The Opportunity for Escape of Engineered Genes from Transgenic Crops

J.F. Hancock, R. Grumet, and S.C. Hokanson

Department of Horticulture, Michigan State University, East Lansing, MI 48824

Much of the concern about the commercialization of transgenic crops has focused on the movement of transgenes into populations of wild relatives via pollen flow (Brown et al., 1984; Colwell et al., 1985; Dale, 1992; Ellstrand, 1988; Ellstrand and Prentice, 1995; Goy and Duesing, 1996; Rissler and Mellon, 1993; Tiedje et al., 1989). If these engineered traits confer a selective advantage, introgression and subsequent evolution might lead to more noxious agricultural weeds (Keeler, 1988; Rissler and Mellon, 1993) and even disrupt natural ecosystem balances by enhancing the fitness of wild relatives (Ellstrand and Hoffman, 1990; Raybould and Gray, 1993; Regal, 1988; Rissler and Mellon, 1993). The genes themselves could directly confer a selective advantage, or unique epistatic interactions might arise between engineered and native genes that result in higher fitness (Keeler, 1989; Mooney and Bernardi, 1990; Rissler and Mellon, 1993).

Experience with the release of conventionally bred crops could be used as a guide in predicting the likelihood of escape of genes from crops into native populations. Hybridization and introgression have been occurring between cultivated and wild species since humans began agriculture (Anderson, 1949, 1961; DeWet and Harlan, 1975; Hancock, 1992; Harlan, 1965). Harlan (1965) originally described the interaction between cultigens and wild populations of *Sorghum* Moench., *Triticum* L. (wheat), and *Hordeum* L. (barley). More recently, crop-wild hybridization has been documented between a broad array of crops, including wild and domesticated gourds (*Cucurbita* L.) (Kirkpatrick and Wilson, 1988), rice (*Oryza* L.) (Chu and Oka, 1970; Langevin et al., 1990), maize (*Zea* L.) (Doebley, 1990), oil seed rape (*Brassica* L.) (Jorgensen and Anderson, 1994; Palmer et al., 1983), carrot (*Daucus* L.) (Wijnheijmer et al., 1989), beet (*Beta* L.) (Boudry et al., 1993; Santoni and Berville, 1992), foxtail millet (*Setaria* Beauv.) (Till-Bottrand et al., 1992), pearl millet (*Pennisetum* Rich.) (Brunken et al., 1977), potato (*Solanum* L.) (Urgent, 1970), radish (*Raphanus* L.) (Klinger et al., 1991), raspberries (*Rubus* L.) (Jennings, 1988; Luby and McNichol, 1995), and wheat (*Triticum* L.) (Zohary, 1971, 1976).

Most geneticists would agree that it is

unlikely that natural and engineered traits will have different patterns of gene dispersal (Raybould and Gray, 1993; Rees et al., 1991; Regal, 1988; Simonsen and Levin, 1988; Williamson, 1988; Yang, 1988); however, some have argued that comparisons with conventional crop releases are not appropriate, since engineered genes might be inherently different than native genes due to their exotic sources (Rissler and Mellon, 1993). To answer this question, Hokanson (1995) recently compared gene movement between a morphological marker and engineered neomycin phosphotransferase gene (NPT) in melon and found no difference in their pattern of dispersal. Engineered traits may provide selective advantages unique to the native species, but there is little reason to believe that patterns of pollen flow will be significantly different between natural and engineered traits.

With regard to the potential for gene escape, many factors are thought to influence the extent of gene flow and establishment (Antonovics, 1971; Ellstrand and Hoffman, 1990; Hamrick, 1987; Handel, 1983a; Levin, 1981; Manasse, 1992): 1) proximity of compatible wild relatives, 2) the fitness of hybrids, 3) mating system and mode of pollination, 4) mode of seed dispersal, and 5) the selective value of the engineered trait. Comprehensive data exist within the literature for the first four questions and is the primary focus of this paper. Herein, we briefly review the ecological literature as it relates to each of these questions, and then we describe the available information on the engineered crop species tested under APHIS (Animal and Plant Health Inspection Service) oversight in the United States. We also briefly describe the potential selective advantage of engineered traits, although, to our knowledge, very few controlled experiments have been conducted on the fitness of engineered genotypes in either agricultural or native environments (Bergelson, 1994; Crawley et al., 1993).

PROXIMITY OF COMPATIBLE WILD RELATIVES

Most crops have wild relatives somewhere (Table 1), and the progenitors of our crop species often survive in extensive populations next to cultivated fields (DeWet and Harlan, 1975; Harlan, 1965, 1992). These native populations are frequently encouraged to thrive in some less-developed nations by traditional methods of agriculture (Ellstrand and Hoffman, 1990).

Reproductive isolating barriers can exist at several pre- and post-zygotic levels, but in many instances a high level of interfertility exists between proximal wild and cultivated

species (Table 1). At least 7 crop species with added transgenes have compatible native relatives in the United States, including apple (*Malus pumila* Mill.), cranberry (*Vaccinium macrocarpon* Ait.), pepper (*Capsicum annuum* L.), plum (*Prunus domestica* L.), strawberry (*Fragaria × ananassa* Duch.), sunflower (*Helianthus annuus* L.), and squash (*Curcubita pepo* L.). Several others, including alfalfa (*Medicago sativa* L.), beets (*Beta vulgaris* L.), carrot (*Daucus carota* L.), oats (*Avena sativa* L.), rapeseed (*Brassica napus* L.), and rice (*Oryza sativa* L.), have congeners which are naturalized weeds somewhere in the United States (Ellstrand and Hoffman, 1990). Ellstrand and Hoffman (1990) list a total of eight vegetable species in California alone that have potential wild mates in that state—asparagus (*Asparagus officinalis* L.), broccoli (*Brassica oleracea* L.), carrot, cauliflower (*Brassica oleracea*), celery (*Apium graveolens* L.), lettuce (*Lactuca sativa* L.), onion (*Allium cepa* L.), and potato (*Solanum tuberosum* L.). Of the seven crops currently approved for transgenic commercialization in the United States (Table 1), two have compatible wild relatives in the continental United States (rapeseed and squash), four in South America and Mexico [cotton (*Gossypium hirsutum* L.), maize, potato, and tomato (*Lycopersicon esculentum* Mill.)], and one in China [soybean (*Glycine max* (L.) Merr.)]. Cotton also has compatible relatives in Hawaii and the Caribbean (DeJode and Wendel, 1992).

FITNESS OF HYBRIDS

Most crop species can survive in the wild for a generation or two, even without the addition of adaptive genes. When local floras representing California (Munz and Keck, 1973), the southern United States (Radford et al., 1968), and eastern parts of the United States (Gleason and Cronquist, 1963) were examined, we found 11 crops that have come under APHIS oversight that escape and persist in native environments (Table 2). In fact, vagrants of almost all crops can be found somewhere in the world, particularly where their progenitors occur naturally. For example, Harlan (1965) reports that most important grain species are found growing next to farmers' fields.

Not only do many crop genotypes survive in the wild, but in many instances they exist as successful weeds in agro-ecosystems. In a list of the weediness of crop plants, Keeler (1989) identified carrot, lettuce, oat, radish, rice, sunflower, and sweetpotato as being potential weeds in the United States. More recently, a spontaneous *Cucurbita pepo*, similar to the Texas gourd, has become a weed problem in

Received for publication 16 Jan. 1996. Accepted for publication 8 Apr. 1996. Thanks to Norman Ellstrand, who stimulated this manuscript and carefully reviewed an early draft. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

Table 1. Compatible wild relatives of crops engineered in the United States and tested under APHIS oversight (Source: Ellstrand and Prentice, 1994; Hancock, 1992; Smartt and Simmonds, 1995; Zohary and Hopf, 1993). Engineered crops currently approved for commercialization in the United States are underlined (APHIS records, unpublished).

	Crop	Compatible wild relatives	Location	Level of cross fertility ^a	Natural hybrids reported
Alfalfa	<i>Medicago sativa</i> L.	Wild <i>M. sativa</i>	Near East/Mediterranean	1	Yes
		<i>M. glomerata</i> Balb.	S. Europe/N. Africa	1	Yes
Apple	<i>Malus domestica</i> Borkh.	Many	N. America/Europe/China/Asia	1	Yes
Barley	<i>Hordeum vulgare</i> L.	Wild <i>H. vulgare</i> (<i>H. spontaneum</i>)	Near East	1	Yes
Beet	<i>Beta vulgaris</i> L.	Wild <i>B. vulgaris</i>	Europe to China	1	Yes
Carrot	<i>Daucus carota</i> L.	Wild <i>D. carota</i>	Europe/Mediterranean/N. America	1	Yes
<u>Cotton</u>	<i>Gossypium hirsutum</i> L.	Wild <i>G. hirsutum</i>	Meso-America/Caribbean	1	No
		<i>G. barbadense</i> L.	S. America	2	Yes
		Several others	Locally at several locations	2–3	Yes
Cranberry	<i>Vaccinium macrocarpon</i> Ait.	Wild <i>V. macrocarpon</i>	Eastern North America	1	Yes
		<i>V. oxycoccus</i> L.	Circumboreal	3	No
Cucumber	<i>Cucumis sativus</i> L.	Wild <i>C. sativus</i>	Asia	1	Yes
Eggplant	<i>Solanum meloena</i> L.	Wild <i>S. meloena</i>	India	1	Yes
		<i>S. incanum</i>	India/Africa/Asia	1	Yes
		Several others	Mostly India	2–3	No
Lettuce	<i>Lactuca sativa</i> L.	<i>L. serriola</i> L.	Mediterranean	1	Yes
		<i>L. virosa</i> L.	Mediterranean	1	Yes
		<i>L. saligna</i> L.	Mediterranean	1	Yes
<u>Maize</u>	<i>Zea mays</i> L.	Several native teosinte (<i>Z. mays</i>)	Mexico	2–3	Variable
Melon	<i>Cucumis melo</i> L.	Wild <i>C. melo</i>	Africa	1	Yes
		<i>C. metuliferus</i> Naud.	Africa	2	No
		<i>C. anguria</i> L.	Africa	2	No
Pea	<i>Pisum sativum</i> L.	Wild <i>P. sativum</i>	Near East/Mediterranean	1	Yes
		<i>P. fulvum</i> Sibth. & Sm.	Mediterranean	2	No
Peanut	<i>Arachis hypogea</i> L.	<i>A. monticola</i>	S. America	1	No
		Several others	S. America	3	No
Pepper	<i>Capsicum annuum</i> L.	Wild <i>C. annuum</i>	S. America/Mexico/southern U.S.	1	Yes
		Many species	S. America/Mexico	1–3	Yes
Plum	<i>Prunus domestica</i> L.	<i>P. spinosa</i> L.	Europe	1	Yes
		<i>P. insititia</i> L.	Asia	1	Yes
		<i>P. cerasifera</i> Ehrh.	Asia	1	Yes
		Many others	Europe/Asia/China/N. America	1–2	Yes
<u>Potato</u>	<i>Solanum tuberosum</i> L.	Wild <i>S. tuberosum</i>	S. America	1	Yes
		Many others	S. America	2–3	Yes
<u>Rapeseed</u>	<i>Brassica napus</i> L. (and hybrids with <i>B. campestris</i> L.)	Wild <i>B. napus</i>	Mediterranean	1	Yes
		Wild <i>B. campestris</i>	Mediterranean/N. America	2	Yes
		<i>B. juncea</i> (L.) Czern.	Mediterranean	2	Yes
		Several others	Mediterranean	2–3	Variable
Rice	<i>Oryza sativa</i> L.	Wild <i>O. sativa</i>	Asia	1	Yes
		<i>O. rufipogon</i> Griff.	Africa/China/S. America	1	Yes
		<i>O. nivara</i> Sharma et Shastri	Asia/China	1	Yes
		Several others	Asia, China/Africa/S. and Central America	2–3	Yes
<u>Soybean</u>	<i>Glycine max</i> (L.) Merr.	<i>G. soya</i> L.	China	1	No (?)
		<i>G. gracilis</i> Skvortz.	China	1	Hybrid (?)
<u>Squash</u>	<i>Cucurbita pepo</i> L.	<i>C. texana</i> Gray	South-central U.S./Mexico	1	Yes
		<i>C. fraterna</i> L.H. Bailey	South-central U.S./Mexico	1	Yes
Strawberry	<i>Fragaria ×ananassa</i> Duch.	<i>F. virginiana</i> Duchn.	N. America	1	Yes
		<i>F. chiloensis</i> (L.) Duchn.	Chile/California	1	Yes
Sugar cane	<i>Saccharum officinarum</i> L.	<i>S. spontaneum</i> L.	New Guinea/India/Asia/Africa	1	Yes
Sunflower	<i>Helianthus annuus</i> L.	Wild <i>H. annuus</i>	Western North America	1	Yes
		Several other species	Western North America	1–2	Yes
Tobacco	<i>Nicotiana tabacum</i> L.	Many	Americas/Australia	1–3	Yes
<u>Tomato</u>	<i>Lycopersicon esculentum</i> Mill.	Wild <i>L. esculentum</i>	S. America/Mexico	1	Yes
		Many others	Mostly S. America	1–3	Variable
Watermelon	<i>Citrullus lanatus</i> (Thunb.) Mats. & Nakai	Wild <i>C. lanatus</i>	Africa	1	Yes
		<i>C. colocynthis</i> (L.) Schrad.	N. Africa/W. Asia	1–2	Yes
Wheat	<i>Triticum aestivum</i> L.	Feral <i>T. aestivum</i>	Near East	1	Yes
		Numerous 2× and 4× species	Near East	2–3	Yes

^a1 = hybridization easy, hybrids generally fertile; 2 = partial seed set/variable F₁ fitness; 3 = hybridization possible, but difficult, hybrids weak with low fertility.

Arkansas and Mississippi cotton fields (Decker-Walters et al., 1995). All of these species except sweetpotatoes and radish have been engineered and tested under APHIS oversight (Table 1).

The fitness of crop/congener hybrids is generally assumed to be low under field conditions, with a few exceptions (Klinger and Ellstrand, 1994; Langevin et al., 1990), but

successful hybrids have been found between most crops and wild populations (Table 1). Evidence for introgression has been presented for apple (Clapham et al., 1987; Zohary and Hopf, 1993), alfalfa (Stace, 1975), beet (Boudry et al., 1993; Hornsey and Arnold, 1979; Santoni and Berville, 1992; Stace, 1975), carrot (St. Pierre and Bayer, 1991; Wijnheijmer et al., 1989), *Chenopodium* L. (Wilson and Manhart,

1993), cotton (Brubaker et al., 1993; Wendel et al., 1992), plum (Stace, 1975, 1991), rapeseed (Palmer et al., 1983), rice (Langevin et al., 1990; Oka and Chang, 1961), rye (*Secale cereale* L.) (Sun and Corke, 1992; Zohary, 1971), and sunflower (Arias, 1994; Heiser, 1978). Only soybean and peanut have not been reported to produce wild/congener hybrids. However, *Glycine max* and *Glycine soya* L.

can be artificially crossed with some success (Singh and Hymowitz, 1988; Zhu et al., 1995), and there is a soybean taxon, *Glycine gracilis* Skvortz., that is intermediate in appearance between them and that could be a hybrid (Hymowitz and Singh, 1987).

MATING SYSTEM AND MODE OF POLLINATION

Most pollen travels only a few meters from its source, but the tails of the distribution are very long and of a generally unspecified distance (Colwell, 1951; Handel, 1982, 1983b; Hokanson et al. (1996). Wind-carried pollen has been found hundreds of kilometers from its point of origin (Ehrlich and Raven, 1969; Moore, 1976), and insects have been shown to carry viable pollen for at least 1 km (Devlin and Ellstrand, 1990; Ellstrand and Marshall, 1985).

Probably the best information on gene movement between populations has come from reports of accidental matings among crop populations and the generation of recommended

isolation distances for the production of pure seed lines (Ellstrand and Hoffman, 1990; Levin and Kerster, 1974). Most wind-pollinated species require distances of less than 200 m, while most insect-pollinated crops require distances of more than 500 m. The average for 35 insect-pollinated species is 657 m, while that for wind-pollinated species is 244 m (data from Levin and Kerster, 1974). Numerous examples have been given of long-distance gene dispersal in wild relatives of crop species. For example, Ellstrand and his group provided several estimates of inter-populational gene flow in wild radish populations and discovered high levels of movement between populations isolated by 1000 m and more (Devlin and Ellstrand, 1990; Ellstrand and Marshall, 1985; Ellstrand et al., 1989; Klinger et al., 1991, 1992). In small recipient populations, 3% to 18% of the seeds were produced from inter-populational hybridizations and there was no reduction in gene flow with isolation distances ranging from 150 to 1000 m (Ellstrand et al., 1989). Likewise, Kirkpatrick and Wilson (1988) measured substantial gene flow in

excess of 1300 m between experimental populations of the Texas gourd, *Cucurbita texana* Gray, and cultivars of *Cucurbita pepo* L. Kohn and Casper (1992) found gene flow up to 0.7 km between patches of *Cucurbita foetidissima* HBK., with inter-patch siring 0 to 48% of the seeds. Wilson and Manhart (1993) found high levels of hybridization between cultivated *Chenopodium quinoa* Willd. (Andean grain chenopod) and a North American relative, *C. berlandieri* Moq., at 500 m from the cultivated plot. Isolation distances in excess of 1000 m are usually recommended for pure seed production of most outcrossed crops (Ellstrand and Hoffman, 1990; George, 1985).

In general, outcrossed species have a wider pattern of pollen distribution than inbred ones. Again, if we use the data generated for isolation distances in crop species (Levin and Kerster, 1974), we find that most self-fertilized species require isolation distances of 200 m, while most outcrossing species require distances of 1000 m or more. The averages are: 385 m for 14 predominantly selfing species, 493 m for 16 mixed species, and 846 m for 21 outcrossed species.

Most of our engineered crops have pollination modes that will result in wide dispersal. More than 60% are outcrossed or mixed pollinated, and a high proportion of these are insect-pollinated (Table 3). In this group are alfalfa, apple, carrot, cotton, cranberry, cucumber, melon, plum, pepper, rapeseed, strawberry, squash, sunflower, tobacco, and watermelon. Only barley, rice, and wheat are both highly inbred and wind-pollinated.

MODE OF SEED DISPERSAL

Seeds are generally dispersed in a leptokurtic fashion like pollen, but the tails can be very long (Levin and Kerster, 1974; Harper, 1977). Many seeds have long-distance dispersal mechanisms, such as wings to catch air currents, stickers that attach to animal fur, and hard seedcoats that survive trips through the digestive tracts of animals.

Only limited quantitative information is available on the seed dispersal distances of wild species, but some general trends are apparent. Gravity-dispersed seeds usually travel only a few meters and most seeds are clumped about the mother (Sheldon and Burrows, 1973). Explosive or plumose seeds travel a little bit further, 1 to 10 m, with a more even distribution (Burrows, 1973; Levin and Kerster, 1968; Muller, 1955; Sheldon and Burrows, 1973). Animal-dispersed seeds are often clumped about the mother plant due to gravity, but can have by far the longest tails in the dispersal curve. Mammals and birds can have territories of dozens of kilometers (Bullock and Primack, 1977; Darley-Hill and Johnson, 1981; Lack, 1966; Lanner and Vander Wall, 1980), and bird migration distances can span hundreds of kilometers (Cruden, 1966). Human beings have played a particularly important role in plant evolution by carrying native collected and crop seeds long distances, planting them next to compatible native populations, and providing disrupted sites for population expansion

Table 2. Survival outside of agricultural fields of crop species tested under APHIS oversight (according to local floras).

Rarely escape	Eggplant, cucumber, lettuce, maize, pepper, sugar cane
Occasionally escape/nonpersistent	Carrot, cotton, melon, pea, potato, soybean, squash, strawberry, tobacco, tomato, watermelon
Occasionally escape/persistent	Apple, barley, beet, cranberry, plum, peanut, rice, wheat
Commonly escape/persistent	Alfalfa, rapeseed, sunflower

Table 3. Breeding system, pollination mode, and seed dispersal mechanism of crop species engineered in the United States and tested under APHIS oversight.

Crop	Species	Breeding system ^z	Pollination mode ^y	Seed dispersal mechanism ^x
Alfalfa	<i>Medicago sativa</i>	O	I	A
Apple	<i>Malus ×domestica</i>	O	I	A
Barley	<i>Hordeum vulgare</i>	S	W	G
Beet	<i>Beta vulgaris</i>	O	W	G
Carrot	<i>Daucus carota</i>	O	I	W
Cotton	<i>Gossypium hirsutum</i>	S	I	G
Cranberry	<i>Vaccinium macrocarpon</i>	V	I	A
Cucumber	<i>Cucumis sativus</i>	O	I	A
Eggplant	<i>Solanum melogena</i>	S	I (?)	A
Lettuce	<i>Lactuca sativa</i>	S	I	G
Maize	<i>Zea mays</i>	O	W	A
Melon	<i>Cucumis melo</i>	O	I	A
Pea	<i>Pisum sativum</i>	S	I	A
Peanut	<i>Arachis hypogea</i>	S	I	G
Pepper	<i>Capsicum annuum</i>	V	I	A
Plum	<i>Prunus domestica</i>	O	I	A
Potato	<i>Solanum tuberosum</i>	S ^w	I	A
Rapeseed	<i>Brassica napus</i>	S	I	S
	<i>B. campestris</i>	O	I	S
Rice	<i>Oryza sativa</i>	S	W	G
Soybean	<i>Glycine max</i>	S	I	A
Squash	<i>Cucurbita pepo</i>	O	I	A
Strawberry	<i>Fragaria ×ananassa</i>	O	I	A
Sugar cane	<i>Saccharum officinarum</i>	O	W	G
Sunflower	<i>Helianthus annuus</i>	O	I	G
Tobacco	<i>Nicotiana tabacum</i>	V	I	G
Tomato	<i>Lycopersicon esculentum</i>	S	I	A
Watermelon	<i>Citrullus lanatus</i>	O	I	A
Wheat	<i>Triticum aestivum</i>	S	W	G

^zS = predominantly selfed, V = variable, O = predominantly outcrossed.

^yI = insect, W = wind.

^xG = gravity, S = shattering, W = wind, A = animal.

^wMany cultivars are sterile.

(Anderson, 1949; Hancock, 1992; Salisbury, 1961).

Most of our engineered crops have long-distance seed dispersal mechanisms. More than 65% produce a capsule or fruit, and as a result are animal-dispersed (Table 3). Humans are probably the primary dispersers of most of these, but hard-seeded fruits like strawberry and cranberry are probably moved long distances in the gut of birds and mammals. Others, like barley, cotton, rice, and wheat, have no special dispersal mechanisms and as a result are listed as gravity-dispersed, but these too can be moved long distances by humans.

CONCLUSIONS

Genes will readily escape from most if not all of our transgenic crops, depending on where they are planted. Virtually all crops have native, highly interfertile relatives somewhere in the world, and numerous hybrids have already been reported between almost all conventionally bred crops and their natural progenitors. In addition, most crop species have long-distance pollen and seed dispersal mechanisms.

Since transgenes will move readily from crop species into adjacent congeners, the key question about the release of transgenic crops is not whether engineered genes will escape, but rather the nature of the genes themselves (Kareiva et al, 1991; Raybould and Gray, 1993; Rees, 1991; Regal, 1988; Simonsen and Levin, 1988; Williamson, 1988; Yang, 1988). Ellstrand and Hoffman (1990), Keeler (1985, 1989), and Regal (1988) already have stressed that the significance of escape will vary with the adaptive nature of the gene. Crawley et al. (1993) recently showed that the simple incorporation of kanamycin resistance or herbicide tolerance did not increase the invasive potential of oilseed rape sown artificially into natural habitats. However, these experiments do not exclude the possibility that other genes, which improve tolerance to biotic and abiotic stress, might have a more dramatic effect. Engineered traits that dramatically change abiotic tolerances, such as to salinity or extreme temperature, might generate a more aggressive natural competitor. Improved resistance to biotic stresses also might have an impact in free-living systems, although, to our knowledge, no one has noted a dramatic change in natural systems after the introduction of conventionally bred resistance genes.

One of the engineered traits most often mentioned as a potential danger is herbicide tolerance (Rissler and Mellon, 1993). The incorporation of herbicide tolerance could produce new noxious weeds, if the genes spread to native species already capable of invading crop ecosystems. In fact, Mikkelsen et al. (1996) recently found in small plots that transgenic oilseed rape (*Brassica napus* L.) readily passed on glufosinate tolerance to its weedy relative *Brassica campestris* L. One of the worst weeds in the United States and the rest of the world, Johnsongrass [*Sorghum halepense* (L.) Pers.], could become even more difficult to control if herbicide genes were

allowed to escape from its partially compatible relative, sorghum [*S. bicolor* (L.) Moench]. To date, sorghum has not been engineered in the United States, but its agricultural importance makes it a logical candidate.

As far as we know, herbicide resistance has not been conventionally bred into crops, so there is no previous experience to guide us, but the introgression of other crop genes into natural populations has on occasion produced new noxious weeds through mimicry (Barrett, 1983). Weedy relatives of rice, millet, chenopod, teosinte, amaranths, and sorghum invade agricultural fields and look almost identical to their related crop species, until their inflorescences shatter just before harvest (Harlan et al., 1973; Sauer, 1967; Wilson and Heiser, 1979). There are weedy forms of wild oats, rye, and beet that are thought to have been the result of crop/congener introgression (Boudry et al., 1993; Chang, 1976; Hornsey and Arnold, 1979; Santoni and Berville, 1992; Sun and Corke, 1992; Suneson et al., 1969; Zohary, 1971).

It should be noted that even if immigrant genes are selectively disadvantageous, they can still become established in native species, if the recipient populations are very small or the rate of migration is very high (Ellstrand et al., 1989; Glidden, 1994; Jain and Bradshaw, 1966; Slatkin, 1985; Wright, 1969). One of the axioms of invasion biology is that invaders are more likely to succeed when they have a large founding population (Mooney and Drake, 1990). In fact, the importance of selection on population differentiation becomes almost insignificant when the migration rate is higher than or equal to the selection coefficient (Ellstrand and Marshall, 1985). Genes established in this manner could reduce the fitness of native populations and even lead to extinction. Rissler and Mellon (1993) have suggested that this swamping effect could result in the loss of potentially useful populations in some of the centers of diversity for food crops.

In summary, transgenes likely will move quickly from engineered crop species into natural ecosystems whenever populations of compatible relatives are in close proximity. In assessing the environmental risk of transgenes in crops with nearby relatives, the research emphasis should be placed on determining whether the transgene will be selectively advantageous in native populations and not whether it will escape. In the United States we only have about 10 native crop relatives into which transgenes can escape, but native relatives of all our crop species are found somewhere in the world. The risk of transgene escape via crop/congener hybridization must be considered when releasing transgenes to other countries where these native populations reside.

Literature Cited

- Anderson, E. 1949. Introgressive hybridization. Wiley, New York.
- Anderson, E. 1961. The analysis of variation in cultivated plants with special reference to introgression. *Euphytica* 10:79–86.
- Antonovics, J. 1971. The effects of a heterogeneous environment on the genetics of natural populations. *Amer. Naturalist* 59:593–599.
- Arias, D.M. 1994. Evolution of the domesticated sunflower, *Helianthus annuus* L. Asteraceae. PhD Diss., Claremont Graduate School, Claremont, Calif.
- Barrett, S.C.H. 1983. Crop mimicry in weeds. *Econ. Bot.* 37:255–282.
- Bergelson, J. 1994. Changes in fecundity do not predict invasiveness: A model study of transgenic plants. *Ecology* 75:249–252.
- Boudry, P., M. Mörchen, P. Saumitou-Laprade, Ph. Vernet, and H. VanDijk. 1993. The origin and evolution of weed beets: Consequences for the breeding and release of herbicide-resistant transgenic sugar beets. *Theor. Appl. Genet.* 87:471–478.
- Brown, J.H., R.K. Colwell, R.E. Lenski, B.R. Levin, M. Lloyd, P.J. Regal, and D. Simberloff. 1984. Report on workshop on possible ecological and evolutionary impacts of bioengineered organisms released into the environment. *Bul. Ecol. Soc. Amer.* 65:436–438.
- Brubaker, C.L., J.A. Koontz, and J.F. Wendel. 1993. Bidirectional cytoplasmic and nuclear introgression in the new world cottons, *Gossypium barbadense* and *G. hirsutum*. *Amer. J. Bot.* 80:1203–1208.
- Brunken, J., J.M.J. DeWet, and J.R. Harlan. 1977. The domestication and morphology of pearl millet. *Econ. Bot.* 31:163–174.
- Bullock, S.H. and R.B. Primack. 1977. Comparative experimental study of seed dispersal on animals. *Ecology* 58:681–686.
- Burrows, F.M. 1973. Calculation of the primary trajectories of plumed seeds in steady winds with variable convection. *New Phytol.* 72:647–664.
- Chang, T.T. 1976. The origin, evolution, dissemination and diversification of African and Asian rice. *Euphytica* 25:425–441.
- Chu, Y. and H. Oka. 1970. Introgression across isolating barriers in wild and cultivated *Oryza* species. *Heredity* 23:1–22.
- Clapham, A.R., T.G. Tutin, and D.M. Moore. 1987. *Flora of the British Isles*. Cambridge Univ. Press, Cambridge, U.K.
- Colwell, R. 1951. The use of radioactive isotopes in determining spore distribution patterns. *Amer. J. Bot.* 38:511–523.
- Colwell, R.K., E.A. Norse, D. Pimentel, F.E. Sharples, and D. Simberloff. 1985. Genetic engineering in agriculture. *Science* 229:111–112.
- Crawley, M.J., R.S. Hails, M. Rees, D. Kohn, and J. Buxton. 1993. Ecology of transgenic oilseed rape in natural habitats. *Nature* 363:620–623.
- Cruden, R.W. 1966. Birds as agents of long-distance dispersal for disjunct plant groups of the temperate western hemisphere. *Evolution* 20:517–532.
- Dale, P.J. 1992. Spread of engineered genes to wild relatives. *Plant Physiol.* 100:13–15.
- Darley-Hill, S. and W.C. Johnson. 1981. Acorn dispersal by the bluejay (*Cyanocitta cristata*). *Oecologia* 50:231–232.
- Decker-Walters, D., T. Andres, and T. Walters (eds.). 1995. "Texas gourd" becomes a weed problem in Mississippi cotton fields. *Cucurbit Network News* 2(1):4.
- DeJode, D.R. and J.F. Wendel. 1992. Genetic diversity and origin of the Hawaiian island cotton, *Gossypium tomentosum*. *Amer. J. Bot.* 79:1311–1319.
- Devlin, B. and N.C. Ellstrand. 1990. The development and application of a refined method for estimating gene flow from angiosperm paternity analysis. *Evolution* 44:248–259.
- DeWet, J.M.J. and J.R. Harlan. 1975. Weeds and domesticates: Evolution in the manmade habi-

- tat. Econ. Bot. 29:99–107.
- Doebley, J. 1990. Molecular evidence for gene flow among *Zea* species. *Bioscience* 40:443–448.
- Ehrlich, P.R. and P.H. Raven. 1969. Differentiation of populations. *Science* 165:1228–1232.
- Ellstrand, N.C. 1988. Pollen as a vehicle for the escape of engineered genes?, p. s30–s32. In: J. Hodgson and A.M. Sugden (eds.). *Planned release of genetically engineered organisms. Trends in biotechnology/trends in ecology and evolution special publication*. Elsevier Publications, Cambridge, U.K.
- Ellstrand, N.C., B. Devlin, and D.L. Marshall. 1989. Gene flow by pollen into small populations: Data from experimental and natural stands of wild radish. *Proc. Natl. Acad. Sci. USA* 86:9044–9047.
- Ellstrand, N.C. and C.A. Hoffman. 1990. Hybridization as an avenue of escape for engineered genes. *BioScience* 40:438–442.
- Ellstrand, N.C. and D.L. Marshall. 1985. Interpopulation gene flow by pollen in wild radish, *Raphanus sativus*. *Amer. Naturalist* 126:606–616.
- Ellstrand, N.C. and H.C. Prentice. 1994. Evaluating the opportunities for the escape of engineered crop genes. Final Rpt. Contract #97.0682/91. Uppsala Univ., Sweden.
- Ellstrand, N.C. and H.C. Prentice. 1995. Will transgenes escape into natural populations? *Amer. J. Bot.* 82:68. (Abstr.)
- George, R.A.T. 1985. *Vegetable seed production*. Longman, New York.
- Gleason, H.A. and A. Cronquist. 1963. *Manual of vascular plants of northeastern United States and adjacent Canada*. Van Nostrand Co., New York.
- Glidden, C. 1994. The impact of hybrids between genetically modified crop plants and their related species: Biological models and theoretical perspectives. *Mol. Ecol.* 3:41–44.
- Goy, P.A. and J.H. Duesing. 1996. Assessing the environmental impact of gene transfer to wild relatives. *Bio/Technology* 14:39–40.
- Hamrick, J.L. 1987. Gene flow and the distribution of genetic variation in plant populations, p. 53–66. In: K. Urbanska (ed.). *Differentiation patterns in higher plants*. Academic, London.
- Hancock, J.F. 1992. Plant evolution and the origin of plant species. Prentice-Hall, Englewood Cliffs, N.J.
- Handel, S.N. 1982. Dynamics of gene flow in an experimental population of *Cucumis melo* (Cucurbitaceae). *Amer. J. Bot.* 69:1538–1546.
- Handel, S.N. 1983a. Pollination ecology, plant population structure and gene flow, p. 163–211. In: L. Real (ed.). *Pollination biology*. Academic, Orlando, Fla.
- Handel, S.N. 1983b. Contrasting gene flow patterns and genetic subdivision in adjacent populations of *Cucumis sativus* (Cucurbitaceae). *Evolution* 37:760–771.
- Harlan, J.R. 1965. The possible role of weed races in the evolution of cultivated plants. *Euphytica* 4:173–176.
- Harlan, J.R. 1992. *Crops and man*. 2nd ed. Amer. Soc. Agron., Madison, Wis.
- Harlan, J.R., J.M. J. DeWet, and E.G. Price. 1973. Comparative evolution of cereals. *Evolution* 27:311–325.
- Harper, J.L. 1977. *Population biology of plants*. Academic, London.
- Heiser, G.B. 1978. Taxonomy of *Helianthus* and the origin of domesticated sunflower, p. 31–54. In: J.F. Carter (ed.). *Sunflower science and technology*. Amer. Soc. Agron., Crop Sci. Soc., and Soil Sci. Soc. Amer., Madison, Wis.
- Hokanson, S. 1995. Risk assessment of transgenic plants: Evaluation of border rows as a containment strategy for transgenic pollen and a comparison of pollen dispersal patterns for native and transgenes. PhD Thesis, Michigan State Univ., East Lansing, Mich.
- Hokanson, S., J.F. Hancock, and R. Grumet. 1996. Direct comparison of pollen-mediated movement of native and engineered genes. *Ecol. Applications* (In press).
- Hornsey, K.G. and M.H. Arnold. 1979. The origins of weed beet. *Ann. Appl. Biol.* 92:279–285.
- Hymowitz, T. and R.J. Singh. 1987. Taxonomy and speciation, p. 23–48. In: J.R. Wilcox (ed.). *Soybeans: Improvement, production and uses*. (revised). Amer. Soc. Agron., Madison, Wis.
- Jain, S.K. and A.D. Bradshaw. 1966. Evolutionary divergence among adjacent plant populations. I. The evidence and its theoretical analysis. *Heredity* 21:407–441.
- Jennings, D.L. 1988. *Raspberries and blackberries: Their breeding, diseases and growth*. Academic, London.
- Jorgenson, R.N. and B. Anderson. 1994. Spontaneous hybridization between oilseed rape (*Brassica napus*) and weedy *B. campestris* (Brassicaceae): A risk of growing genetically modified oilseed rape. *Amer. J. Bot.* 81:1620–1626.
- Kareiva, P., R. Manasse, and W. Morris. 1991. Using models to integrate data from field trials and estimate risks of gene escape and gene spread, p. 31–42. In: D.R. MacKenzie and S.C. Henry (eds.). *Biological monitoring of genetically engineered plants and microbes*. Agr. Res. Inst., Bethesda, Md.
- Keeler, K.H. 1985. Implications of weed genetics and ecology for the deliberate release of genetically-engineered crops. *Recombinant DNA Technol. Bul.* 8:165–172.
- Keeler, K.H. 1988. Can we guarantee the safety of genetically engineered organisms in the environment? *CRC Critical Rev. Biotechnol.* 8:85–97.
- Keeler, K.H. 1989. Can genetically engineered crops become weeds? *Bio/Tech.* 7:1134–1139.
- Kirkpatrick, K.J. and H.D. Wilson. 1988. Interspecific gene flow in *Cucurbita*: *C. texana* versus *C. pepo*. *Amer. J. Bot.* 75:519–527.
- Klinger, T., P.E. Arriola, and N.C. Ellstrand. 1992. Crop-weed hybridization in radish (*Raphanus sativus*): Effects of distance and population size. *Amer. J. Bot.* 79:1431–1435.
- Klinger, T., D.R. Elam, and N.C. Ellstrand. 1991. Radish as a model system for the study of engineered gene escape via crop-weed mating. *Conservation Biol.* 5:531–535.
- Klinger, T. and N.C. Ellstrand. 1994. Engineered genes in wild populations. Fitness of crop-weed hybrids of *Raphanus sativus*. *Ecol. Applications* 4(1):117–120.
- Kohn, J.R. and B.B. Casper. 1992. Pollen-mediated gene flow in *Cucurbita foetidissima* (Cucurbitaceae). *Amer. J. Bot.* 79:57–62.
- Lack, D. 1966. *Population studies of birds*. Oxford Univ. Press, London.
- Langevin, S.A., K. Clay, and J.B. Grace. 1990. The incidence and effects of hybridization between cultivated rice and its related weed red rice (*Oryza sativa*). *Evolution* 44:1000–1008.
- Lanner, R.M. and S.B. Vander Wall. 1980. Dispersal of limber pine seed by Clark's nutcracker. *J. For.* 78:637–639.
- Levin, D.A. 1981. Dispersal versus gene flow in plants. *Ann. Missouri Bot. Garden* 68:233–252.
- Levin, D.A. and H.W. Kerster. 1968. Local gene dispersal in *Phlox pilosa*. *Evolution* 22:130–139.
- Levin, D.A. and H.W. Kerster. 1974. Gene flow in seed plants, p. 139–220. In: Th. Dobzhansky, M. Hecht, and W. Steere (eds.). *Evolutionary biology*. Vol. 7. Plenum Press, New York.
- Luby, J.J. and R.J. McNicol. 1995. Gene flow from cultivated to wild raspberries in Scotland: Developing a basis for risk assessment for testing and deployment of transgenic cultivars. *Theor. Appl. Genet.* 90:1133–1137.
- Manasse, R. 1992. Ecological risks of transgenic plants: Effects of spatial dispersion on gene flow. *Ecol. Applications* 2:431–438.
- Mikkelsen, T.R., B. Anderson, and R.B. Jorgensen. 1996. The risk of transgene spread. *Nature* 380:31.
- Mooney, H.A. and J.A. Drake. 1990. The release of genetically designed organisms in the environment: Lessons from the study of the ecology of biological invasions, p. 117–127. In: H.A. Mooney and G. Bernardi (eds.). *Introduction of genetically modified organisms into the environment*. SCOPE 44. John Wiley and Sons, Chichester, U.K.
- Moore, P. 1976. How far does pollen travel? *Nature* 260:280–281.
- Muller, P. 1955. Verbreitungsbiologie der Blütenpflanzen. *Verh. Geobot. Inst. Zurich. Publ.* 30.
- Munz, P.A. and D.D. Keck. 1973. *A California flora*. Univ. of California Press, Berkeley.
- Oka, H.I. and W.T. Chang. 1961. Hybrid swarms between wild and cultivated rice species, *Oryza perennis* and *O. sativa*. *Evolution* 15:418–430.
- Palmer, J.D., C.R. Shields, D.B. Cohen, and T.J. Orton. 1983. Chloroplast DNA and the origin of amphiploid *Brassica* species. *Theor. Appl. Genet.* 65:181–189.
- Radford, A.L., H.E. Ahles, and C.R. Bell. 1968. *Manual of the vascular flora of the Carolinas*. The Univ. of North Carolina Press, Chapel Hill.
- Raybold, A.F. and A.J. Gray. 1993. Genetically modified crops and hybridization with wild relatives: A U.K. perspective. *J. Appl. Ecol.* 30:199–219.
- Rees, M., D. Kohn, R. Hails, M. Crawby, and S. Malcolm. 1991. An ecological perspective to risk assessment, p. 9–24. In: D.R. MacKenzie and S.C. Henry (eds.). *Biological monitoring of genetically engineered plants and microbes*. Agr. Res. Inst., Bethesda, Md.
- Regal, P.J. 1988. The adaptive potential of genetically engineered organisms in nature. *TIBTECH* 6:36–38.
- Rissler, J. and M. Mellon. 1993. Perils amidst the promise: Ecological risks of transgenic crops in a global market. Union of Concerned Scientists, Cambridge, Mass.
- St. Pierre, M.D. and R.J. Bayer. 1991. The impact of domestication on the genetic variability in the orange carrot, cultivated *Daucus carota* ssp. *sativus* and the genetic homogeneity of various cultivars. *Theor. Appl. Genet.* 82:249–253.
- Salisbury, E.J. 1961. *Weeds and aliens*. Collins, London.
- Santoni, S. and A. Berville. 1992. Evidence for gene exchange between sugar beet *Beta vulgaris* L. and wild beets: Consequences for transgenic sugar beets. *Plant Mol. Biol.* 20:578–580.
- Sauer, J.D. 1967. The grain amaranths and their relatives—A revised taxonomic and geographic survey. *Ann. Missouri Bot. Garden* 54:103–137.
- Sheldon, J.C. and F.M. Burrows. 1973. The dispersal effectiveness of the achene pappus units of selected Compositae in steady winds with convection. *New Phytol.* 72:665–675.
- Simonsen, L. and B.R. Levin. 1988. Evaluating the risk of releasing genetically engineered organisms. *TIBTECH* 6:27–30.
- Singh, R.J. and T. Hymowitz. 1988. The genomic relationship between *Glycine max* (L.) Merr. and *G. soya* Sieb. and Zucc. as revealed by

- pachytene chromosome analysis. *Theor. Appl. Genet.* 76:705–711.
- Slatkin, M. 1985. Gene flow in natural populations. *Ann. Rev. Ecol. Systematics* 16:393–430.
- Smartt, J. and N.W. Simmonds. 1995. *Evolution of crop plants*. Longman Scientific and Technical, Essex, England.
- Stace, C.A. 1975. *Hybridization and the flora of the British Isles*. Academic, London, U.K.
- Stace, C.A. 1991. *New Flora of the British Isles*. Cambridge Univ. Press, Cambridge, U.K.
- Sun, M. and H. Corke. 1992. Population genetics of colonizing success of weedy rye in northern California. *Theor. Appl. Genet.* 83:321–329.
- Suneson, C.A., K.O. Rachie, and G.S. Khush. 1969. A dynamic population of weedy rye. *Crop Sci.* 9:121–124.
- Tiedje, J.M., R.K. Colwell, Y.L. Grossman, R.E. Hodson, R.E. Lenski, R.N. Mack, and P.J. Regal. 1989. The planned introduction of genetically engineered organisms: Ecological considerations and recommendations. *Ecology* 70:298–315.
- Till-Bottraud, I., X. Reboud, P. Brabant, M. Lefranc, B. Rherissi, F. Vedel, and H. Darmency. 1992. Outcrossing and hybridization in wild and cultivated foxtail millets: Consequences for the release of transgenic crops. *Theor. Appl. Genet.* 83:940–946.
- Urgent, D. 1970. The potato. *Science* 170:1161–1166.
- Wendel, J.F., C.L. Brubaker, and A.E. Percival. 1992. Genetic diversity in *Gossypium hirsutum* and the origin of upland cotton. *Amer. J. Bot.* 79:1291–1310.
- Wijnheijmer, E.H.M., W.A. Brandenburg, and S.J. Ter Borg. 1989. Interactions between wild and cultivated carrots (*Daucus carota* L.) in the Netherlands. *Euphytica* 40:147–154.
- Williamson, M. 1988. Potential effects of recombinant DNA organisms on ecosystems and their components. *TIBTECH* 6:32–35.
- Wilson, H.D. and C.B. Heiser. 1979. The origin and evolutionary relationships of 'Hauzontle' (*Chenopodium nutalliae*) domesticated chenopod in Mexico. *Amer. J. Bot.* 66:198–206.
- Wilson, H. and J. Manhart. 1993. Crop/weed gene flow: *Chenopodium quinoa* Willd. and *C. berlandieri* Moq. *Theor. Appl. Genet.* 86:642–648.
- Wright, S. 1969. *Evolution and genetics of populations*. vol. 2. Univ. of Chicago Press, Chicago.
- Yang, N-S. 1988. Genotypic and phenotypic changes in plant varieties. *TIBTECH* 6:21–23.
- Zhu, T., L. Shi, J.J. Doyle, and P. Keim. 1995. A single nuclear locus phylogeny to soybean based on DNA sequence. *Theor. Appl. Genet.* 90:991–999.
- Zohary, D. 1971. Origin of south-west Asiatic cereals: Wheats, barley, oats and rye, p. 235–263. In: P.H. Davis, P.T. Harper, and I. Hedge (eds.). *Plant life of south-west Asia*. Bot. Soc. of Edinburgh, U.K.
- Zohary, D.E. 1976. Colonizer species in the wheat group, p. 403–412. In: H.G. Baker and G.L. Stebbins (eds.). *The genetics of colonizing species*. Academic, New York.
- Zohary, D. and M. Hopf. 1993. *Domestication of plants in the old world*. Clarendon Press, Oxford, U.K.