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Chapter **20**

MOVEMENT OF CROP TRANSGENES INTO WILD PLANTS

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CONTENTS

1. INTRODUCTION

The technology of genetic engineering is introducing a wide variety of traits into crop plants. One of the first to be field tested is herbicide resistance. Field trials show that herbicide resistance can be a dramatically effective agricultural tool, allowing the crops to survive while general-purpose herbicides of low toxicity and persistence remove or significantly reduce competing weeds (Chapters 14 and 15). Despite these benefits, problems with this technology can be anticipated. Some of these are considered elsewhere in this book. In this chapter we discuss the problems of herbicide- resistant weeds (HRWs) and how these might arise from the widespread development and employment of herbicide-resistant crops (HRCs).

Concern has been expressed over the inadvertent development of HRWs that are harder to control than present weeds (Hauptli et al. 1985; Keeler and Turner 1991; Dyer et al. 1993). This can occur either by the HRC itself becoming a weed where it is not specifically cultivated, or by existing weeds receiving herbicide-resistant genes (HRGs) from a HRC via gene flow, leading to greater difficulty controlling these weeds. In this chapter we mention possible problems from increased weediness attained by HRCs, but focus particularly on the role of gene flow to weedy wild relatives as a potential problem (Keeler and Turner 1991; Dyer et al. 1993), because that is a matter of far greater concern. Other possible weed problems are discussed elsewhere in this book and in Keeler and Turner (1991).

Escape of herbicide resistance should not be regarded as a problem in and of itself. Escape is a problem only if this leads to undesirable consequences. Problems are unlikely in habitats where herbicides are not used, because in the absence of herbicide applications, herbicide-resistant plants will have no particular selective advantage. In heavily herbicided environments, however, herbicide resistance will favor the survival of HRWs, potentially creating a new set of weed problems.

Not all consequences are equally serious. While the most desirable outcome is a crop that survives herbicide application and makes absolutely no contribution to weed populations, many other alternatives are tolerable. For example, a transgenic weed that is resistant to the herbicide of choice but is controllable by alternate methods, e.g., mechanically, does not greatly decrease the usefulness of the resistant crop. Even when a HRW spreads, if it is less costly to control than the plants killed by the herbicide, there is a net gain. While we probably cannot evaluate and weigh these alternatives quantitatively, they are part of all decisions to develop or market a crop, and part of the U.S. Environmental Protection Agency's regulation of plant pesticides under the Federal Insecticide, Fungicide and Rodenticide Act (FIFRA). Every action, including inaction, represents a decision, so all parties are best served by well-considered decisions and actions.

Precise predictions are not possible. We have only incomplete information at present, but even if we knew much more about the interaction of weeds with HRCs, some predictions would fail because the system is dynamic: Ecosystems are continually changing and the resident organisms evolving, so that a novel genotype–environment interaction is always possible. In addition, while

many HRGs occur in nature, some transgene–plant combinations are, or will be, unique. Changing environments and organismal evolution could confound any prediction.

Herbicide resistance confers survival in the presence of substances that otherwise cause severe reduction of plant growth or death. For the purpose of evaluating environmental consequences, the mode of action is less important than the functional phenotype. If the genes produce a herbicide-resistant phenotype, the application of that herbicide will produce strong selection favoring HRWs, including hybrids that received resistance genes from the crop.

We assume for the purposes of this chapter that the only effect of the herbicide resistance gene (and the facilitating DNA introduced as part of the construct) is herbicide resistance, and that it is the only way in which weeds receiving the introduced gene will differ from other local weeds. Thus, we do not consider problems that might arise when there are pleiotropic effects of the inserted genes or genes that alter the phenotype in several ways (e.g., a combined herbicide/virus/pest resistance package). However, accurate risk assessment must include these complex effects (Dyer et al. 1993; see also Chapters 25 and 26). To further simplify our analysis here, our focus is on the U.S.

2. HERBICIDE-RESISTANT WEEDS

2.1. WEED DEFINITIONS

Herbicide-resistant crops have the potential to lead to "worse weeds." "Weed" is a familiar term about which there is much debate as to definition and meaning. The basic, working definition of weed seems to be "a plant in the wrong place," a plant whose presence is objectionable to someone. Trying to cast this into an objective definition, however, has proven quite difficult (e.g., Salisbury 1961; Bucholtz 1967; Perrins et al. 1992a, b). Basically, the concept of a weed is an anthropocentric construction, and thus essentially subjective in nature. Plants may be weeds for quite diverse reasons. They may interfere with human activities because of rapid growth or because, although slow growing, they are hard to remove, or be neither of the above, but are unpalatable or poisonous to livestock. When considering possible weeds of herbicide-resistant cultivated plants, this is a very important point. If biotechnology produces a plant that interferes with someone or something, it has produced a weed, regardless of the taxonomic identity of the species.

2.2. WEED SEVERITY

Plants which are never unwanted are never weeds. There must be species in this category, but they are few. At the other extreme of this spectrum are plants that are unwelcome in most places in which they occur, and that are therefore considered weeds almost universally. For example, cocklebur (*Xanthium strumarium*), a spiny weed of 11 crops in 28 countries with foliage toxic to livestock, is likely to have very few proponents (Holm et al. 1977).

By the definition above, major and especially minor weeds abound. However, no one is going to spend much time or money removing minor weeds. The weeds of chief interest here are species with major economic or environmental impact. For this sort of weed it is easy to find agreement that they should be controlled. In the economic sphere a functional approach to determining that a weed presents a serious problem can be found in its economic impact. Holm et al. (1977) rated the "world's worst weeds" by determining which weeds were problems in the most crops in the most countries, the record being 52 crops in 92 countries (purple nutsedge, *Carex rotundata*). Plants creating problems to multiple crops in multiple countries are clearly serious weeds. Thus, a gradient exists from plants that never bother anyone to interference that dramatically reduces the productivity of major areas of cropland or rangeland. It is most critical to not genetically enhance the plants at the most damaging end of the weed spectrum.

2.3. LINES OF EVIDENCE

To predict the environmental impact of a transgenic crop requires a number of assumptions, none of which actually apply. These assumptions include:

1. the plants will always be responsibly handled
2. the plants will not evolve
3. land use patterns, e.g., agricultural and pasturage systems, will not change significantly
4. human uses of plants will remain the same
5. human evaluation of the worth of different species will remain stable
6. the distribution of people and the way they use the land (e.g., urban/rural) will be stable

Given these assumptions, one way to predict outcome is to gather information based on our historical experience with crops, weeds, and herbicide resistance to determine the relative probabilities of problems.

Science works best from well-controlled, experimental tests of ideas. For transgenic herbicide resistance plants, these do not currently exist, the PROSAMO experiment being a notable exception (Crawley et al. 1993; see also Miller and Gunary 1993). In the absence of adequate experimental evidence we look to other sources of information. All of these must be evaluated for what they can and cannot tell us about transgenic plants.

2.3.1. Cultivated Plants

The record of the cultivated plants into which the genes are inserted provide insight into the behavior of the same plant with herbicide resistance. This is true because only a few genes are being introduced into a large genome and breeders will try to make a transgenic plant that is as much like successful varieties as possible. While more extensive transgenic constructs may be present in the crops of the future, by then we will have field data on our present transgenics to use to evaluate those crops.

2.3.2. Herbicide Resistance Genes

Rather than being just an area of theoretical concern, there have however, been real problems in the field from the evolution of weeds resistant to herbicides. For example, sulfonylurea-resistant populations of prickly lettuce (*Lactuca serriola*), kochia (*Kochia scoparia*), and Russian thistle (*Salsola* sp.) are reducing the utility of sulfonylurea herbicides in and around winter wheat and along roadsides in the northwestern U.S. (Mallory-Smith et al. 1990; Alocer-Ruthling et al. 1992; Thompson et al. 1994; Stallings et al. 1994; Saari et al. 1994; also Chapter 8).

2.3.3. Environment

There is no consensus about the invasibility of environments. Species sometimes invade even intact and apparently healthy natural ecosystems, but stressed or disturbed systems are particularly vulnerable (e.g., croplands, roadsides, and overgrazed rangeland) (Mooney and Drake 1986). Fortunately, many disturbed sites, such as field edges, are easily managed for weed control.

Many of the events which can lead to the escape of transgenes are low probability events. Thus, watching for them at any particular site is likely to fail, but across a large area, they are more likely to occur. Their impact, however, depends on a complex set of local events.

Events with a general low probability can be greatly enhanced by natural selection. Thus, the emergence of herbicide-resistant phenotypes, while still improbable in any particular location, is significantly enhanced by the selection pressure created by the application of herbicides in the area. Except for the occasional case of cross-resistance, this is herbicide specific. Glyphosate resistance can be expected where glyphosate is applied, imidizolinone resistance, not glyphosate resistance,

where imidizolinone is applied. These patterns increase our ability to monitor effectively for the emergence of HRWs.

2.3.4. Lessons from Introduced Species

Experience with introduced species, naturalized species from a different part of the world, has been used frequently to provide information about the behavior of transgenics (e.g., Sharples 1983, Keeler 1985, Tiedje et al. 1989). This has the following justifications:

1. Transgenics are perceived as potentially having novel interactions in an ecosystem, similar to the novel interactions of introduced species.
2. Population growth of naturalized transgenics may parallel the growth of introduced species from low initial numbers to outbreak populations
3. Introduced species produced some of the best data sets on change in number over time and invasion of new environments.
4. Control of introduced species provide some of the clearest studies of the factors that determine plant success.

However, information from introduced species must be treated carefully because these plants are outside their native range and have escaped adapted parasites, diseases, and predators. Transgenics may or may not be outside their range and free of specialist natural enemies. A given HRW is likely to be afflicted by the same consumer pests as those attacking the HRC relative. Furthermore, because they are virtually identical to a crop, most of their herbicide interactions can be readily predicted by the crop to which the HRGs were added. In contrast, an introduced species may have less predictable impact.

2.3.5 Predictions of Experts

Any plant that most weed scientists agree is likely to be a serious weed is just that. Predictive power for this category is excellent. This is based largely on knowledge of which plants are weedy somewhere in the world: the best predictor of whether a plant is potentially weedy here is that it is weedy somewhere else. There are lists of plants that are considered potential threats to U.S. agriculture (Zimdahl 1983), and noxious weed lists of weeds legally barred from entry to parts of the world where they do not currently occur (Foy et al. 1983). These plants are likely to produce further weed problems if provided with herbicide resistance; some already have it.

At the other extreme are plants for which almost no one would anticipate the development of weed problems. This group is probably also sound predictively. Note, however, that one would experience greater unhappiness if surprised by a weed from this group than if one of the noxious weeds fails to expand when introduced to a new site. A failure to predict weediness is more serious than a prediction of weediness that fails.

There remain many species for which there is no consensus on their potential for weediness (e.g., Perrins et al. 1992a, b). For these plants, experimental studies are essential. Expansion of our understanding of the genetics and ecology of weediness should have the most impact on this group. For the present, release of HRCs in this category must be treated on a case-by-case basis.

3. GENERATION OF HERBICIDE-RESISTANT WEEDS

As noted above, herbicide resistance may contribute to weed problems either by increased weediness of the crop or by escape of the resistance genes to compatible weedy relatives. The trait is then problematic or does not depend on whether herbicides are a potent selective factor in the environment of the resistant plants. We consider these problems below.

3.1. HERBICIDE-RESISTANT CROPS AS WEEDS

This alternative is rarely considered in detail because most of the major crops (e.g., corn, soybeans, wheat) are rarely, if ever, seen as weeds, and are readily controlled if they escape (Harlan 1965; and see also Table 1). These assumptions about the behavior of crops are less clearly valid in aseasonal climates, for crops recently domesticated, and for cultivated plants not grown as annual row crops. There are, unfortunately, many plants deliberately introduced as ornamentals, forage plants, or for soil stabilization (i.e., outside a row crop environment) that have become agggressive weeds. Some well-known examples include bermudagrass (*Cynodon dactylon*), Scotch broom (*Cytisus scoparius*), lantana (*Lantana camara*), Dalmatian toadflax (*Linaria dalmatica*), Japanese honeysuckle (*Lonicera japonica*), kudzu (*Pueraria montana* var. *lobata*), multiflora rose (*Rosa multiflora*), and Brazilian peppertree (*Schinus terebinthifolius*) (Foy et al. 1983; Turner 1988).

3.2. ESCAPE OF HERBICIDE RESISTANCE GENES TO WILD RELATIVES

We focus chiefly on weedy wild relatives because compatible wild plants that are already weedy constitute the greatest weed threats. If HRGs move from crops to wild relatives in the area, there is immediate potential for a serious weed problem because (1) herbicide resistance in the crop is likely to be accompanied by application of the herbicide, generating selection for the resistance, and (2) if the wild relatives were effective weeds before becoming herbicide resistant, they will be even more difficult to control as HRWs. This has the potential to significantly reduce the utility of the herbicide resistance trait and the herbicide.

With only rare exceptions, all our crops have wild relatives somewhere in the world, so escape of the transgenes is a strong possibility somewhere. The necessary conditions for the movement of an HRG from an HRC to a wild plant through pollen flow is as follows: dispersal of viable herbicide-resistant pollen from the HRC; interfertility between the HRC and a wild relative, leading to viable hybrids; and opportunity to cross, which is the presence of crop and weed in sufficiently close proximity that viable pollen reaches the compatible wild population.

3.2.1 Dispersal of Viable Pollen

Transgenes can only reach weed populations if carried to weeds on viable pollen. If the crop produces no pollen or no viable pollen, there will be no gene flow. Whatever the abundance and distribution of their compatible weedy relatives, such crops will not produce HRW populations.

This covers most, but not quite all, conditions. It is conceivable that an abandoned HRC plant could be fertilized by pollen from wild relatives and serve as the pistillate (female) parent for a hybrid seed. The hybrid seed, germinating under favorable conditions, might subsequently found (establish) a new, resistant population. For this to occur, the pistillate parent HRC would have to escape harvesting, and its hybrid seeds would have to survive to germinate, grow, and reproduce. In a cropland environment the conditions for this are sufficiently restrictive that we will not consider it further.

The potential for gene flow via pollen depends on three primary factors: (1) the amount of pollen produced, (2) the longevity of the pollen, and (3) the means of pollen transport. Secondarily it may be affected by selection on any genes expressed in the recipient gametophyte.

The amount of pollen produced per plant varies over several orders of magnitude, from tens of grains in some water-pollinated or cleistogamous (closed-flowered) species, to billions of grains in some wind-pollinated species (Stanley and Linskens 1974; Faegri and Iverson 1975; Frankel and Galun 1977). In general, wind-pollinated species (Table 2) produce the greatest amounts of pollen, followed by outcrossing species with animal pollinators (Table 3), and finally species that are facultative or obligate inbreeders (Table 4) producing the least pollen (Faegri and Iverson 1975; Cruden 1977). Studies of different varieties of crop species show genetic variation in the amount of pollen produced (Oberle and Goertzen 1952; Beri and Anand 1971; cited in Frankel and Galun

TABLE 1 Weediness of 60 Herbaceous U.S. Crop Plants[a]

Crop Name	Weedy?	Location and Severity if Weedy[b,c]
Apiaceae/Umbelliferae		
Apium graveolens, celery	No	
Daucus carota, carrot	Yes	S: 1 Af, 1 CAm, USA; C: 8, incl. Can; X: 22 other countries
Pastinaca sativa, parsnip	Yes	C: Arg, Can, Sov; X: 2 SAm, NZ, USA
Petroselinum sp. parsley	No	
Asteraceae/Compositae		
Carthamus tinctorius, safflower	Yes	X: Turkey
Cichorium endivia, endive, escarole	Yes	S: Egypt
Cynara scolymus, artichoke	No	*Note: C. cardunculus* S: Arg, Aus, USA; hybridizes freely with *C. cardunculus;* some taxonomists consider them conspecifics
Helianthus annuus, sunflower	Yes	S: Mx, USA; P: Arg
H. tuberosus, sunchoke, Jerusalem artichoke	Yes	X: USA
Lactuca sativa, lettuce	No	
Brassicaceae/Cruciferae		
Brassica rapa var. *rapa* oilseed rape/turnip	Yes	S: Can, 2 SAm, 3 CAm; P: 3 Eu, 4 SAm, 1 CAm, 1Af, NZ; C: 10 countries, HA 2 Eu, Aus Jpn 2Af; X: 16 other countries
B. napus, oilseed rape, rutabaga, swede	Yes	P: USA
B. oleracea, broccoli, Brussels sprouts, cabbage, cauliflower, collards, kale, kohlrabi	No	Its apparent progenitor, *B. maritima,* is not considered weedy either
Raphanus sativus, radish	Yes	P: Arg
Rorippa nasturtium-aquaticum (*Nasturtium officinale*), watercress	Yes	C: 3 A, 1 Eu, USA
Chenopodiaceae		
Beta vulgaris, beet, sugarbeet	Yes	S: Egypt; X: USA
Spinacia oleracea, spinach	No	
Convolvulaceae		
Ipomoea batatas, sweet potato	Yes	C: Taiwan; X: 1 A, 1 CAm
Cucurbitaceae		
Citrullus lanatus, watermelon	Yes	C: 2 Oc

TABLE 1 (continued) Weediness of 60 Herbaceous U.S. Crop Plants[a]

Crop Name	Weedy?	Location and Severity if Weedy[b,c]
Cucumis melo, melon	Yes	P: 1 SAm
Curcumis sativus, cucumber	Yes	C: Aus; X: 2 A
Cucurbita maxima, squash	No	
Curcurbita moschata, squash	No	
Cucurbita pepo, pumpkin, summer squash	Yes	X: 1 Car, 1 Oc
Euphorbiaceae		
Ricinus communis, castor, castor bean	Yes	P: 1 Af, USA; C: 1 A, 1 Oc, 2 CAm, 4 Af, HA; X: 36 other countries
Fabaceae/Leguminosae		
Arachis hypogaea, peanut	Yes	C: Taiwan
Cicer arietinum, chickpea, garbanzo	No	Unknown in wild
Glycine max, soybean	No	
Lens culinaris (L. esculenta), lentil	No	
Medicago sativa, alfalfa	Yes	P: Aus; C: 1 Eu, 2 A; X: 2 A, 1 Oc, USA
Phaseolus lunatus, lima bean	Yes	X: USA
Phaseolus vulgaris, French bean	No	
Pisum sativum, pea	No	Unknown in wild
Vicia faba, broad bean	Yes	P: 1 Af; C: 1 A
Liliaceae		
Allium ampeloprasm, leek	Yes	C:1 Eu, 1 A
Allium cepa, onion	Yes	C: 1 Eu
Allium sativum, garlic	Yes	X: CAm
Asparagus officinalis, asparagus	Yes	C: 1 Eu; X: 1 Oc
Linaceae		
Linum usitatissimum, flax	Yes	P:USA, X: 1 SAm, 2 A, Aus
Malvaceae		
Gossypium hirsutum, cotton	No	
Abelmoschus esculentus (= Hibiscus esculentus), okra	Yes	C: 1 Af; X: 1 Af, 2 A

TABLE 1 (continued) Weediness of 60 Herbaceous U.S. Crop Plants[a]

Crop Name	Weedy?	Location and Severity if Weedy[b,c]
Poaceae/Gramineae		
Avena sativa, oats	Yes	P: Arg
Hordeum vulgare, barley	Yes	C: USA
Oryza sativa, rice	Yes	S: 2 SAm, 2 As, 1 CAm, 1 Af, USA; P: 1 Af, 1 SAm; C: 1 Oc, 1A; X: 17 other countries; taxonomic debates put red rice (variously *O. rufipogon* and *O. sativa* var. *rufipogon*) in and out of *O. sativa;* in any event, they hybridize
Panicum miliaceum, millet	Yes	P: 1 A, USA; X: Med
Pennisetum glaucum, pearl millet	No	
Saccharum officinarum, sugarcane	Yes	C: Taiwan
Secale cereale, rye	Yes	P: USA; C: 1 SAm, 1 Eu, 1 A; X: 1A, USA; weedy annual *Secale* sp. are considered *S. cereale* by some authors (Simmonds 1976)
Sorghum bicolor, sorghum	Yes	S: USA (shattercane is a weedy race of the crop)
Triticum aestivum, bread wheat	Yes	C: USA; X: Nepal
Triticum turgidum, durum wheat	No	
Zea mays, maize, corn	Yes	C: USA
Polygonaceae		
Rheum rhaponticum, rhubarb	No	
Solanaceae		
Capsicum annuum, bell pepper, chili pepper, green pepper, paprika, red pepper, sweet pepper	Yes	X: Aus, 1 A
Capsicum annuum var. *frutescens,* chili pepper, pepper, tabasco	Yes	X: 1 A, 1 CAm, 1 Oc, 1 Af
Lycopersicon esculentum, tomato	Yes	C: 1 A; X: 1 CAm, USA; the weedy tomato is *L. esculentum* var. *ceratiforme, the* cherry tomato
Nicotiana tabacum, tobacco	Yes	C: HA
Solanum melongena, aubergine, eggplant	Yes	X: 1 A
Solanum tuberosum, potato, white potato	Yes	S: USA; C: 1 Eu

[a] Major sources: Crockett 1977; Holm et al. 1979; Schery 1972; Bridges 1992.

[b] Locations: NAm = North America, CAm = Central America, SAm = South America, A = Asia, Af = Africa, Eu = Europe, Oc = Oceania, USA = United States, Sov = former Soviet Union, Can = Canada, HA = Hawaii, Med = countries around the Mediterranean Sea, Mx = Mexico, Arg = Argentina, Aus = Australia, NZ = New Zealand, Jpn = Japan, Car = countries around the Caribbean Sea.

[c] Severity of weed problem: S = serious, P = principal, C = common, X = present and weedy, but importance uncertain (after Holm et al. 1979), S = troublesome weed of several crops and states, P = troublesome weed of a few or one crop or state, C = common weed, as listed in Bridges (1992).

1977). Superimposed on this genetic variation is ecological variation that results from differences in year-to-year conditions. Soloman (1979) reported that standard deviations are normally 80% of mean production values. There is also site-to-site variation that influences the overall vigor of the plant, and plant density effects that result in isolated plants producing more pollen than those growing in more dense stands (Faegri and Iverson 1975).

As pollen completes development in the anther, it loses water and becomes dormant (Dumas et al. 1986; Hoekstra 1992; Hoekstra et al. 1992). Successful germination and fertilization depend on controlled rehydration to break dormancy. The degree of dehydration that induces dormancy is a variable that is a predictor of pollen longevity. Most pollen is shed in a highly desiccated state with a water content of between 4 and 20% (Platt-Aloia et al. 1986; Luza and Polito 1987). Some species, such as those in the Poaceae and Cucurbitaceae, have pollen that have a much higher water content (>40%) and a higher susceptibility to death by dehydration (Kerhoas et al. 1986, 1989; Hoekstra 1992). The life span of these pollen grains is measured in hours rather than days or weeks.

A second generalization applicable to predicting pollen life span is that pollen that undergoes mitosis to form the sperm before it is released from the anther (trinucleate pollen) has a faster metabolism and shorter life span than pollen that divides to produce the sperm after germination on the stigma (binucleate pollen) (Brewbaker 1967). Trinucleate pollen is found in about 30% of angiosperms (Hoekstra and Bruinsma 1978) (see Tables 2, 3, and 4). In contrast to the grasses (trinucleate, higher water content), fruit tree pollen (binucleate, lower water content) often survives for 1 week or more, and pine and date pollen are reported to survive for as long as 1 year when stored indoors under "natural conditions" (Frankel and Galun 1977). Under true field conditions, most pollen probably remains viable for 1 d or less (Soloman 1979; Hoekstra 1992).

The functional longevity of pollen also can be limited by pollinators. For example, ants and honey bees both secrete substances that inhibit pollen germination, so that pollen that has been in contact with an ant or in the cobiculas of bees for >24 h rarely germinates (Faegri and van der Pijl 1979, Hull and Beattie 1988). Pollen

TABLE 2   Outbreeding, Wind-Pollinated Economic Plants

Scientific Name	Common Name
Beta vulgaris	Beet (3n)[a,c]
Ceratonia siliqua	Carob
Ricinus communis	Castor
Cocos nucifera	Coco palm (2n)[b]
Corylus spp.	Hazelnut (2n)[b]
Humulus lupulus	Hop (2n)[b]
Morus alba, M. nigra	Mulberry (2n)[b]
Zea mays	Maize (3n)[a,c]
Olea europaea	Olive (2n)[b]
Pennisetum glaucum	Pearl millet (3n)[a,c]
Carya illinoinesis	Pecan
Pistacia vera	Pistachio
Populus spp.	Poplar (2n)[b]
Secale cereale	Rye (3n)[a,c]
Spinacea oleracea	Spinach (3n)[a,c]
Saccharum robustum, S. spontaneum, S. sinense S. officinarum	Sugarcane[a]
Juglans regia	Walnut

[a]   Family known to have trinucleate pollen.
[b]   2n, Genus or species known to have binucleate pollen.
[c]   3n, Genus or species known to have trinucleate pollen.

From Brewbaker 1967; Frankel and Galun 1977.

TABLE 3 Outbreeding, Animal-Pollinated Economic Plants

Scientific Name	Common Name
Allium porrum	Leek (2*n*)[a]
A. schoenoprasum	Chives (2*n*)[a]
A. cepa	Onion (2*n*)[a]
Ananas comosus	Pineapple (2*n*)[a]
Asparagus officinalis	Asparagus
Brassica oleracea	Cabbage, kale (3*n*)[b,c]
B. napus	Swedes, rapes (3*n*)[b,c]
B. rapa var. *rapa*	Turnip (3*n*)[b,c]
Carthamus tinctorius	Safflower[c]
Castanea spp.	Chestnut (2*n*)[a]
Citrullus lanatus	Watermelon
Cucumis melo	Melon (2*n*)[a]
C. sativus	Cucumber (2*n*)[a]
Cucurbita spp.	Squash (2*n*)[a]
Daucus carota	Carrot[c]
Diospyros kaki	Persimmon (2*n*)[a]
Fragaria ananassa	Strawberry (2*n*)[a]
Helianthus annuus	Sunflower (3*n*)[b,c]
H. tuberosus	Jerusalem artichoke (3*n*)[b,c]
Ipomoea batatas	Sweet potato (3*n*)[b,c]
Malus pumila	Apple (2*n*)[a]
Medicago sativa	Alfalfa (2*n*)[a]
Mentha piperita	Peppermint
Persea americana	Avocado (2*n*)[a]
Petroselium sp.	Parsley[c]
Prunus spp.	Cherry (2*n*)[a]
Prunus	Plum (2*n*)[a]
P. dulcis	Almond (2*n*)[a]
Pyrus communis	Pear
Raphanus sativus	Radish (3*n*)[b,c]
Rosa spp.	Rose (2*n*)[a]
Rubus spp.	Raspberry
Theobroma cacao	Cacao (2n)[a]

[a] (2*n*) Genus or species known to have binucleate pollen.
[b] (3*n*) Genus or species known to have trinucleate pollen.
[c] Family known to have trinucleate pollen.

From Brewbaker 1967; Frankel and Galun 1977.

TABLE 4 Normally Inbreeding Economic Plants

Scientific Name	Common Name
Abelmoschus esculentus	Okra
Apium graveolens	Celery[a]
Arachis hypogaea	Peanut
Avena spp.	Oat (3*n*)[a,c]
Capsicum annuum	Pepper (2*n*)[b]
Cicer arietinum	Chick pea
Citrus spp.	Citrus (2*n*)[b]
Glycine max	Soybean
Gossypium arboreum, G. barbadense, G. herbaceum, G. hirsutum	Cotton (2*n*)[b]

TABLE 4   (continued) Normally Inbreeding Economic Plants

Scientific Name	Common Name
Hordeum vulgare	Barley[a]
Lactuca sativa	Lettuce (3*n*)[a,c]
Lens culinaris	Lentil
Linum usitatissimum	Flax (3*n*)[a,c]
Lycopersicon esculentum	Tomato (2*n*)[b]
Nicotiana rusticua, N. tabacum	Tobacco (2*n*)[b]
Oryza sativa	Rice[a]
Panicum miliaceum	Proso millet[a]
Pastinaca sativa	Parsnip[a]
Phaseolus lunatus	Lima bean (2*n*)[b]
Pisum sativum	Pea (2*n*)[b]
Prunus persica	Peach/nectarine (2*n*)[b]
P. armeniaca	Apricot (2*n*)[b]
Sesamum orientale	Sesame (2*n*)[b]
Solanum melongena	Eggplant (2*n*)[b]
S. tuberosum	Potato (2*n*)[b]
Sorghum bicolor	Sorghum[a]
Triticosecale	Triticale[a]
Triticum spp.	Wheat (3*n*)[a,c]
Vicia faba	Broad bean (2*n*)[b]
Vitis vinifera	Grape (2*n*)[b]

[a]   Family known to have tinucleate pollen.
[b]   2N, Genus or species known to have binucleate pollen.
[c]   3N, Genus or species known to have trinucleate pollen.

From Brewbaker 1967; Frankel and Galun 1977.

survival is also adversely affected by high temperature, the presence of ultraviolet radiation, and repeated cycles of wetting and drying.

In wind- (Table 2) and animal-mediated (Table 3) pollination pollen dispersal shows a leptokurtic distribution (Stanley and Linskens 1974). The average distances that viable pollen is transported by different vectors has been estimated as a few hundred meters for wasps and flies; several hundreds of meters for bees, birds, and small mammals; and, depending on wind speed and the height of the flower, from a few dozens of meters to several kilometers for airborne pollen (Stanley and Linskens 1974; Pacini 1992).

Crops vary as to whether pollination is required. Many species are raised for foliage (e.g., lettuce, cabbage) or for root parts (e.g., potatoes, carrots), so pollen production need only occur in seed producers' fields. Most cultivars are currently fertile, but it should be possible to breed for male sterility as an HRG containment mechanism.

Much more difficult in terms of gene containment are crops for which seeds or fruits are the product. These include the melons and squashes, but also tomatoes, fruit and nut trees, and the cereal grains. The size of the pollen cloud produced by wind-pollinated plants and the distances flown by common pollinators are large enough that effective removal of wild relatives that spontaeously occur within such a large pollen dispersal radius may be impractical. All other factors being equal, outcrossing HRCs producing viable pollen have a higher likelihood of producing herbicide-resistant hybrids with compatible wild relatives.

In terms of the containment of HRC pollens, this means that the mode of pollination, pollen longevity, and crop type combine to influence the probability of gene escape. For some, e.g. *Brassica* mustards and pines *(Pinus* spp.), escape of HRGs from a HRC are a virtual certainty. For others, e.g., celery or onions, this is much less probable.

3.2.2. Interfertility

Interfertility is required for hybridization, no matter how far the viable pollen disperses. Herbicide-resistant crops that are incompatible with any wild species can be disregarded as potential sources for escape of HRGs. The data on compatibility relations probably exist for most crops, but are not readily accessible. This information is critical for an analysis of and strategies for the containment of HRGs. We hope this discussion will induce researchers who know of interfertility data with wild relatives to assemble the data, evaluate it, and make it accessible to others.

A very few crop species have no close wild relatives, e.g., castor (*Ricinus communis*) (Simmonds 1976), so that their HRGs would remain contained within the HRC. A few other crops have no known compatible wild relatives, e.g., watercress (*Rorippa nasturtium-aquaticum*) and broad bean (*Vicia faba*). These too will not release herbicide resistance to wild populations.

The most common situation, however, is that the crop is a member of a genus comprised of other species, some compatible, some incompatible, and others for which interfertility is not known. Often, but certainly not always, the congeners about which compatibility with the crop are unknown consist of species that are relatively uncommmom or at least not weedy. Thus, some interfertility data gaps are to be expected and should not necessarily constitute a major stumbling block to risk analysis and containment.

For some crops, the probability of transgene escape is 1.0. These crops have abundant weedy wild relatives with which they freely exchange genes, for example, sorghum and johnsongrass, rice and red rice, oats and wild oats (see below). The development and field deployment of herbicide-resistant plants of these crops is tantamount to also providing the gene to these weeds.

In general, one can expect compatible wild relatives to be other members of the same genus. However, in some notable examples crops hybridize with species in other genera. The wheat group is a dramatic example. Species of *Triticum* (wheats), *Secale* (ryes), *Hordeum* (barleys), and *Aegilops* (goat grasses) can hybridize in nature (e.g., Simmonds 1976). Similarly, *Zea* (maize) crosses with wild species of *Teosinte* (teosinte) (Doebley 1990). These are relatively stable taxonomic units with gene flow between them. In other cases evolving taxonomic understanding may be responsible for expanding and contracting genus boundaries. Groups known to us in which exchange beyond the same genus should be evaluated are *Brassica* (e.g., with *Sinapis*) and *Abelmoschus* (okra) with *Hibiscus*. Other cases may well exist or be created by future nomenclatural changes.

3.2.3. Proximity

The opportunity for hybridization is created by the proximity of the wild, compatible relative to within the distance of maximum viable pollen flow of the crop, which might be termed "reproductive sympatry." It is important to bear in mind that proximity is a dynamic rather than static variable. Crops are continually planted in new as well as old areas, and weeds colonize new areas, creating new infestations as well as spreading outward from existing infestation foci. Due to the high degree of long distance transport of people and their goods, the dispersal and naturalization of weeds to new, distant areas is now commonplace.

4. IMPACT

The mere existence of a HRW is not necessarily a problem. The HRW becomes a problem only where the herbicide to which it is resistant is applied. Under our simplifying assumption that the HRG has no other pleiotropic effects, environments where the herbicide is applied are the only places where the resistance gene is advantageous and where HRW spread would be favored.

The argument is sometimes made that the added HRGs should confer a genetic load, setting transgenic herbicide resistance or any herbicide-resistant plants at a disadvantage in nonherbicided environments, leading to their demise. Indeed, some studies have shown HRWs, e.g.,

triazine-resistant weeds, to be less fit outside the herbicide environment (Conard and Radosevich 1979; Warwick and Black 1981; Holt and Radosevich 1983; Jacobs et al. 1988). However, other studies indicate that this is not necessarily the case with resistance to other groups of herbicides, e.g., the sulfonylureas (Alocer-Ruthling et al. 1992; Thompson et al. 1994).

Crawley et al. (1993) point out the critical importance of genotype by environmental interactions in determining fitness, so one should be very careful about the genetic load assumption. In particular, many plants appear to successfully carry tremendous loads of nontranscribed DNA that are replicated each generation, or, in the case of polyploids, multiple apparently functional copies of every locus (e.g., Bennett 1987). In a large genome the additional DNA and the production of an additional protein may not constitute a significant cost. Likewise, plant species, especially weeds, are found in a diversity of environments, from those rich in water and nutrients to very resource-poor environments. While lineages in poor conditions may be under strong selection for efficiency, those in rich environments may show considerable inertia, carrying irrelevant genes for long periods of time. Herbicide resistance transgenes certainly constitute a potential cost to the plant, potentially reducing its fitness. Whether the cost is sufficient to cause selection against plants carrying nonadvantageous transgenes in nature is probably a function of complex local conditions and should not necessarily be counted on in weed control strategies.

4.1. BIOLOGICAL IMPACT

Biological problems may arise from the movement of HRGs into wild populations. Where the herbicide is applied, HRGs are expected to be strongly selected for, and the population should evolve to contain primarily or entirely plants carrying the HRGs. This strong selection should have a number of side effects. Alleles linked to the advantageous alleles should be carried to high frequency as well, via hitchhiking effects (e.g., Futuyma 1986). Total genetic diversity should decline, at least initially, because linkage disequilibrium should cause replacement of the existing variation with alleles associated with herbicide resistance alleles, not as diverse or certainly different from those of the wild population.

Where the herbicide is not applied, HRGs should confer no fitness advantage. If they are neutral or nearly neutral in the absence of herbicide, they can be expected to simply add to the genetic variation in the population. Sheer addition of genetic variation may be considered desirable (e.g., Templeton 1986) because it gives the population more evolutionary flexibility. If, however, massive numbers of genes from the crop come into an adjacent wild population, they could swamp the native population, so that every seed is a hybrid, greatly reducing effective variation and compromising the ability of the population to respond evolutionarily.

While theoretical genetic models for the fate of particular new neutral or nearly neutral alleles show them being rather rapidly lost due to chance events (e.g., Crow and Kimura 1970), this should not be applied to HRGs, except as they occur by random mutation. If large numbers of hybrids that carry the HRG are produced, then one begins with a relatively high frequency of the herbicide resistance alleles in the wild population and, in the absence of selection against the herbicide resistance allele, it should drift in the wild population for a very long time (Figure 1). Functionally, one can assume that once introduced into wild population from a large planting of an HRC, the HRGs will be permanently present in the population of wild relatives at the site. If the wild relatives are weeds, the herbicide can never again be applied without the rapid production of HRWs.

If the HRG is slightly deleterious in the absence of herbicide, for whatever reason, then the frequency will drop steadily each generation, eventually reaching zero (Figure 2). However, unless the gene is strongly deleterious, many generations are required.

An alternative outcome is that so many herbicide resistance alleles of lower fitness are added to the wild population that they lower the fitness of the wild population, for example, by reducing the mean number of seeds per plant, enough to endanger the survival of the wild population. If the
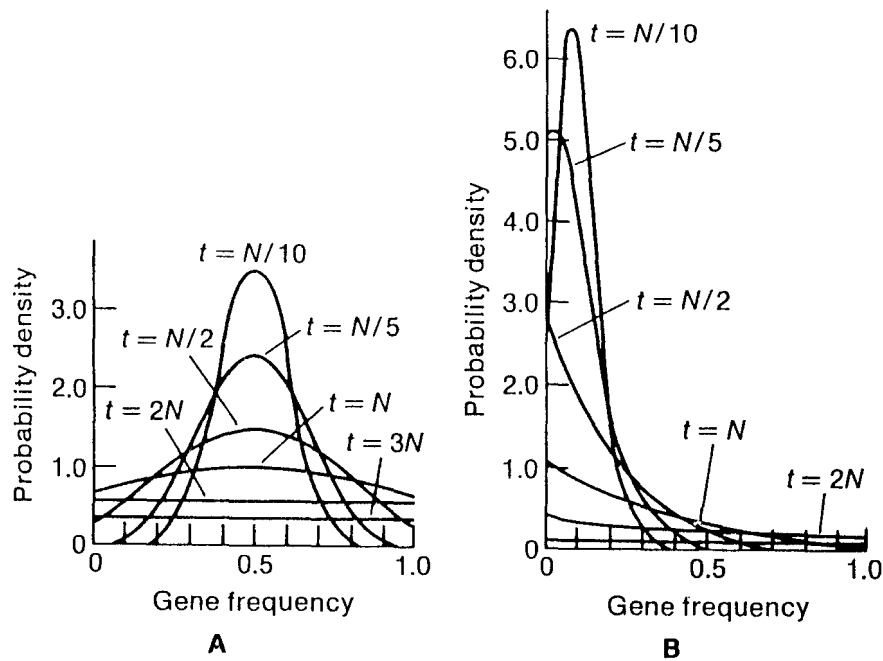
FIGURE 1   Removal of herbicide resistance genes will be very slow in the absence of selection against them. (A) Probability distribution of allele frequencies when the initial allele frequency is 0.5 (as might happen in the hybrid seed of wild relatives next to a field). t = time in generations, N is the effective population size. (B) Same, with initial allele frequency of 0.1. Proportion of populations fixed at 0 or 1 is not shown. (After Futuyma 1986.)
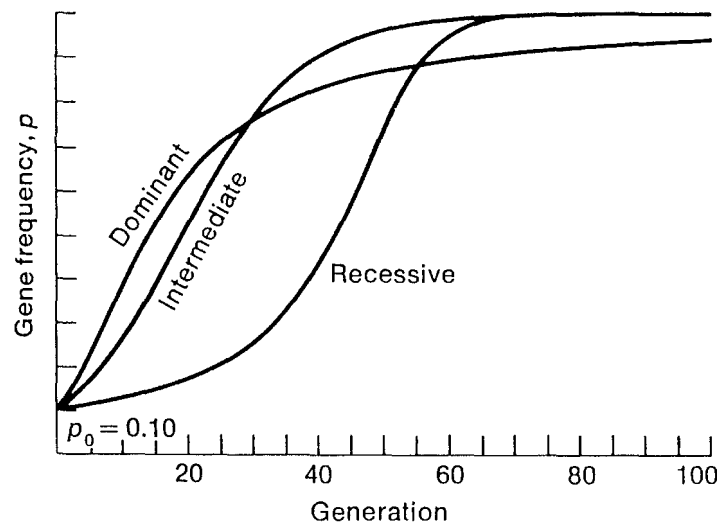

FIGURE 2   Dynamics of allele frequency change. Elimination of slightly unfit herbicide resistance genes from wild populations will take many generations. Drawn is the rise of a wild-type allele that is more fit than the transgene. Because transgenes are expected to be dominant, the right-hand curve (wild-type allele recessive) is the most applicable curve. Fitnesses used were 1, 1, 0.8 for wild-type dominant case; 1, 0.9, 0.8 for co-dominance; and 1, 0.8, 0.8 for wild-type recessive. (After Futuyma and Young 1986.)

wild population is a noxious weed, this is a beneficial side effect of using the HRC. If the wild population represents an important genetic resource, e.g., of wild germplasm for breeding or a rare native species, then this poses a potentially serious risk and action should be taken to prevent it.

Thus, genetic impact depends on how many genes are received by the wild population, whether those are advantageous, neutral, or disadvantageous, and how we value the population of wild relatives.

4.2. ECONOMIC IMPACT

The economic consequences of HRWs are potentially immense. The chief economic impact of weeds is in agriculture, where they reduce crop yield and quality by competing for limited resources. Agricultural weeds also reduce harvest efficiency and have other negative economic impact. Agricultural weed problems are universal and continuous. The agricultural losses due to weeds, including control costs, total about $15.2 billion annually in the U.S. (Chandler 1991). While machine and hand cultivation are used extensively to eliminate weeds, herbicides are the primary weapon, constituting about 62% of all pesticides applied in the U.S. (Szmedra 1991).

One challenge in the development of herbicides for weed control has been to find herbicides that do not also damage the crop. Reducing a complex story to its simplest parts, with genetic engineering, a HRC can be used so that the herbicide of choice can be applied to control the weeds, in some cases literally saving the crop. The emergence of HRWs threatens this technology specifically, and the utility of herbicides generally. Transgenic HRWs have not evolved, but naturally occurring HRWs have repeatedly threatened canola production in western Canada (Jensen and Bandeen 1979; Jana and Naylor 1982; LeBaron 1984; Beversdorf 1987), and are on the verge of threatening winter wheat production in the northwestern U.S. (Mallory-Smith et al. 1990; Stallings et al. 1994; Thompson et al. 1994).

4.3. CROP/WEED SYSTEMS OF CONCERN

The likelihood of escape of herbicide resistance into weed populations and consequent increased weed control problems varies greatly among different crops. Specifically, some species apparently do not reproduce sexually, have no relatives in North America, and are not compatible with relatives anywhere (e.g., rhubarb), therefore, weed problems from escape of herbicide resistance can be essentially disregarded. At the other extreme are crops that outcross during crop production, have seriously weedy close relatives widely distributed in North America, and hybridize freely with those relatives (e.g., sorghum). A few are native species (e.g., sunflower), whose relatives are not only weedy and compatible, but represent an indigeous gene pool many would prefer not to contaminate with introduced genes.

Table 5 is an attempt to summarize readily available data on the distribution of the weedy wild relatives of 60 important crop plants. While it contains a number of data gaps, it outlines the nature of the missing data and the level of our ignorance. Of the 60 crops, only 11 do not have congeners that are considered weeds somewhere in the world. Fifteen more do not have weedy wild congeners reported for the U.S. That leaves the majority, 34 (57%), with weedy wild relatives reported for the U.S. Hybridization with wild relatives is clearly known for only 15 (25%) of the crops.

From this analysis we can see (1) that pertinent reproductive and distributional data are apparently lacking for many crops; (2) that large geographic areas, such as countries, are very unsatisfactory ways to look for proximity of a weed; and (3) that information about abundance and distribution is constantly changing and needs continual updating. It shows, most importantly, the need to generate a database on the pollination system, interfertility relationships, and distribution of wild relatives of cultivated plants in order that informed decisions about the risks of escape of genes such as those for herbicide resistance can be made. The tables in this chapter are intended as a beginning in this effort.

TABLE 5 Distribution of Weedy Wild Relatives of 60 Herbaceous Crop Plants and Potential for Hybridization between Crop and Wild Relatives

Species	No. of Congeneric Species Reported as Weeds	If So, How Weedy, Where?[a,b]	Compatibility of Crop and Relatives?
Apiaceae			
Apium graveolens	4	*A. leptophyllum* S: HA; P: 1 SAm, 1 Af;C: 5; X: 6 more) 2 spp. C in 3 countries, 1 X	Hybrids?
Daucus carota	9	6 C in 8 countries	Hybrids?
Pastinaca sativa	0		Does not hybridize with wild congeners
Petroselinum sativum	1	*P. segetum* C: Eu	Does not hybridize with wild congeners
Asteraceae			
Carthamus tinctorius	8	*C. lanatus* S: Aus, C 2 countries, X 5 *C. oxyacantha* S: 2A, X 2 countries; 6 more C–X weeds	Not compatible with weedy wild relatives, will hybridize with wild relatives that are not considered weedy
Cichorium endivia	3	*C. intybus* S: 1 SAm, 3 Eu 1 A; P: 2, Eu 1 A, 2 Med; C: 9 incl. USA; X 12 *C. pumilum* P: Isr; C	Hybrids? 3 spp.
Cynara scolymus	3	*C. cardunculus* S: Arg, Aus; P: 1 Eu, X 4 2 C	Free hybridization between *C. scolymus* and *C. cardunculus*
Helianthus annuus	6	S: *H. ciliaris* USA; X: *H. californicus, ciliaris, grosseserratus, maximiliani, petiolaris,* and *tuberosus*	1 hybridizes freely with *H. annuus* (*H. petiolaris*)
H. tuberosus	6	Only *H. annuus* (c.f.) S: Mex; P: Arg, USA	Does not hybridize with any weedy congeners
Lactuca sativa	19	*L. capensis* P:1 Af; *L. floridana* C: USA; *L. scariola* P: 1 Med, *L. serriola* P: USA; C: 1 Af, Aus, Can, Med 1 SAm; *L. taraxacifolia* P: 1 Af	Hybridizes with some wild relatives (*L. serriola, L. virosa, L. saligna;* C: 1 A, Aus)
Brassicaceae			
Brassica campestris	13	*B. juncea* P: Can; C: Arg, Aus; X: 1 Oc, 1 CAm, USA; *B. kaber* P: Can; C: 1 Med, USA; *B. rapa* P: SAm; C: 1 Af, 2 Eu, USA; *B. tournefortii* P: Aus; C 1 Med; X 1 Oc; *B. nigra* (=*Sinapis nigra*) S USA, C: 10 countries, X: 7 countries	*B. campestris* hybridizes with *B. nigra* and *B. napus*
B. napus	14	See *B. campestris*	Hybridizes readily with *B. campestris* (McNaughton 1978)
B. oleracea	14	See *B. campestris*	Hybridizes with European wild congeners that are not considered weedy
Rorippa nasturtium-aquatica	1	*Rorippa* sp. P: A; C: 6 in; 8 X (incl. 2 in USA) 2 *Nasturtium* spp. X: 1 country each	Watercress is incompatible with wild relatives
Raphanus sativus	2	*R. raphanistrum* S: A, Af, Eu, Oc, SAm, USA; *R. microcarpus* C: Eu	Hybridizes with *R. raphanistrum, R. maritimus,* and *R. landra*

TABLE 5 (continued) Distribution of Weedy Wild Relatives of 60 Herbaceous Crop Plants and Potential for Hybridization between Crop and Wild Relatives

Species	No. of Congeneric Species Reported as Weeds	If So, How Weedy, Where?[a,b]	Compatibility of Crop and Relatives?
Chenopodiaceae			
Beta vulgaris	0	No weedy congeners; incompatible with wild congeners	
Spinacia oleracea	0	No weedy congeners; incompatible with wild congeners	
Convolvulaceae			
Ipomoea batatas	57	*I. cordofana* P: Af; *I. hederacea* S: USA; *I. lacunosa* S: USA; *I. pandurata* S: USA; *I. purpurea* S: USA; *I. tiliacea* P: SAm; *I. triloba* P: Oc; S: CAm, HA, USA; *I. wrightii* P: USA	*I. batatas* is not very fertile, but is compatible with *I. triloba* and others of the *I. batatas* complex
Cucurbitaceae			
Citrullus lanatus	1	C: Aus	Incompatible with weedy relatives
Cucumis melo	8	*C. myriocarpus* P: Aus; *C. anguria* P: USA	Hybridizes with wild relatives that are not considered weeds
C. sativus	8	See *Cucumis melo*; also *C. melo* P: SAm	Hybridizes with *C. hardwickii* in Asia, which is not considered very weedy (Simmonds 1976)
Cucurbita maxima	4	*C. texana* P: USA; *C. pepo* X: USA	Hybridizes with nonweedy congeners in SAm
C. moschata	4	*C. texana* P: USA; *C. pepo* X: USA	Hybridizes with nonweedy congeners in SAm
C. pepo	3	See *C. maxima*	Hybridizes with nonweedy congeners in SAm
Euphorbiaceae			
Ricinus communis	0	No other species in genus	No compatible relatives
Fabaceae			
Arachis hypogaea	0	No weedy congeners	Hybridizes with nonweedy congeners, including *A. monticola*
Cicer arietinum	0	No weedy congeners	No hybrids with other members of this genus of 39 southern Asian species
Glycine max	2	*G. soya* C: Jpn, another sp. X: Af	Hybridizes with *G. soya* to produce weedy *G. gracilis*
Lens culinaris	0	No *Lens* sp. are weedy	Interfertile with *L. orientalis*, which is not considered weedy (Hancock 1992)
Medicago sativa	20	*M. lupulina* P: A; C: USA; *M. polymorpha* C: USA; 10 other spp. C (total of 17 countries)	Hybridizes with *M. sativa* var. *falcata*, to make "*M. varia*" populations
Phaseolus lunatus	7	*P. lathyroides* P: Aus; C: HA, A; *P. trilobus* P: A	Hybrids?

TABLE 5 (continued) Distribution of Weedy Wild Relatives of 60 Herbaceous Crop Plants and Potential for Hybridization between Crop and Wild Relatives

Species	No. of Congeneric Species Reported as Weeds	If So, How Weedy, Where?[a,b]	Compatibility of Crop and Relatives?
P. vulgaris	7	See *P. lunatus*	Hybrids occur, although in general there is little geographical overlap between wild and cultivated species; the hybrids are hard to classify, leading to taxonomic problems defining the species.
Pisum sativum	1	*P. elatius* C: NAf, Por	*P. arvense* and *P. elatius* (the latter is weedy)
Vicia faba	25	*V. sativa* S: A, Eu USA; P: A, Oc; C, X: 27 countries; *V. cracca* P: 1 Eu, USA; *V. hirsuta* P: A; *V. narbonensis* P: NAf; *V. villosa* P: USA; 13 more spp. C somewhere in the world	Does not hybridize with wild congeners (Hancock 1992)
Liliaceae			
Allium ampeloprasm	13	*A. macrostemon* P: A; *A. nigrum* P: NAf; *A. vineale* P: Aus, Tur, USA; *A. canadense* P: USA; 4 spp. C somewhere	
A. cepa	13	See *C. ampeloprasm*	
A. sativum	13	See *C. ampeloprasm*	
Asparagus officinalis	1	1 *A. lucidus* C: A	Long history in cultivation, wild relatives in southern Asia
Linaceae			
Linum usitatissimum	5	*L. peyroni* C: NAf	Forms fertile hybrids with *L. africanum* and *L. angustifolium*, and 5 others, of which *L. angustifolium* is considered a weed
Malvaceae			
Gossypium hirsutum	0	No *Gossypium* spp. are weeds [the one report (*G. tomentosum*, Holt et al. 1977) is for the rare and endangered Hawaiian endemic cotton so this appears to be an error)	Hybridizes with wild congeners that are not weedy
Abelmoschus esculentus	0	No *Abelmoschus* spp. are weedy	Okra is incompatible with its wild relatives
Poaceae			
Avena sativa	10	*A. barbata* P: Eu X: USA; *A. byzantina* P: Arg, Af; *A. fatua* S: Arg, Aus, Can, Eu, SAf, USA; P: CAm, SAm; C, X: 34 more countries; *A. sterilis* spp. *ludoviciona* S: Aus, Eu; P: Af, A; *A. sterilis* S: Aus, Med; *A. strigosa* S: Af; 2 others C in 3 countries	Hybridizes with very weedy *A. fatua* despite ploidy differences (Thomas and Jones 1976)

TABLE 5 (continued) Distribution of Weedy Wild Relatives of 60 Herbaceous Crop Plants and Potential for Hybridization between Crop and Wild Relatives

Species	No. of Congeneric Species Reported as Weeds	If So, How Weedy, Where?[a,b]	Compatibility of Crop and Relatives?
Hordeum vulgare	13	*H. jubatum* S: AL; C: Can, USA; *H. murinum* S: Aus, Oc; P: Med; C, X 24 countriesu, including USA (X); *H. leporinum* P: Aus; X: Arg, USA; 7 others are C in 8 countries (*H. pusillum* USA)	Chiefly hybridizes with *H. spontaneum* which is sometimes considered part of *H. vulgare*
Oryza sativa	6	*O. punctata* S: Af; *O. barthii* P: Af; *O. perennis* P: 1 Af; 1 other is C in 1 country	Taxonomic debates put red rice (variously *O. rufipogon* and *O. sativa* var. *rufipogon*) in and out of the same species as cultivated rice.
Panicum miliaceum	59	*P. fasciculatum* S: CAm, SAm; P: SAm; C: As; X: USA; *P. maximum* S: Aus, SAm, CAm, Af, HA; P: 1 Car, SAm, Af, CAm; C: 3 countries; X: 22, incl. USA; *P. repens* S: Af, Eu, HA, Oc, As; P: 2 Oc Af, C: 5 countries, incl. USA	Hybrids?
Pennisetum glaucum	13	*P. japonicum* P: Jpn; *P. macrourum* P: Aus; *P. pedicellatum* S: Af, As; P: Aus; *P. polystachyon* S: As; P: As; *P. purpureum* S: SAm, Af; C: HA, Oc, CAm; X: 14 countries, incl. USA	Hybrids?
Saccharum officinarum	4	*S. behghalense* P: As; *S. spontaneum* S: As, Oc; P: As, CAm; X: 20 countries; 2 spp. X in 2 countries	All *Saccharum* sp. are interfertile (Hancock 1992)
Secale cereale	1	*S. montanum* X: Tur	Weedy annual *Secale* sp. are close enough to rye to be considered *S. cereale* by some authors (Simmonds 1976)
Sorghum bicolor	11	*S. bicolor* ssp. *arundinacuum* P: SAm; X: Af; *S. halepense* P: Arg, Aus, SAm, CAm, Oc, Eu, HA, As, Med, USA; S: Oc, SAm, Af, Eu, CAm; C: 18 other countries; *S. bicolor* spp. *arundinacuum* S: Af; P: Af, USA; C: 3 other countries; *S. vulgare*, *S. bicolor* ssp. *bicolor* P: As, SAm; C: 2 countries, 2 spp. C in 3 countries 5 spp. X (2 in USA)	*S. bicolor* (2x) hybridizes freely with the serious weed *S. halepense* (4x) (Ellstrand and Hoffman 1990)
Triticum aestivum	1	*T. ramosum* X: Eu, As	Hybridizes infrequently with *Aegilops (Triticum) cylindrica*, jointed goatgrass (a P weed in incl. USA)
T. turgidum	2	*T. aestivum* X: As; *T. ramosum* X: Eu, As	Hybrids form with *Secale*, *Hordeum*
Zea mays	0	No members of *Zea* are weeds	Hybridizes with teosinte (*Zea* spp.), but teosintes not considered weedy

TABLE 5 (continued) Distribution of Weedy Wild Relatives of 60 Herbaceous Crop Plants and Potential for Hybridization between Crop and Wild Relatives

Species	No. of Congeneric Species Reported as Weeds	If So, How Weedy, Where?[a,b]	Compatibility of Crop and Relatives?
Polygonaceae			
Rheum rhaponiticum	0	No weeds in *Rheum*	Propagated asexually by dividing clumps, seeds infertile; does not hybridize with congeners
Solanaceae			
Capsicum annuum	2	*C. frutescens* X: As, CAm, Oc, Med; *C. baccatum* X: Med	Hybridizes with congeners that are not considered weeds
C. annum var. frutescens	2	See *C. annuum*	Hybridizes with congeners that are not considered weeds
Lycopersicon esculentum	2	2 spp. X: both in Per	Yes?
Nicotiana tabacum	7	*N. glauca* C: Aus, HA, Af; X: SAm, Oc, USA; *N. longiflora* C: Arg; *N. suaveolus* C: Aus; 4 spp. X in 1 country each (*N. trigonophylla* USA)	Cultivated tobacco is the hybrid of two semiweeds of SAm
Solanum melongena	66	*S. alatum* P: Med; *S. americanum* P: USA; *S. auriculatum* P: Aus; *S. carolinense* P: USA; C: Can; *S. dubium* P: Af; *S. dulcamara* C: USA; . *elaeagnifolium* S: Af, USA; P: Aus; C: Arg, Af; X: SAm, CAm, USA; *S. glauco-phyllum* P: Arg; *S. gracilius* P: SAm; *S. grossedentatum* P: Af; *S. hystrix* P: Aus; *S. nigrum* S: A, Aus, HA, Med, Oc, USA; P: Af, Can, CAm, Eu, SAm; C 14 other countries, incl. USA; X: 32 others); *S. nodiflorum* S: HA; C: Af; *S. ptycanthum* P: USA; *S. rostratum* S: Mx, USA; C: 1 Af, Aus; *S. saccaroides* P: USA; *S. torvum* S: Oc; P: A, Af, Aus, Oc; C: 3 other countries, incl. USA; *S. triflorum* P: Aus, USA; *S. tuberosum* P: USA; *S. villosum* S: Med; C: 1 Af; X: USA; *S. xanthocarpum* P: 1 A, As; 23 spp. C weeds somewhere	Hybridize?
S. tuberosum	66	See *S. melongena*	Hybridizes with relatives in the subsection *Potato* which are not considered weeds (Hancock 1992)

[a] Locations: NAm = North America, CAm = Central America, SAm = South America, A = Asia, Af = Africa, Eu = Europe, Oc = Oceania, USA = United States, Sov = former Soviet Union, AL = Alaska, Per = Peru, Can = Canada, HA = Hawaii, Med = countries around the Mediterranean Sea, Mx = Mexico, Arg = Argentina, Aus = Australia, NZ = New Zealand, Jpn = Japan, Car = countries around the Caribbean Ocean, Isr = Israel, NAf + North Africa, Por = Portugal, Tur = Turkey, SAf = South Africa.

[b] Severity of weed problem: S = serious, P = principal, C = common, X = present and weedy, but importance uncertain (after Holm et al. 1979), S = troublesome weed of several crops and states, P = troublesome weed of a few or one crop or state, C = common weed, as listed in Bridges (1992).

[c] Major sources: Crockett 1977; Holm et al. 1979; Schery 1972; Bridges 1992.

We briefly discuss below examples of crops for which problems with HRG escape are probable in the U.S. These highlight a challenge as well as a warning; significant ingenuity will be required to provide crops with HRGs or other potentially beneficial genes that do not exacerbate weediness in weedy, compatible wild relatives.

4.3.1. Oats

Oats (*Avena sativa*) are valued for the relatively high protein and fat content of the seeds, and are chiefly a crop of north temperate areas such as North America, northern Europe, and Russia (Langer and Hill 1982). Wild oat, *Avena fatua*, is grown as a crop in Scotland, but is a serious agricultural weed elsewhere in the world (Thomas and Jones 1976; Jana and Naylor 1982). Wild oat is weedy in grainfields, rangelands, and other environments in the U.S. and southern Canada (Reed and Hughes 1970; Bridges 1992). Although *A. fatua* is hexaploid and *A. sativa* is diploid, they freely hybridize (Thomas and Jones 1976).

4.3.2. Canola

Canola (*Brassica napus* and *B. rapa;* rapeseed) is an important oilseed crop in North America and elsewhere. The crop is sometimes itself weedy as an escape from cultivation (Rollins 1981). The canola industry of the northwestern U.S. and southwestern Canada has already experienced serious problems with spontaneous development of herbicide-resistant wild mustards (*Brassica* spp.) interfering with crop production (Beversdorf 1987; Chapter 21). This experience perhaps most clearly emphasizes the potential of new HRWs to cause problems. *B. napus* and *B. rapa* are themselves weedy, and along with *B. nigra* are widespead weeds of orchards and cultivated fields, and along ditchbanks and roadsides in North America (Reed and Hughes 1970; Rollins 1981; Whitson et al. 1992; Hickman 1993). Canola outcrosses in order to produce seed. Pollination has been well studied, and it is clear that gene flow from canola to wild *Brassica* spp. is "virtually inevitable" (e.g., papers in McCammon and Dwyer 1990).

4.3.3. Artichoke

Artichoke (*Cynara scolymus*) is an important specialty crop in California. Artichoke thistle or cardoon (*C. cardunculus*), is an aggressive colonizer of grasslands and a difficult to control weed of northern San Francisco Bay area counties and southern coastal California. The northern coastal infested region is close to the primary artichoke growing area immediately to the south. The crop and the weed are highly interfertile, and are sometimes considered to comprise a species complex (Thomsen et al. 1986).

4.3.4. Sunflower

Sunflower (*Helianthus annuus*) is grown as an oilseed crop and edible seed crop in the north-central U.S., and much of the grower seed production is done in California. Sunflower is a cultivated race of the native North American annual, *H. annuus*. Wild sunflowers, including *H. annuus* itself, are widespread weeds throughout the U.S. in grainfields and other cultivated fields, roadsides, and waste areas (Reed and Hughes 1970). Other native annual, weedy sunflowers include *H. bolanderi* and *H. petiolaris* (Robbins et al. 1970; Bridges 1992; Whitson et al. 1992). Gene flow between cultivated and wild annual sunflowers is probably common (Heiser et al. 1969; Heiser 1976). Wider crosses with perennial congeners have been made, for example, with *H. tuberosus*, but these are typically not as fertile (Heiser 1976).

4.3.5. Lettuce

Lettuce (*Lactuca sativa*) is a major leafy crop in North America. *L. sativa* is a diploid ($2n = 18$), primarily self-fertilized herbaceous annual. It is probably derived from prickly lettuce, *L. serriola* (Schery 1972). Prickly lettuce is a major weed throughout much of the U.S. in irrigated fields,

orchards, and along roadsides (Reed and Hughes 1970; Bridges 1992; Whitson et al. 1992). Lettuce and prickly lettuce have the same number of chromosomes ($2n = 18$) and are interfertile (Mallory-Smith et al. 1993). The spontaneous evolution of resistance to sulfonylurea herbicides is a growing concern in the northwestern U.S. (Mallory-Smith et al. 1990; Alocer-Ruthling et al. 1992). Sulfonylurea resistance has been successfully transferred by hand pollination from resistant prickly lettuce to Bibb lettuce (Mallory-Smith et al. 1990, 1993).

4.3.6. Rice

Rice (*Oryza sativa*), an aquatic grass, is a major grain crop grown in flooded fields in California and the south-central states. Red rice is a diiferent, weedy biotype of rice, distinguished by a pigmented pericarp and other morphological and physiological differences (Langevin et al. 1990). Red rice is a serious weed of rice fields, irrigation/drainage canals, and other wet areas in the south-central U.S. (Smith et al. 1977). Measures of hybridization rates between sympatric populations of rice and red rice found that hybrid seed set in red rice varied from 1 to 52% in sampled fields of six rice cultivars (Langevin et al. 1990). Langevin et al. (1990) also report that the hybrids generally were taller and had larger flag leaves than either cultivated rice or red rice, and the hybrids produced more tillers than red rice.

4.3.7. Radish

Radish (*Raphanus sativus*) is a root crop widely grown in North America. Wild radish is currently considered conspecific with the crop radish, but is undoubtedly a different, interfertile biotype. Wild radish generally lacks the well-developed fleshy taproot of cultivated radish. Wild radish is a widespread weed in California, infesting cereal grains (where it is particularly trouble-some) and other cultivated crops, roadsides, and waste areas (Robbins et al. 1970; Bridges 1992; Whitson et al. 1992). In a study of radish–wild radish hybridization Klinger et al. (1991) documented gene flow from radish to surrounding experimental plantings of wild radish, and detected gene flow to the most distant plots (1000 m) of wild radish. Klinger et al. (1992) found that hybridization rates declined with increasing linear distance between radish and wild radish, and also that there was a complex effect of recipient (wild radish) population size. In a field plot experiment, the hybrids had greater fruit and seed production and equalled wild radish in the other reproductive characters measured (Klinger and Ellstrand 1994).

4.3.8. Sorghum

Sorghum (*Sorghum bicolor*) is a diploid ($2n = 20$) annual grown for grain (chiefly for animal food), silage, and syrup in the U.S. (Schery 1972). Sorghum hybridizes freely with johnsongrass, *S. halepense,* a rhizomatous, perennial tetraploid ($2n = 40$) (Schery 1972; Baker 1974). Johnsongrass was intentionally introduced to North America as a forage grass (Foy et al. 1983), but has become a troublesome weed of cultivated fields, ditch banks, and waste areas throughout the warmer parts of the U.S. (Reed and Hughes 1970; Bridges 1992). It it listed as the sixth worst weed in the world (Holm et al. 1977).

Other crop–weed systems also may be of concern. Wheat, for example, as grown in the U.S., is primarily the hexaploid *Triticum aestivum.* There are no weedy species of *Triticum* in the U.S., and in general no species of *Triticum* has naturalized at all. However, the wheat group hybridizes freely across generic lines, so that in fact *Triticum* is compatible with *Aegilops, Hordeum,* and *Secale.* This means that HRGs could go to other crops, to wild *Hordeum* or *Secale* spp., at least in principle, because there are some weeds in these genera. Furthermore, *Aegilops cylindracea,* jointed goat grass, is a serious weed of wheat fields and partially compatible with *T. aestivum.* Not many hybrids form, and although they probably do not send many genes back to the jointed goat-grass populations (Donald and Ogg 1991), exchange with weed populations is definitely possible.

Furthermore, in the high plains of Colorado, Nebraska, the Dakotas, and western Kansas, where irrigation is impossible, wheat is grown on a fallow–wheat–fallow–wheat rotation, in which one of the worst weed problems is carryover wheat from previous years. Herbicide tolerance may be a blessing in the first year and a curse in subsequent years.

5. MANAGEMENT

Despite the great potential and increasing importance of other weed control options (Turner et al. 1992) and unwanted environmental side effects of some herbicides, herbicides constitute a very important means of weed control. The escape of herbicide resistance genes to wild, weedy plants could cause more severe weed problems, and presents a very real threat to the efficacy of herbicides as a weed control option. Therefore, management strategies that prevent, or reduce the likelihood and frequency of HRG escape through containment methods are advisable, as are mitigation plans in the event of HRG escape to wild plants.

5.1. PREVENTION/CONTAINMENT

A policy of avoidance of engineering herbicide resistance into high-risk crop–weed systems is an absolutely effective means of avoiding the transgene escape problem altogether. For now, we recommend this "abstinence" policy for the aforementioned eight crops (oats, canola, artichoke, sunflower, lettuce, rice, radish, sorghum) of special concern in the U.S. We also urge researchers to develop compatibility barriers between these crops and their presently compatible weedy relatives, so as to be able to safely take advantage of transgenic advances in the future (see below).

Containment includes the use of various genetic, ecological, and cultural methods to reduce the likelihood of HRG escape. They vary in their probable effectiveness, and none are as absolutely effective as the prevention method above. All are unproven for this specific application.

5.1.1. Genetic

Genetic containment methods include "suicide genes," interfertility barriers, and male sterility. The use of suicide genes, genes whose expression is autocidal upon escape (hybridization), amounts to an ultimate, although untried, transgene containment method in plants. The event triggering the autocidal expression upon HRG escape could be some part of the cytological process of hybridization/recombination itself, or as suggested by Ellstrand and Hoffman (1990), an inevitable part of the weed's (but not the crop's) environment. They suggest, for example, an autocidal trait expressed in seeds and triggered by exposure to cold temperatures. This could be effective for temperate crops. Crop plants could be modified to reduce their interfertility with wild relative by various methods, for example, by producing one or more unpaired chromosomes (aneuplody) in the genome, which would prevent successful hybridization (Keeler and Turner 1991). Where the crop product is not a seed or fruit requiring fertilization, male-sterile cultivars could be developed to greatly reduce the likelihood of HRG escape (Ellstrand and Hoffman 1990; Keeler and Turner 1991).

5.1.2. Ecological

The most effective ecological containment method is spatial isolation, where HRCs are isolated by distance from compatible wild relatives. For soybeans *Glycine max*, the wild relatives are currently confined to Asia. Soybeans grown in the United States are well isolated from these wild relatives. Transoceanic isolation, of course, is a drastic example of containment by spatial isolation. On a local scale, spatial isolation will probably be effective only for self-fertilizing crops, and should not be relied upon for outcrossing crops (Klinger et al. 1992). An isolation distance of 500 m should suffice for most selfers (George 1985; Ellstand and Hoffman 1990). This method is dependent on

an accurate knowledge of pollen dispersal, wild plant distribution at the local scale, and interfertility relationships. The success of this method also can be affected by such complex factors as the behavior of biotic pollinators, wind movement, and the nature of intervening vegetation. One also should be mindful of the dynamic nature over time of the spatial distributions of crop plantings and wild plants, especially for weeds with excellent colonizing abilities. Klinger et al. (1992) point out the near impossibility of weed eradication even on a local scale.

All other ecological containment strategies are even less reliable than spatial isolation. For example, disjunct flowering phenologies can constitute another ecological containment method, but its effectiveness is reduced by phenological outliers and unusual seasons.

5.1.3. Cultural

Simple cultural practices can sometimes contribute to HRG containment (Ellstrand and Hoffman 1990). Where the crop product is vegetative, complete harvesting of the crop before flowering will preclude pollen production. The planting of nontransgenic plants of the crop surrounding the transgenic crop may serve to capture most of the otherwise outwardly bound transgenic pollen, although the complexities of pollination render this a method that is not necessarily dependable by itself for containing the transgenic pollen of outcrossing crops.

Wrubel et al. (1992) and Miller and Gunary (1993) are critical of the data available assessing the risk of escape of transgenes. Production of large amounts of inadequate science makes it hard to validly evaluate the lessons learned from our heavily regulated system of testing transgenics in the environment. We urge that both basic and applied scientists with environmental training address the problems of risk asssessment as critically as possible in order to set environmental release on a sound scientific basis. There will be more serious loss of public confidence if, having claimed we tested for safety, we have a problem, than if no tests were made. Regulatory agencies can assist in this process by being quite explicit about how common an event must be before it must be prevented and by approving mitigation plans rather than requiring prevention of rare events.

5.2. MITIGATION

Mitigative methods impede the survival and spread of transgenic HRWs. The types of crop and weed control (herbicide rotations and mixtures and mechanical cultivation) rotation strategies discussed by Gessel and Segel (1990) and Saari et al. (1994) to reduce the likelihood of spontaneous evolution of HRWs also should be effective in reducing the likelihood of survival and spread of transgenic HRWs. If utilized routinely as a management strategy, the effect would be to create a general landscape unfavorable to HRWs, whether transgenic or nontransgenic in origin. This is an important reason to avoid engineering multiple herbicide resistance into crops. In terms of mitigating the effects of a specific HRG escape event, speed of detection is obviously important. Readily detectable marker genes linked to HRGs could facilitate the speedy detection and mitigative response to HRG escape to wild plants.

REFERENCES

Alocer-Ruthling, M., Thill, D.C., and Shafi, B. 1992. Differential competitiveness of sulfonylurea resistant and susceptible prickly lettuce (*Lactuca serriola*). *Weed Technol.* 6: 303.

Alocer-Ruthling, M., Thill, D.C., and Mallory-Smith, C. 1992. Monitoring the occurrence of sulfonylurea-resistant prickly lettuce (*Lactuca serriola*). *Weed Technol.* 6: 437.

Baker, H.G. 1974. The evolution of weeds. *Annu. Rev. Ecol. Systematics* 5: 1.

Bennett, M.D. 1987. Variation in genomic form in plans and its ecological implications. *New Phytol.* 106(Suppl.): 177.

Beversdorf, W.D. 1987. Classical approaches to the development of herbicide tolerance in crop cultivars. In *Biotechnology in Agriculture and Chemistry*. Ed. by LeBaron, H.M., Mumma, R.O., Honeycutt, R.C., and Duesing, J.H. Amerrican Chemical Society, Washington, D.C., chap. 8.

Brewbaker, J.L. 1967. The distribution and phylogenetic significance of binucleate and trinucleate pollen grains in the angiosperms. *Am. J. Bot.* 54: 1069.

Bridges, D.C., Ed. 1992. *Crop Losses Due to Weeds in the United States — 1992*. Weed Science Society, Champaign, IL.

Bucholtz, K.P. 1967. Report of the terminology committee. *Weed* 15: 388.

Chandler, J.M. 1991. Estimated losses of crops to weeds. In *Handbook of Pest Management in Agriculture*, Vol. 1. Ed. by Pimentel, D. Boca Raton, FL, p. 53.

Conard, S.G. and Radosevich, S.R. 1979. Ecological fitness of *Senecio vulgaris* and *Amaranthus retroflexus* biotypes susceptible and resistant to atrazine. *J. Appl. Ecol.* 16: 171.

Crawley, M.J., Halle, R.S., Rees, M., Kohn, D., and Buxton, J. 1993. Ecology of transgenic oilseed rape in natural habitats. *Nature* 363: 620.

Crow, J.F. and Kimura, M. 1970. *An Introduction to Population Genetics Theory*. Harper & Row, New York.

Cruden, R.W. 1977. Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. *Evolution* 31: 32.

Doebley, J. 1990. Molecular evidence for gene flow among *Zea* species. *Bioscience* 40: 443.

Donald, W. and Ogg, A. 1991. Biology and control of jointed goatgrass (*Aegilops cylindrica*), a review. *Weed Technol.* 5: 3.

Dumas, C., Kerhoas, C., Gay, G., and Gaude, T. 1986. Water content, membrane state and pollen physiology. In *Biotechnology and Ecology of Pollen*. Ed. by Mulcahy, D.L., Mulcahy, G.B., and Ottaviano, E. Springer-Verlag, New York, p. 333.

Dyer, W.E., Hess, F.D., Holt, J.S., and Duke, S.O. 1993. Potential benefits and risks of herbicide-resistant crops produced by biotechnology. *Hort. Rev.* 15: 367.

Ellstrand, N.C. 1988. Pollen as a vehicle for the escape of engineered genes? *Trends Biotechnol.* 6: 530.

Ellstrand, N.C., Devlin, B., and Marshall, D.L. 1989. Gene flow by pollen into small populations: data from experimental and natural stands of wild radish. *Proc. Natl. Acad. Sci. U.S.A.* 86: 9044.

Ellstrand, N.C. and Hoffman, C.A. 1990. Hybridization as an avenue of escape for engineered genes. *BioScience* 40: 438.

Elton, C.S. 1958. *The Ecology of Invasions by Animals and Plants*. Chapman & Hall, London.

Faegri, K. and Iverson, J. 1975. *Textbook of Pollen Analysis*, 3rd ed. Hafner Press, New York.

Faegri, K. and van der Pijl, L. 1979. *The Principles of Pollination Ecology*. Pergamon Press, Oxford.

Foy, C.L., Forney, D.R., and Cooley, W.E. 1983. History of weed introductions. In *Exotic Plant Pests and North American Agriculture*. Ed. by Wilson, C.L. and Graham, C.L. Academic Press, New York, chap. 4.

Frankel, R. and Galun, E. 1977. *Pollination Mechanisms, Reproduction and Plant Breeding*. Springer-Verlag, Berlin.

Futuyuma, D.J. 1986. *Evolutionary Biology*, 2nd ed. Sinauer Associates, Sunderland, MA.

George, R.A.T. 1985. *Vegetable Seed Production*. Longmans Press, New York.

Gessel, J. and Segel, L.A. 1990. Herbicide rotations and mixtures: effective strategies to delay resistance. In *Managing Resistance to Agrochemicals*. Ed. by Green, M.B., LeBaron, H.M., and Moberg, W.K. American Chemical Society, Washington, D.C., chap. 30.

Hancock, J.F. 1992. *Plant Evolution and the Origin of Crop Species*. Prentice-Hall, Englewood Cliffs, NJ.

Hancock, J.F. and Luby, J.J. 1993. Genetic resources at our doorstep: the wild strawberries. *BioScience* 43: 141.

Harlan, J.R. The possible role of weed races in the evolution of cultivated plants. *Euphytica* 14: 173.

Hauptli, H., Newell, N., and Goodman, R.M. 1985. Genetically engineered plants: environmental issues. *Bio/Technology* 3: 437.

Heiser, C.B., Smith, D.M., Clevenger, S.B., and Martin, W.C. 1969. The North American sunflowers (*Helianthus*). *Mem. Torrey Bot. Club* 22: 1.

Heiser, C.B. 1976. Sunflowers (*Helianthus* - Compositae). In *Evolution of Crop Plants*. Ed. by Simmonds, N.W. Longmans Press, London, chap. 13.

Hickman, J.C. Ed. 1993. *The Jepson Manual: Higher Plants of California*. University of California Press, Berkeley.

Hoekstra, F.A. 1992. Stress effects on the male gametophyte. In *Sexual Plant Reproduction*. Ed. by Cresti, M. and Tiezzi, A. Springer-Verlag, Heidelberg, p. 193.

Hoekstra, F.A. and Bruinsma, J. 1978. Reduced independence of the male gametophyte in angiosperm evolution. *Ann. Bot.* 42: 759.

Hoekstra, F.A., Crowe, J.H., Crowe, L.M., and van Bilsen, D.G.L. 1992. Membrane behavior and stress tolerance in pollen. In *Angiosperm Pollen and Ovules*. Ed. by Ottaviano, E., Mulcahy, D.L., Sari Gorla, M., and Mulcahy, G.B. Springer-Verlag, Heidelberg, p. 177.

Holm, L.G., Pancho, J.V., Herberger, J.P., and Plunknett, D.L. 1979. *A Geographical Atlas of World Weeds*. Wiley, New York.

Holm, L.G., Plunknett, D.L., Pancho, J.V., and Herberger, J.P. 1977. *The World's Worst Weeds*. University of Hawaii Press, Honolulu.

Holt, J.S. and Radosevich, S.R. 1983. Differential growth of two common groundsel (*Senecio vulgaris*) biotypes. *Weed Sci.* 31: 112.

Hull, D.A. and Beattie, A.J. 1988. Adverse effects on pollen exposed to *Atta texana* and other North American ants: implications for ant pollination. *Oecologia* 75: 153.

Jacobs, B.F., Duesing, J.H., Antonovics, J., and Paterson, D.T. 1988. Growth performance of triazine-resistant and -susceptible biotypes of *Solanum nigrum* over a range of temperatures. *Can. J. Bot.* 66: 847.

Jana, S. and Naylor, J.M. 1982. Adaptation for herbicide tolerance in populations of *Avena fatua*. *Can. J. Bot.* 60: 1611.

Jensen, K.I.N. and Bandeen, J.D. 1979. Triazine resistance in annual weeds. In *Maize*, Ciba Geigy Tech. Monogr. Ed. by Haflinger, E. Ciba Geigy, p. 55.

Jones, M.D. and Newell, L.C. 1946. Pollination cycles and pollen dispersal in relation to grass improvement. *Univ. Neb. Coll. Agric. Res. Bull.* No. 148.

Keeler, K.H. 1985. Implications of weed genetics and ecology for the deliberate release of genetically-engineered crop plants. *Recombinant DNA Tech. Bull.* 8: 165.

Keeler, K.H. 1989. Can genetically engineered crops become weeds? *Bio/Technology* 7: 1134.

Keeler, K.H. and Turner, C.E. 1991. Management of transgenic plants in the environment. In *Risk Assessment in Genetic Engineering*. Ed. by Levin, M.A. and Strauss, H.S. McGraw-Hill, New York, chap. 9.

Kerhoas, C., Gay, G., Duplan, J.C., and Dumas, C. 1986. Water content evolution in *Cucurbita pepo* during aging: a NMR study. In *Biotechnology and Ecology of Pollen*. Ed. by Mulcahy, D.L., Mulcahy, G.B., and Ottaviano, E. Springer-Verlag, New York, p. 502.

Kerhoas, C., Gay, G., Duplan, J.C., and Dumas, C. 1989. Viability of *Cucurbita pepo* pollen: biophysical and structural data. *Planta* 179: 165.

Kirkpatrick, K.J. and Wilson, H.D. 1989. Interspecific gene flow in *Cucurbita: C. texensus* vs. *C. pepo*. *Am. J. Bot.* 75: 519.

Klinger, T., Elam, D.R., and Ellstrand, N.C. 1991. Radish as a model system for the study of engineered gene escape rates via crop-weed mating. *Conserv. Biol.* 5: 531.

Klinger, T., Arriola, P.E., and Ellstrand, N.C. 1992. Crop-weed hybridization in radish (*Raphanus sativus*): effects of distance and population size. *Am. J. Bot.* 79: 1431.

Klinger, T. and Ellstrand, N.C. 1994. Engineered genes in wild populations: fitness of weed-crop hybrids of *Raphanus sativus*. *Ecol. Appl.* 4: 117.

Langer, R.H.M. and Hill, G.D. 1982. *Agricultural Plants*. Cambridge University Press, Cambridge, U.K.

Langevin S.A., Clay, K., and Grace, H.B. 1990. The incidence and effects of hybridization between cultivated rice and its related weed, red rice (*Oryza sativa* L.). *Evolution* 44: 1000.

LeBaron, H.M. 1984. Herbicide resistance in plants — future needs. *Weeds Today* 4: 2.

Luza, J.G. and Polito, V.S. 1987. Effects of desiccation and controlled rehydration on germination *in vitro* of pollen of walnut (*Juglans* spp.). *Plant, Cell Environ.* 10: 487.

Mallory-Smith, C.A., Thill, D.C., and Dial, M.J. 1993. ID-BR1: sulfonylurea herbicide-resistant lettuce germplasm. *HortScience* 28: 63.

Mallory-Smith, C.A., Thill, D.C., and Dial, M.J. 1990. Identification of sulfonylurea herbicide-resistant prickly lettuce (*Lactuca serriola*). *Weed Technol.* 4: 163.

Mallory-Smith, C.A., Thill, D.C., Dial, M.J., and Zemetra, R.S. 1990. Inheritance of sulfonylurea herbicide resistance in *Lactuca* spp. *Weed Technol.* 4: 787.

McCammon, S.L. and Dwyer, S.G., Eds. 1990. *Proceedings, Workshop on Safeguards for Planned Introduction of Transgenic Oil Seed Crucifers*. U.S. Department of Agriculture/Washington, D.C.

Miller, H.I. and Gunary, D. 1993. Serious flaws in the horizontal approach to biotechnology risk assessment. *Science* 262: 1500.

Mooney, H.A. and Drake, J.A. 1986. *Ecological Effects of Introduced Species in North America and Hawaii*. Springer-Verlag, New York.

Pacini, E. 1992. Transport mechanisms of pollen — a short review. In *Sexual Plant Reproduction*. Ed. by Cresti, M. and Tiezzi, E. Springer-Verlag, Heidelberg, p. 69.

Perrins, J., Williamson, M., and Fitter, A. 1992. A survey of differing views of weed classification: implications for regulation of introductions. *Biol. Conserv.* 60: 47.

Perrins, J., Williamson, M., and Fitter, A. 1992. Do annual weeds have predictable characters? *Acta Oecol.* 13: 517.

Platt-Aloia, K.A., Lord, E.M., DeMason, D.A., and Thomson, W.W., 1986. Freeze fracture observations on membranes of dry and dehydrated pollen from *Collomia, Phoenix*, and *Zea*. *Planta* 168: 291.

Proctor, M. and Yeo, P. 1972. *The Pollination of Flowers*. Taplinger Publishing, New York.

Reed, C.F. and Hughes, R.O. 1970. *Selected Weeds of the United States*, U.S. Department of Agriculture/Agricultural Research Service, Agric. Handb. No. 366. U.S. Government Printing Office, Washington, D.C.

Robbins, W.W., Bellue, M.K., and Ball, W.S. 1970. *Weeds of California*. California Department of Agriculture, Sacramento.

Rollins, R.C. 1981. Weeds of the Cruciferae (Brassicaceae) in North America. *J. Arnold Arboretum* 62: 517.

Saari, L.L., Cotterman, J.C., and Thill, D.C. 1994. Resistance to acetolactate synthase inhibiting herbicides. In *Herbicide Resistance in Plants: Ecology and Mechanisms*. Ed. by Powles, S.B. and Holtum, J.A. CRC Press, Boca Raton, FL, chap. 4.

Salisbury, E. 1961. *Weeds and Aliens*. Collins, London.

Schery, R.W. 1972. *Plants for Man*. Prentice-Hall, Englewood Cliffs, NJ.

Sharples, F.E. 1983. Spread of organisms, with novel genotypes: thoughts from an ecological perspective. *Recombinant DNA Tech. Bull.* 6: 43.

Simmonds, N.W., Ed. 1976. *Evolution of Crop Plants*, Longmans Press, London.

Smith, R.J., Jr., Flinchum, W.T., and Seaman, D.E. 1977. *Weed Control in U.S. Rice Production*. U.S. Department of Agriculture/Agricultural Research Service, Agric. Handb. No. 497, U.S. Government Printing Office, Washington, D.C.

Soloman, A.M. 1979. Pollen. In *Aerobiology: The Ecological Systems Approach*. Ed. by Edmonds, R.L. Dowden, Hutchinson & Ross, Stroudsburg, PA, p. 41.

Stallings, G.P., Thill, D.C., and Mallory-Smith, C.A. 1994. Sulfonylurea-resistant Russian thistle (*Salsola iberica*) survey in Washington state. *Weed Technol.* 8: 258.

Stanley, R.G. and Linskens, H.F. 1974. *Pollen: Biology, Biochemistry, Management*. Springer-Verlag, New York.

Szmedra, P.I. 1991. Pesticide use in agriculture. In *Handbook of Pest Management in Agriculture*. Vol. 1. Ed. by Pimentel, D. Boca Raton, FL.

Templeton, A.R. 1986. Coadaptation and outbreeding depression. In *Conservation Biology: The Science of Scarcity and Diversity*. Ed. by Soule, M. Sinauer Associates, Sunderland. MA, p. 105.

Thomas, H. and Jones, H. 1976. Origins and identification of weed species of *Avena*. In *Wild Oats in World Agriculture*. Ed. by Jones, D.P. Agricultural Research Council, London, p. 1.

Thomsen, C.D., Barbe, G.D., Williams, W.A., and George, M.R. 1986. Escaped artichokes are troublesome pests. *Calif. Agric.* 40(3-4): 7.

Thompson, C.R., Thill, D.C., and Shafi, B. 1994. Growth and competitiveness of sulfonylurea-resistant and -susceptible kochia (*Kochia scoparia*). *Weed Sci.* 42: 172.

Tiedje, J.M., Colwell, R.K., Grossman, Y.L., Hodson, R.E., Lenski, R.E., Mack, R.N., and Regal, P.J. 1989. The release of genetically engineered organisms: a perspective from the Ecological Society of America. *Ecology* 70: 297.

Turner, C.E. 1988. Ecology of invasions by weeds. In *Weed Management in Agroecosystems: Ecological Approaches*. Ed. by Altieri, M.A. and Liebman, M. CRC Press, Boca Raton, FL, chap. 4.

Turner, C.E., Anderson, L.W., Foley, P., Goeden, R.D., Lanini, W.T., Lindow, S.E., and Qualset, C.O. 1992. Biological approaches to weed management. In *Beyond Pesticides: Biological Approaches to Pest Management in California*. Ed. by Madden, J.P. and Schroth, M.N. University of California, Berkeley, chap. 2.

Warwick, S.I. and Black, L. 1981. The relative competitiveness of atrazine susceptible and resistant populations of *Chenopodium album* and *C. strictum. Can. J. Bot.* 59: 689.

Whitson, T.D., Burrill, L.C., Dewey, S.A., Cudney, D.W., Nelson, B.E., Lee, R.D., and Parker, R. 1992. *Weeds of the West*. Western Society of Weed Science, Newark, CA.

Wilson, H.D. 1990. Gene flow in squash species. *BioScience* 40: 449.

Zamir, D. and Gadish, I. 1987. Pollen selection for low temperature adaptation in tomato. *Theor. Appl. Gen* 74: 545.

Zimdahl, R L. 1983. Where are the principal exotic weed pests? In *Exotic Plant Pests and North American Agriculture*. Ed. by Wilson, C.L. and Graham, C.L. Academic Press, New York, chap. 7.