out the potentially harmful effects of transgenes on nontarget organisms (e.g., Losey et al. 1999), as well as the possibility that transgenes might escape from cultivation via hybridization.

Less than twenty years ago, the prevailing view among plant biologists was that crop-wild hybridization was infrequent and largely inconsequential. However, shortly thereafter, a few wise souls (e.g., Colwell et al. 1985; Goodman and Newell 1985) realized that such hybridization might serve as a conduit for the escape of engineered genes from crop fields into wild plant populations. If transgenes were to find their way into natural populations, they might provide the basis for the evolution of increasingly weedy and/or invasive plants (Raybould and Gray 1994). Alternatively, such gene flow might result in an erosion of genetic diversity in the recipient populations and, ultimately, might drive such populations extinct. Spurred on by these possibilities, a number of researchers (including Ellstrand and colleagues) spent much of the 1990s investigating the potential for gene flow into wild populations. What they found was troubling: crop plants often can (and do) hybridize with their wild relatives, sometimes over surprisingly long distances. And far from being a geographically localized phenomenon, there is evidence that some crops have the potential to hybridize throughout much of their range of cultivation (Burke et al. 2002).

In *Dangerous Liaisons,* Ellstrand provides the first synthesis of the science underlying the crop-wild hybridization debate. In view of the current political scene, a book such as this is especially timely and likely to be of great general interest. It is therefore not surprising that Ellstrand has targeted his book at a very broad audience, ranging from policy makers and conservation managers to individuals well versed in the minutiae of plant evolutionary genetics. To pull this off, Ellstrand organized the book into a series of more or less freestanding chapters. These chapters are aggregated into three sections that provide the reader with an introduction to fundamental evolutionary concepts (Part I: ''Foreplay''); an exhaustive review of what's known about spontaneous hybridization between cultivated plants and their wild relatives (Part II: ''Caught in the Act''); and a discussion of the significance of such hybridization in an evolutionary context, with a special emphasis on GM crops and strategies that we might employ to minimize the risks associated with gene escape (Part III: ''Dangerous Liaisons?'').

One thing that really stood out as I read this book is the almost complete lack of data on the effects of transgenes once they find their way into wild populations. Thus, I think that it's safe to say that we still don't know very much about the risks associated with transgene escape. If there is any lingering uncertainty about the fact that crop-wild hybridization is taxonomically and geographically widespread, this book should erase all doubt. Where the uncertainty remains is in the arena of what these genes will do following their escape. We have known for decades that the rate of spread of an allele is governed mainly by its effect on fitness, rather than by the migration rate (e.g., Fisher 1937; Slatkin 1976; Rieseberg and Burke 2001). However, researchers have largely focused on the latter. This is not to say that past studies documenting crop-wild gene flow have been without merit; indeed, it is just those sorts of studies that have alerted us to the potential for transgene escape. However, our focus going forward needs to be on the fitness effects of the gene(s) in question, rather than on overall rates of hybridization. This point certainly isn't lost on Ellstrand, who devotes a substantial chunk of Part I to a discussion of the evolutionary consequences of gene flow, and then revisits this issue in Part III. The critical concern here is that the sorts of traits that are typically the target of genetic manipulation—such as pest or pathogen resistance and tolerance of various abiotic stresses—might be highly advantageous in the wild. Thus, even rare transgene escapees could easily become established and begin to spread across the range of the recipient taxon.

Although fitness-related measures are not necessarily good predictors of invasiveness (Bergelson 1994), the fitness of an allele remains the best predictor of its likelihood and rate of spread. Fitness-related measures are, therefore, currently our best means of assessing the environmental risks associated with transgene escape. However, as previously noted, little was known about the fitness effects of transgenes in the wild until very recently. In the time since *Dangerous Liaisons* went to press, two studies chronicling these effects following transgene escape into wild sunflower populations were pub-

Dangerous Liaisons? When Cultivated Plants Mate with Their Wild Relatives. Norman C. Ellstrand. 2003. Johns Hopkins Univ. Press, Baltimore and London. xx + 244 pp. HB $65.00, ISBN 0-8018-7405-X.

lished. In one case, a transgene that provides cultivated sunflower with resistance to *Sclerotinia sclerotiorum* (i.e., white mold) was found to have no detectable effect on fitness in a wild sunflower genetic background, even when the plants were faced with a severe pathogen challenge (Burke and Rieseberg 2003). In contrast, Snow et al. (2003) showed that a Bt transgene had a positive impact on fecundity of wild sunflowers in one locality. Assuming that the findings of Burke and Rieseberg (2003) are generalizable over time, the white mold resistance gene would be predicted to have little, if any, impact on the evolutionary dynamics of wild sunflower populations. However, the Bt transgene might be expected to spread across at least a portion of the range of wild sunflower, possibly resulting in the evolution of a more troublesome weed. The disparate results of these two studies highlight the importance of performing risk assessment on a gene-by-gene basis. Unfortunately, this is a tall order. Proper risk assessment needs to not only take into account the various genetic backgrounds upon which a transgene might find itself, but also needs to be replicated across both space and time. This last point is especially troubling, because strong but episodic selection can have a major influence on the evolutionary trajectory of a population (e.g., Grant and Grant 2002), yet may be rare enough to avoid detection.

What about cases where we've done the work, and the risks clearly outweigh the benefits? Can we tip the balance by mitigating the risks? Ellstrand devotes his final chapter to a discussion of whether and how to manage gene flow into wild populations, describing a number of possible containment strategies, ranging from geographic or temporal isolation to genetic failsafes. Unfortunately, none of these containment strategies is foolproof. Furthermore, a recent theoretical study revealed that even very low failure rates (on the order of 10^{-3}) might allow for the rapid escape and establishment of a moderately favored transgene (Haygood et al. 2004). Thus, it seems unlikely that current strategies will be sufficient to contain the worst offenders.

All in all, I found this to be an accessible, well-written book that is certain to become a valuable reference for anyone with even a passing interest in the subject. Moreover, I found it truly refreshing to read such an even-handed treatment of a topic that has stirred up so much controversy. It is my hope that the publication of this treatise marks a turning point in research on crop-wild hybridization. Once we know that a certain crop hybridizes, additional (or more precise) estimates of the rate of gene flow into wild populations will do little to advance the field. What we need is a better idea of what these genes will do when they get out. Given the potential benefits of genetic modification, we shouldn't turn our backs on GM crops from the outset. Rather, we need to work toward identifying genes that provide the greatest benefit with the least attendant risk. When coupled with one or more gene flow mitigation strategies, such risk assessment is almost certainly our best way forward. After all, as Ellstrand notes in his closing passage, an ounce of prevention is worth a pound of cure.

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Book Review Editor: D. Futuyma