

BOOK REVIEW

**HYBRIDIZATION BETWEEN CROPS AND WILD PLANTS IN
THE AGE OF GENETIC ENGINEERING:
NEW RISKS OR NEW PARADIGMS?¹**

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The global debate about genetically modified (GM) crops remains heated and highly polarized. In 2003, almost 68 million hectares of such crops were grown worldwide by an estimated 7 million farmers in 18 countries, an area which continues to grow year by year at a double-digit rate (James, 2003). Most (73%) of the area was occupied by herbicide-tolerant soybean, maize, canola, and cotton. Most of the rest was insect-resistant (Bt) maize and cotton, but the stacking of these traits and the cultivation of crops with other traits such as virus resistance has continued to increase. Eleven of the countries growing GM crops last year were in the developing world where farmers appear increasingly keen to adopt the technology. By contrast, Europe, with minor exception (a small acreage of Bt maize) continues to oppose both the commercial cultivation of GM crops and, as far as trade rules allow, their importation. European consumers demand labeling and segregation of the products of such crops, and, led by highly successful and well-trusted environmentalist nongovernment organizations, the public have consistently opposed their cultivation on the grounds of potential environmental damage. Recently the UK government, displaying what is arguably a bizarre sense of proportionality, has banned transgenic herbicide tolerant sugar beet and canola because management of the crop could exacerbate the decline in farmland biodiversity, especially farmland birds, whilst taking no action either to reduce the widespread growth of winter sown, as opposed to spring, crops (identified as a major factor in the decline of several of the bird species concerned), or to prevent the extensive conversion of pasture to year-on-year forage maize (which has a huge environmental impact).

One aspect of this debate that has created considerable angst has been the problem of gene flow—specifically the “escape” of transgenes into surrounding populations of other crops or of related wild plants. Both the scientific challenges and the potential difficulties for accurate and sensible risk assessment of gene flow from GM crops were recognized very early (Colwell et al., 1985), and the possible spread of novel genes in the environment was highlighted as “an important uncertainty” in risk assessment in the report of the Royal Commission on Environmental Pollution in 1989 (RCEP, 1989). The likelihood of widespread genetic “pollution” and the spectre of “superweeds” created by gene flow has been a central plank in the anti-GM stance of several pressure groups (e.g., Greenpeace; Fronwald and Straus, 1998). A burgeoning scientific

research program on the measurement and possible consequences of gene flow (e.g., Lutman, 1999; Den Nijs et al., 2004) has been accompanied by growing investment in research into molecular and other methods of gene containment, or mitigation of the effects of gene escape (Daniell, 2002; Gressel, 2002). Gene flow is a hot topic.

Into this maelstrom arrives this extremely timely volume by Professor Norman Ellstrand of the University of California, Riverside. Professor Ellstrand, more than most, has been responsible for alerting a wider audience than research scientists to the fact and ubiquity of hybridization between crops and their wild relatives. This remains the clearly stated aim of his book. Indeed, it is structured specifically to appeal to a broad audience and the author invites different kinds of reader to approach the book differently, suggesting that evolutionary plant geneticists may like to skip or skim some chapters, whilst practical scientists such as policy makers could jump around from chapter to chapter and yet others take a “linear approach.” The overall effect, if like me, you do take a linear approach, is rather curious; the style and language changes abruptly from place to place to address the various audiences. Thus at times we are told that stray pollen grains “have considerably more significance than a stolen kiss” or that beet plants have “children” and “grandchildren,” whereas key technical concepts such as “effective population size” or words such as “ribosomal DNA markers” are introduced elsewhere into the text without qualification or explanation. This makes for something of a roller coaster read but, as was no doubt the intention, provides something to suit most tastes. The more waggish mode is used to headline the sections of the book. Part 1 “Foreplay” introduces the subject of hybridization and gene flow and considers some of its evolutionary consequences, part 2 “Caught in the Act” examines the evidence that can be used to detect that hybridization has occurred and catalogs the many examples of crop/wild relative hybridization and possible introgression, and part 3 “Dangerous Liaisons?” deals with the potential impacts of gene flow to wild relatives and the “special” case of genetically engineered plants. Embedded within these main sections is a three-part narrative “The Case of the Bolting Beets,” which, under the headlines “Long-Distance Romance,” “Detectives Arrive at the Scene,” and “The Cloudy Crystal Ball,” gradually unfurls the fascinating (and from the GM risk assessment point of view, highly relevant) story of the origins of weed beet in European agriculture via hybridization between wild sea beet *Beta vulgaris* subsp. *maritima* and the domesticated sugar beet *Beta vulgaris* subsp. *vulgaris*. (Incidentally, the playful style

¹ *Dangerous Liaisons? When Cultivated Plants Mate with Their Wild Relatives*, Norman C Ellstrand. The John Hopkins University Press. 2003. 264 pp., 6 illus. ISBN 0-8018-7405-X (hardcover, \$65.00).

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is very infectious—I wanted to call this review “Professor Shows Wild Sex is the Norm.”)

In a book explicitly designed to have more or less stand-alone bits, which are the best bits? For me, they are the core chapters 7 and 8, which detail what is actually known about crop/wild relative hybridization, and the ultimately balanced account of the issues presented by gene flow from GM crops, covered in the two final chapters.

Many people will recognize the core chapters as an extension of an earlier review (Ellstrand et al., 1999) of the known cases of spontaneous hybridization between the most widely grown crop plants and their wild relatives. This is the most original part of the book and covers a field to which Professor Ellstrand and his students have made a unique and extensive contribution. If there is anyone left out there who believes that hybridization between domesticated and wild plants is an exceptional event they should read this thoroughly researched account covering most of the world’s crops. In all but three of the 25 main crops looked at in detail, there is some evidence for natural hybridization somewhere in the world with one or more relatives, and in all but seven of the 28 species represented by those crops, there is modern molecular evidence to support the existence of hybrids. A fuller list of 81 cultigens in which there is evidence of crop/wild relative hybridization contains only 33 examples in which hybridity has been deduced from morphological evidence alone. However, evidence of the occurrence of hybrids is not the same thing as saying that gene flow, which includes introgression and the incorporation of a gene into a natural population, is a ubiquitous feature of contemporary agriculture—a subject to which I will return later.

The two final chapters deal with the specific problems presented by GM crops (Ch. 11), in which the traits inserted by recombinant DNA methods are almost unexceptionally inherited in a dominant mode (which, it is important to note, exposes them more rapidly to selection), and discuss the possibilities of containing or limiting gene flow into wild populations (Ch. 12), either by methods such as physical separation and buffer zones (rightly concluded to be costly and largely ineffective in most cases) or the sorts of genetic engineering technologies alluded to earlier (which actually bring additional risk assessment issues).

What about the other bits? In a relatively slim volume (just over 200 pages of text), one cannot include everything of relevance, and what goes in will always be a matter of choice. Professor Ellstrand’s decision to focus on one-way hybridization, (i.e., where, at least initially, genes are transferred *from* the cultivated plant *to* the wild relative) and also largely to ignore natural ecosystems, obviously makes sense in the context of a discussion of transgene escape from GM crops. However it leaves out research areas that undoubtedly have something to offer in addressing the book’s central question. For example, missing from the introductory chapters is a sense of the antiquity of the subject of spontaneous crop/related plant hybridization; needless to say, the topic did not begin with the GM crop debate. Even Charles Darwin (remarkably not cited) refers to the serious contamination of his cabbage seed stocks by kale plants growing half a mile away (Darwin, 1876). It was actually surprising to be told that the prevailing view in the late 1980s was that hybridization between crops and their wild relatives occurred infrequently, if at all. Extensive true gene flow (*sensu* Futuyma [1998] in which a gene is successfully incorporated from one population into another) may have

been thought to be rare in such circumstances (and, as it turns out, probably still is), but the frequent occurrence of crop/wild hybrids was surely acknowledged by many (see e.g., Stace, 1975). Such hybridization was certainly described in the literature on introgression, natural gene exchange between wild relatives and crops in the reverse direction, the evolution of crop mimics, and of crop–weed–wild complexes. This literature, given the one-way focus of the book, has much less prominence than it probably deserves. Similarly, the extensive work in the fields of ecological and conservation genetics on the genetic structure of natural plant populations and the interplay between gene flow and natural selection is barely included. Surely it is these literatures that we are going to have to research both for understanding and for relevant models to predict whether or not, in specific cases, gene flow from GM crops is likely to have a negative impact on the environment. The work on the evolution of herbicide tolerant weeds provides a striking example.

From the viewpoint of assessing the potential risks of cultivating GM crops, the central question posed by the book’s title (are the liaisons between crops and wild relatives in some sense “dangerous”?) is correctly identified as comprising two specific questions. Will hybridization between GM crops and wild relatives lead to the creation of weedy or invasive species (or, more specifically, the evolution of increased weediness in existing wild relatives)? Will hybridization between GM crops and wild relatives increase the risk of extinction of any wild taxa? These are really reverse sides of the same ecological genetic question and are critically dependent on the changes in plant fitness that result from hybridization and subsequent introgression. Some of the evidence needed to consider these questions, garnished from what we have learned from crops produced by traditional plant breeding, is gathered in part 3 of the book, especially Chapter 9.

Dealing with the second question first; we are given a table containing nine examples of hybridization with a cultivated species that appears to be endangering one or more wild populations. Although most of the examples provide data that shows that hybridization has occurred, in only one case, that of natural hybridization of cultivated rice *Oryza sativa* with an endemic wild rice *Oryza rufipogon* subsp. *formosana* in Taiwan, is there evidence of decreased fitness in the wild populations. There is a similar problem with judging how much extinction of wild populations may have occurred as a result of hybridization with a domestic species, although “the overall impression of experts in the field is that it is not rare” (p. 155). The author, who suggests that extinction may be very rapid, hence the lack of examples, observes that the topic “has enjoyed more speculation than data collection” (lovely phrase!) (p. 155) and points out that there is a great deal of relevant research that can be done in this area.

The first question (Will gene flow from GM crops produce weedier or more invasive plants?) is in many ways the key question that the title of this book suggests it has set out to address. It is certainly number one among the frequently asked questions about gene flow and GM crops, a central concern of all risk assessments performed by regulators, and has been repeatedly invoked by environmentalists as a reason to refuse consent to release particular crops. In view of this, it will come as a huge disappointment to many readers to realize that we actually know almost nothing about the consequences of gene flow from crops—GM or conventional. Having been convinced that it happens, and on a larger scale than envisioned

heretofore, we arrive at the crunch “so what?” question, only to discover a virtually data-free zone. To be fair, Professor Ellstrand does set out some examples that hint at the generalization that gene flow from domesticates tends to result in an increase of genetic diversity in the wild, and offers some possible explanations for this. And there is a smallish body of research literature that allows us to make some intelligent guesses about the really vital risk assessment question of invasiveness. In fact, Professor Ellstrand goes further and lists 13 (of 16) cases in which hybridization between a cultivated plant and a wild relative have “preceded the evolution of increased aggressiveness of the wild taxon” (p. 152) (Five of these involved the evolution of new taxa and eight were examples of adaptive evolution.) He goes on to conclude from this that hybridization between wild plants and their domesticated relatives “has resulted in some plants that have created hardship for humankind and others that have disrupted natural ecosystems” (p. 154) and, by comparison with a data set (of 28 examples) not published in the book, that “the chances of a domesticated-wild hybrid becoming a problem plant are an order of magnitude greater than if both hybridizing parents are wild species” (p. 154). This surprising, and for some readers no doubt alarming, conclusion becomes less surprising if the data are reexamined in the light of the author’s definition of “wild” plants, given (on p. 10) as “those that are essentially free-living, that is, those that grow and reproduce without being deliberately planted and cared for.” This categorization clearly includes agricultural weeds and the species commonly found in peri-agricultural and frequently disturbed biotopes. And sure enough, the 13 examples of increased aggressiveness include no less than nine weeds of agricultural fields, and of the other four at least two, *Rhododendron ponticum* and *Nasturtium sterile*, are arguably inappropriate analogs for cases of gene flow from domestic crops (their success as invaders can also be given more parsimonious non-genetic “explanations” involving the exploitation of vacant niches).

The distinction between agricultural or disturbed-land weeds and plant species invasive of natural or semi-natural habitats is an extremely important one from the point of view of ecological risk assessment of GM crops. But it is one that is rarely made explicit. A potential weed is a potential agricultural problem and the risk of one resulting from gene flow, or increased weediness of the GM plant, must be set in the context of potential agricultural solutions. Weed management and control strategies have developed alongside evolving weed problems to variously cope with the threats to crop yield. Thus, an assessment of the risks of, say, creating a herbicide-tolerant weed as a result of gene flow from the crop must consider what strategies are available for risk mitigation or management, such as alternative herbicides or changes in farm practice, and decide what is relatively “safe” in that case; no agriculture is entirely risk free. (In fact, such a weed has been reported from the canola fields of Canada (Warwick et al., 2003), probably since the text of *Dangerous Liaisons* was completed, adding to the 130 or so herbicide-tolerant weeds produced by the selective action of herbicides on weed populations.) By contrast, the creation by gene flow of a hybrid that becomes more invasive of natural ecosystems is a very different prospect (and could in theory be a potential nightmare) and is one of the major reasons why GM crops receive regulatory oversight and why they should be scrutinized on a case-by-case basis. One is bound to say, however, that Professor Ellstrand’s data actually lend more support to those who

maintain that, as a general rule, hybrids that receive genes from modern crops are likely to be less fit in natural habitats because they are invariably linked to genes expressing traits selected during domestication, such as seed shattering and lack of dormancy (e.g., Conner et al., 2003; Stewart et al., 2003). It seems that, despite widespread crop/wild plant hybridization there have been virtually no “escapes.” Until we have more case studies (and not ones that use fecundity as a substitute for fitness but undertake actual life history analysis—see Bullcock, 1999 and Crawley et al., 2001), data such as those provided in this volume, whilst confirming that mechanisms exist for the evolution of more serious crop weeds, give limited clues to the potential for invasiveness and disturbance of natural ecosystems.

Despite this, I feel sure that the book will be widely acclaimed and play an important part in the debate about GM crops. Regulators, policy makers, and the scientists who advise politicians (described by the author as being “in the trenches”) will find the extensive information on hybridization in the world’s crops and their wild relatives useful and through it gain access to other studies relevant to their own countries. Those scientists in the European trenches, where the debate is rarely leavened by humor and where the distinction between what is dangerous, undesirable, or plain daft has become almost irreversibly blurred, will no doubt have winced at the book’s title, even with the question mark, but should read it nonetheless. Students of evolution and plant genetics will find the introduction to the subject informative and clear. The text is rich in quotable phrases (which one predicts will be selected by both sides in the debate as appropriate) and, as indicated earlier, the book can be read at several levels.

Finally, what about the case of the bolting beets? Is it an exception that proves the rule? Whilst it certainly shows what can happen when cultivated plants mate with their wild relatives, unfortunately for Professor Ellstrand’s line of argument, weed beets were created by gene flow *into* the seed crops *from* the annual wild beet (sea beet is an annual in the southern part of its range), and hybrid seed were then transported with the crop to the sugar beet production areas in the north where they created an agricultural weed problem. Although the mechanism exists for this type of gene transfer to happen with a transgenic crop, it is hardly a good analogy for gene flow from a GM crop into populations of a wild relative—where the hybrids must survive in the habitat of the wild plant. To me, the most illuminating aspect of the bolting beet story is how little gene flow, if any, has occurred in the north between the crop or weed and the wild sea beet relative. In recent studies using molecular markers, by Joel Cuguen and his colleagues at the University of Lille, populations of sea beet on the north French coast displayed no evidence of gene flow by pollination with beet in nearby fields, but, intriguingly, from the distribution of the cytoplasmic male sterility marker gene, demonstrated clear evidence of seed-mediated gene flow into these populations (the likely vector being tractor tires or sea wall engineers) (Arnaud et al., 2003). Similarly, and despite decades of exposure to pollen from coastal sugar beet fields containing weed beets, the bolting gene has not been found in any wild sea beet populations along the French channel coast or the coast of England (Van Dijk et al., 1997) Sea beet is a perennial plant in these northern sea wall and salt marsh populations. Suggesting that annual beets are less fit in such habitats, this example surely provides yet further testimony to the power and ubiquity of natural selection.

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