1 Introduction and Overview of Resistance

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CONTENTS

1.1 INTRODUCTION

Humans have struggled against the negative impact of weeds since the cultivation of crops commenced around 10,000 B.C.[1] Weed control technologies have evolved from hand-weeding to include primitive hoes (6000 B.C.), animal-powered implements (1000 B.C.), mechanically powered implements (1920 A.D.), biological control (1930 A.D.), and chemical (herbicide) control (1947 A.D.).[1] Since the introduction of the first selective herbicides, 2,4-D and MCPA, in 1947, herbicides have had a major positive impact on world agricultural production, initially in developed nations and more recently in developing nations.[2] Herbicides are often the most reliable and least expensive method of weed control available, and the success of herbicides is largely responsible for the abundant and sustained food production necessary to support an increasing world population.[3] The availability of herbicides has allowed plant breeders to move from taller, more competitive crop varieties to shorter, higher-yielding crop varieties.[4] The efficacy and cost-effectiveness of herbicides has led to heavy reliance on them in the developed world. Nevertheless, there are some real and perceived problems with herbicides. In recent years there has been increased concern about residues and associated food safety issues, their adverse impact on the environment,[5] and the widespread occurrence of herbicide-resistant weeds.[6] The focus of this book is on the last of these concerns.

1.2 RESISTANCE

Pesticide resistance evolved in insects, fungi, and bacteria long before it was observed in weeds.[7] Resistance evolves following persistent selection for mutant genotypes that may be pre-existing or arise *de novo* in weed populations.[7] Herbicide-resistant weeds were predicted shortly after the introduction of herbicides.[8,9] Given the examples of pesticide resistance in insects and fungi it seemed inevitable that the continuous or frequent use of the same herbicide against the same populations of weeds would eventually result in resistant weeds. The first herbicides to be used persistently over large areas were 2,4-D and MCPA. Fortunately, these auxinic herbicides are not prone to rapid selection for resistance and, with the exception of 2,4-D-resistant *Daucus carota*,[10,11] resistance was not reported until the appearance of triazine herbicide-resistant weeds (Section 1.2.3.1) in the early 1970s.[12,13]

1.2.1 Resistance Defined

In the context of this book, *resistance*, unless otherwise stated, denotes the evolved capacity of a previously herbicide-susceptible weed population to withstand a herbicide and complete its life cycle when the herbicide is used at its normal rate in an agricultural situation.

Target-site resistance is the result of a modification of the herbicide-binding site (usually an enzyme), which precludes a herbicide from effectively binding. This is the most common resistance mechanism.

Cross-resistance occurs where a single resistance mechanism confers resistance to several herbicides. *Target-site cross-resistance* can occur to herbicides binding to the same target site (enzyme). Good examples are the two classes of herbicide chemistry (aryloxyphenoxypropionates and cyclohexanediones). While chemically dissimilar, both inhibit the enzyme acetyl coenzyme A carboxylase and resistant biotypes frequently exhibit varying levels of target-site cross-resistance in both. Some target sites may have more than one domain, e.g., the targeted protein in photosystem II has separate domains that bind triazine-type herbicides and phenolic-type herbicides.[14]

Nontarget-site resistance is resistance due to a mechanism(s) other than a target-site modification. Nontarget-site resistance can be endowed by mechanisms such as enhanced metabolism, reduced rates of herbicide translocation, sequestration, etc. Such mechanisms reduce the amount of herbicide reaching the target site.

Nontarget-site cross-resistance occurs when a single mechanism endows resistance across herbicides with different modes of action. Such mechanisms are usually unrelated to the herbicide target site. Examples are cytochrome P450–based nontarget-site cross-resistance,[15–17] and glutathione transferase–based resistances,[18–20] which degrade a spectrum of herbicides that have different sites of action.

Multiple-resistance occurs when two or more resistance mechanisms are present within individual plants or a population. Depending on the number and type of mechanisms, a population and/or individual plants within a population may simultaneously exhibit multiple-resistance to many different herbicides.

While there has not been international standardization on terminology, this book uses the above-defined terms of resistance, target-site and nontarget-site resistance, and multiple-resistance throughout.[21]

1.2.2 Learning from the History of Resistance

At this moment in time, and in this introductory chapter on herbicide resistance, it is informative to look back over the past 30 years. Prior to 1970, the few reports or observations of weeds exhibiting reduced levels of control with 2,4-D or other early herbicides received little notice or concern among farmers or scientists. Minor interspecific and intraspecific differences or shifts in selectivity among weed populations were very common following the use of herbicides. This was to change dramatically with the first clear evidence of evolved resistance to the triazine herbicides. The triazine herbicides provided excellent weed control; however, even with the remarkably effective and consistent triazine herbicides, missed or escaped weeds were often observed under certain soil and climatic conditions.

The first report of triazine resistance in the previously very susceptible *Senecio vulgaris* populations in a Washington State nursery (U.S.A.) in the late 1960s[12] rightfully received much attention. The weed had evolved an extremely high level of resistance that was genetically transferred to its progeny.[22,23] Many realized that this was likely a harbinger of things to come. Holm et al.,[24] in their major and classic work on world weeds, stated, "This discovery [i.e., resistance to triazines] has proven to be one of the most important events since the inception of weed science. If triazine-resistant weeds are not controlled by some other means, the resistant biotype rapidly predominates, reproduces and becomes a solid infestation that can no longer be controlled by the herbicide. If only triazine herbicides are available to control weeds in that crop, the farmer may no longer be able to produce the crop of choice."

Not long after this first report of triazine-resistant *S. vulgaris* another equally important discovery was made. In 1975, S. Radosevich, a graduate student with Dr. F. M. Ashton at the University of California, Davis, wrote a letter to Dr. Homer M. LeBaron of Ciba-Geigy in which he stated that isolated chloroplasts from triazine-resistant *S. vulgaris* were insensitive to simazine. Radosevich and Appleby[25] had earlier confirmed that there were no differences between the susceptible and resistant biotypes of *S. vulgaris* in herbicide uptake, distribution, or metabolism, whereas it was well known that maize and other tolerant crops avoided injury because they are able to metabolize atrazine.[26] In 1976, Radosevich and DeVilliers published the first report confirming that the triazine resistance in this weed was due to alteration of the target site. This evidence was the first documentation of what would later become many cases of target-site-based resistance to triazine and, ultimately, many other herbicides. They further reported that these triazine herbicide–insensitive chloroplasts were capable of continuing photosynthesis in the presence of simazine or atrazine.

Earlier research had demonstrated that chloroplasts isolated from crop species resistant to triazine herbicides were susceptible to triazines. Moreland[27] had reported that photosynthesis in isolated chloroplasts was equally inhibited by simazine, whether they came from resistant maize or susceptible spinach. Radosevich (1977) soon documented that triazine-resistant common *Chenopodium album* and *Amaranthus retroflexus*, which had recently been found in Washington State maize fields and elsewhere, also had chloroplasts that were insensitive to atrazine. These discoveries on the mechanism of triazine herbicide resistance were more unexpected, and had greater impact on weed science and management, than the original evolution of triazine-resistant weeds.

During the 1970s, many additional important weed species were reported to be resistant to triazine herbicides and several other herbicides. These were widely scattered independent outbreaks in the United States, Canada, and Europe. Some species (e.g., *Amaranthus* spp., *Chenopodium* spp., *Conyza canadensis, Kochia scoparia, Solanum nigrum, Echinochloa crus-galli, Senecio vulgaris,* and *Poa annua*) have evolved resistance to the triazine herbicides frequently and in many locations (Table 1.3). The majority of triazine-resistance cases have occurred from separate evolutionary events and have not been caused by the spread of resistant seed or propagules.[28,29] However, there has been some evolution of triazine resistance along roadsides and rights-of-way, where vehicles have dispersed seed. Triazine resistance has also appeared in orchards and roadsides throughout the world from the persistent use of simazine. In North America, *K. scoparia, Bromus tectorum*, and *S. vulgaris* have mostly evolved resistance to triazine herbicides in roadsides, railways, nurseries, or perennial crops. By 1980, 32 weed species (26 broadleafs and 6 grasses) had evolved resistance to triazine herbicides.

A significant scientific benefit flowing from the work on triazine-resistant weeds has been the increased knowledge and understanding of herbicide-binding sites and modes of action. As further discussed in Chapter 3, the availability of two biotypes identical except for herbicide resistance, due to a small change at the herbicide-binding domain on a protein in the thylakoid membrane, provided a powerful tool to study the mechanisms of photosynthesis, herbicide mechanisms of action, and other physiological and molecular genetic processes.[30–32] Indeed, the target (binding site) has been isolated and crystallized from resistant and susceptible photosynthetic bacteria,[33] leading to a Nobel Prize in medicine, not because the research dealt with herbicide resistance, but because of its universal implications for drug binding, design, and resistance.

1.2.3 When and Where Resistance Evolved

Although the above-mentioned first reports of triazine-resistant weeds were of concern to weed scientists they were not initially of practical significance to most growers, as they were very limited and localized in area, and were usually well controlled with other herbicides. Even among scientists, herbicide-resistant weeds were mostly of academic interest and few were researching how they should be managed. However, it was becoming obvious that the problem deserved greater attention. During 1977, LeBaron organized an informal but enthusiastic meeting at the Weed Science Society of America (WSSA) convention held in Dallas, Texas on February 10, 1978. From this first discussion, research efforts were coordinated and LeBaron organized a formal 1-day symposium, held the following year at the WSSA meeting in San Francisco on February 8, 1979. Of the 14 papers, 8 were presented by scientists from the United States, 4 by scientists from Canada, and 1 each by scientists from Germany and Israel. Dr. J. Gressel agreed to work with LeBaron to edit a book from these papers. The landmark book, *Herbicide Resistance in Plants*, was published in 1982. Chapters in this first book on herbicide resistance included the remarkable progress on photosynthetic mechanisms and herbicide-binding sites,[30] the potential of new herbicide-resistant crops,[22,34] models for predictions of future herbicide-resistant weeds,[35] and physiological responses and fitness of susceptible and resistant weed biotypes.[36] This book was well received and brought to the attention of weed scientists, plant physiologists, and many others the practical and scientific importance of herbicide-resistant weeds.

From these beginnings catalyzed by the first cases of triazine resistance, resistance has evolved in the field to almost all herbicide chemistries and modes of action (Table 1.1) and in almost all cropping systems (Tables 1.2 and 1.3). In many cases researchers have simply stated that resistant weeds occur in "cropland" without specifying a crop. Thus, the fact that a resistant weed biotype is not listed under a particular crop does not necessarily mean that it has not been found in that crop (Table 1.2). The evolution of resistant populations has been slow to appear with some herbicides (Figure 1.1), but resistance continues to evolve to almost all herbicide modes of action being used (Figure 1.2).

In August 2000 the International Survey of Herbicide-Resistant Weeds recorded 235 herbicide-resistant weed biotypes in 47 countries.[37] A new resistant biotype refers to the first instance of a weed species evolving resistance to one or more herbicides in a herbicide group. Up-to-date information on the International Survey of Herbicide-Resistant Weeds can be found on the Web (http://www.weedscience.com).[37] There has been a relatively steady increase in the number of new cases of resistance (approximately nine new cases per year) since 1980 (Figure 1.1). In the 5-year period from 1978 to 1983, scientists around the world documented 33 new cases of triazine-resistant weeds (Figure 1.2). More recently, ALS- and ACCase-herbicide-resistant weeds have accounted for a large portion of the resistant species (Figure 1.2). The first cases of glyphosate-resistant weeds have appeared recently in Australia[38,39] and Malaysia.[40] Importantly, the Malaysian *Eleusine indica* resistant to glyphosate[41] has been reported to have target-site resistance due to a mutation in the EPSP-synthase gene.[40] Considering the recent rapid adoption of glyphosate-resistant crops, more cases of glyphosate resistance are likely; however, it is expected that resistance to glyphosate will appear less frequently than for most herbicide modes of action, following a pattern similar to that observed for phenoxy herbicides (Figure 1.2).

TABLE 1.1
The Occurrence of Herbicide-Resistant Weed Biotypes to Different Herbicide Groups

Herbicide Group	WSSA[a] Code	HRAC[b] Code	Australian Code	Example	Resistant Weed Biotypes		
					Dicots	Monocots	Total
ALS inhibitors	2	B	B	Chlorsulfuron	44	20	64
Triazines	5	C1	C	Atrazine	42	19	61
Bipyridiliums	22	D	L	Paraquat	18	7	25
ACCase inhibitors	1	A	A	Diclofop-methyl	0	21	21
Synthetic auxins	4	O	I	2,4-D	15	5	20
Ureas/amides	7	C2	C	Chlorotoluron	6	11	17
Dinitroanilines	3	K1	D	Trifluralin	2	7	9
Triazoles	11	F3	C	Amitrole	1	3	4
Chloroacetamides	15	K3	E	Butalochlor	0	3	3
Thiocarbamates	8	N	E	Triallate	0	3	3
Glycines	9	G	M	Glyphosate	0	2	2
Benzoflurans	16	N	K	Ethofumesate	0	1	1
Chloro-carbonic-acids	26	N	J	Dalapon	0	1	1
Nitriles	6	C3	C	Bromoxynil	1	0	1
Organoarsenicals	17	Z		MSMA	1	0	1
Pyrazoliums	8	Z		Difenzoquat	0	1	1
Unknown	25	Z		Flamprop-methyl	0	1	1
				Totals	130	105	235

[a] Retzinger and Mallory-Smith[48]
[b] Schmidt [Scm]

Source: Compiled from data in Reference 37.

TABLE 1.2
The Occurrence of Herbicide-Resistant Weeds in Various Cropping Situations

Category	Crop	No. of Resistant Biotypes
Field Crops	Wheat/barley	57
	Corn	50
	Rice	24
	Soybean	22
	Canola	11
	Cotton	5
	Sugarbeet	4
	Unspecified cropland[a]	62
Vegetables	Vegetables (carrot, lettuce, potato, etc.)	16
Perennial Crops	Orchard (apple, pear, peach, ... including vineyard)	37
	Pasture (clover, alfalfa, pasture seed, etc.)	23
	Forestry	8
	Other perennial (tea, coffee, rubber, mint, etc.)	8
Noncrop	Noncrop (roadside, railway, industrial site)	35

[a] Respondents of the survey only indicated that the resistant biotype was found on “cropland” in their region in general and did not specify all the crops.

Source: Compiled from data in Reference 37.

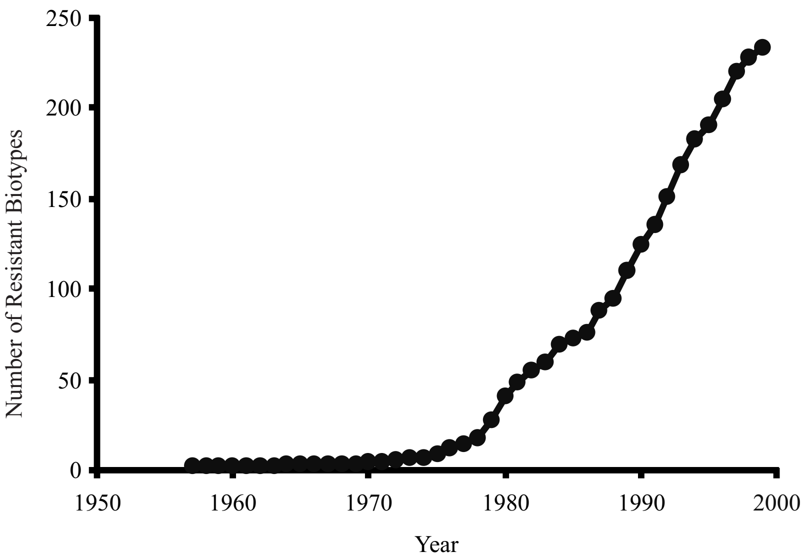

FIGURE 1.1 The chronological increase in the number of herbicide-resistant weeds worldwide.

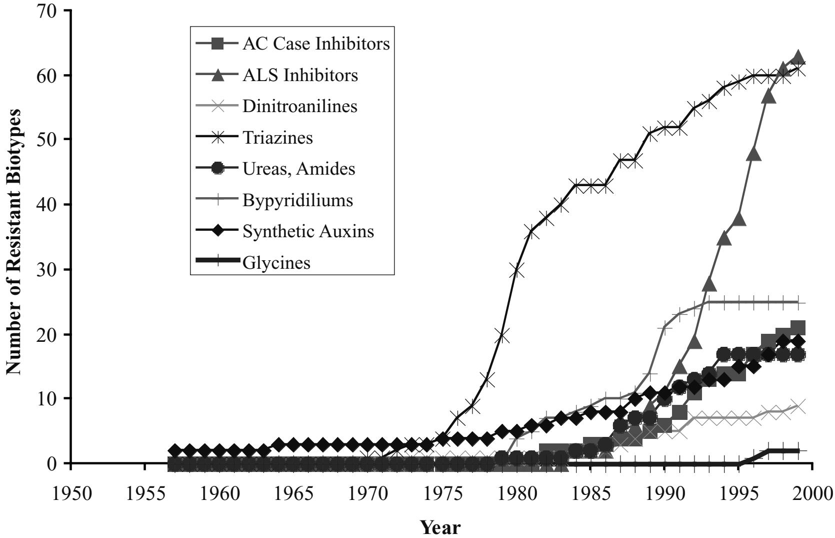

FIGURE 1.2 The chronological increase in the number of herbicide-resistant weeds for several herbicide classes.

1.2.3.1 World Grain Crops

Detailed information on the extent and spread of resistant weed biotypes in the major crops will be provided in subsequent chapters. Here we summarize briefly the resistant weed populations in some of the major crops.

1.2.3.1.1 Wheat

Fifty-seven herbicide-resistant weed biotypes have been identified in wheat and barley (Table 1.2). Grass weeds with resistance to ACCase-inhibiting herbicides and dicot weeds with resistance to ALS-inhibiting herbicides account for the majority of the wheat area infested with herbicide-resistant weeds. Target-site cross-resistance and multiple-resistance in the grass weeds *Lolium rigidum* from Australia and *Alopecurus myosuroides* from Europe are two of the most intractable problems. In some instances there are few remaining herbicides for control of these multiple-resistant biotypes. ACCase-herbicide resistance in weedy *Avena* spp. is widespread in all major wheat-producing regions of the world and multiple-resistant *Avena* spp. are beginning to appear in North America. *Avena* spp. are already among the most serious weeds of cereals, and now they are poised to become the worst herbicide-resistant weed of wheat.

Twenty-four of the herbicide-resistant biotypes occurring in wheat and barley are resistant to ALS-inhibiting herbicides. ALS-herbicide-resistant biotypes of *Kochia scoparia* and *Salsola iberica* now infest more than 60% of wheat fields in the northern United States. In general there have been sufficient alternatives for control of ALS-herbicide-resistant weeds in wheat and barley and the present threat to production is less than that of ACCase-herbicide-resistant grasses (see Chapter 5).

While seven dicot weed species have evolved resistance to synthetic auxin-type herbicides in wheat, none has become a widespread problem and all are easily controlled with alternative modes of action.[37]

1.2.3.1.2 Rice

The *Echinochloa* spp. are major weeds wherever rice is grown and they present growers with the most serious resistance problems in rice (see Chapter 6). Propanil resistance in *E. crus-galli* and *E. colona* has evolved in South America and the United States as a result of elevated levels of the same acylamidase enzyme system that rice uses (nontarget-site-based resistance) to detoxify propanil.[42,43] Target-site cross-resistance to butachlor and thiobencarb has evolved in populations of *E. crus-galli* in China in over 2 million ha.[44] In California (U.S.A.), Fischer et al.[45] identified populations of *E. oryzoides* and *E. phyllopogon* with multiple-resistance (4- to 20-fold) to thiobencarb, molinate, fenoxaprop, and propanil. This has left growers with few alternatives to control *Echinochloa* spp. in some California rice fields (see Chapter 6).

In addition to the above-mentioned grass weed problems of rice there has been a steady increase in the number of sites and the area infested with ALS-herbicide-resistant weeds. Over half of the 24 herbicide-resistant biotypes in rice are resistant to ALS-inhibiting herbicides. With the exception of *Echinochloa* spp., they represent all of the major weed threats to the rice industry. Of particular concern are *Alisma plantago-aquatica* in Italy and Portugal, *Cyperus difformis* and *Sagittaria montevidensis* in Australia and the United States, *Scirpus mucronatus* in Italy and the United States, and *Lindernia* sp. in Asia. The lack of good alternatives in rice for control of some of these species heightens the concern of growers (see Chapter 6).

1.2.3.1.3 Maize

At least 50 herbicide-resistant weed biotypes have evolved resistance in maize production systems worldwide and all but 11 of them are resistant to triazine herbicides (see Chapter 4). The widespread adoption of atrazine for weed control in maize fields resulted in triazine-resistant weeds becoming the first widespread herbicide-resistant weed problem. Triazine-resistant *Chenopodium album* and *Amaranthus* spp. have achieved particular notoriety because of the large areas infested with these biotypes and the fact that they have been identified in 18 countries. *Amaranthus* spp. are of greater concern to growers because they have shown the potential to sequentially evolve multiple-resistance to triazine and ALS herbicides. Two dicot species (*Amaranthus rudis* and *A. palmeri*) and four grasses (*Setaria* spp. and *Sorghum bicolor*) have evolved resistance to ALS herbicides in maize, all in the United States. Even fewer ALS-herbicide-resistant species have evolved in European maize production due to far less usage of ALS herbicides in Europe. Fortunately, the majority of herbicide-resistant weeds in corn can be easily controlled by alternative herbicides (see Chapter 4).

1.2.3.1.4 Soybean

Of the 22 herbicide-resistant biotypes found in soybean, 16 are resistant to ALS herbicides and 3 are resistant to ACCase herbicides. In soybean, five ALS-herbicide-resistant

TABLE 1.3
The Occurrence of Triazine-Resistant Weeds Worldwide

	Species	Common Name	Family	Weed Group	Country and Year
1.	*Abutilon theophrasti*	Velvetleaf	Malvaceae	Dicot	U.S.A. (1984)
2.	*Amaranthus albus*	Tumble pigweed	Amaranthaceae	Dicot	Spain (1987)
3.	*A. blitoides*	Prostrate pigweed	Amaranthaceae	Dicot	Israel (1983), Spain (1986)
4.	*A. cruentus*	Smooth pigweed	Amaranthaceae	Dicot	Spain (1989)
5.	*A. hybridus*	Smooth pigweed	Amaranthaceae	Dicot	U.S.A. (1972), Italy (1980), France (1980), Switzerland (1982), Spain (1985), Israel (1986), South Africa (1993)
6.	*A. lividus*	Livid amaranth	Amaranthaceae	Dicot	Switzerland (1978), France (1981)
7.	*A. palmeri*	Palmer amaranth	Amaranthaceae	Dicot	U.S.A. (1993)
8.	*A. powellii*	Powell amaranth	Amaranthaceae	Dicot	Canada (1977), France (1982), Switzerland (1986), Czech Republic (1989), U.S.A. (1992)
9.	*A. retroflexus*	Redroot pigweed	Amaranthaceae	Dicot	Canada (1980), U.S.A. (1980), Germany (1980), France (1980), Switzerland (1982), Bulgaria (1984), Czech Republic (1985), Spain (1986), Poland (1991), Chile (1995)
10.	*A. rudis*	Common waterhemp	Amaranthaceae	Dicot	U.S.A. (1994)
11.	*Ambrosia artemisiifolia*	Common ragweed	Asteraceae	Dicot	Canada (1976), U.S.A. (1993)
12.	*Arenaria serpyllifolia*	Thymeleaf sandwort	Caryophyllaceae	Dicot	France (1980)
13.	*Atriplex patula*	Spreading orach	Chenopodiaceae	Dicot	Germany (1980)
14.	*Bidens tripartita*	Bur beggarticks	Asteraceae	Dicot	Austria (1979)
15.	*Brachypodium distachyon*	False brome	Poaceae	Monocot	Israel (1975)
16.	*Brassica campestris*	Birdsrape mustard	Brassicaceae	Dicot	Canada (1977)
17.	*Bromus tectorum*	Downy brome	Poaceae	Monocot	France (1981), Spain (1990)
18.	*Capsella bursa-pastoris*	Shepherd's-purse	Brassicaceae	Dicot	Poland (1984)
19.	*Chamomilla suaveolens*	Disc mayweed	Asteraceae	Dicot	United Kingdom (1989)

20.	*Chenopodium album*	Lambsquarters	Chenopodiaceae	Dicot	Canada (1973), Switzerland (1977), U.S.A. (1977), France (1978), New Zealand (1979), Belgium (1980), The Netherlands (1980), Germany (1980), Italy (1982), Czech Republic (1986), Spain (1987), Bulgaria (1989), United Kingdom (1989), Poland (1991), Norway (1994), Chile (1995), Slovenia (1996)
21.	*C. ficifolium*	Figleaved goosefoot	Chenopodiaceae	Dicot	Germany (1980), Switzerland (1986)
22.	*C. polyspermum*	Manyseeded goosefoot	Chenopodiaceae	Dicot	France (1980), Switzerland (1982), Germany (1988)
23.	*C. strictum* var. *glaucophyllum*	Late flowering goosefoot	Chenopodiaceae	Dicot	Canada (1976), Czech Republic (1989)
24.	*Chloris inflata*	Swollen fingergrass	Poaceae	Monocot	U.S.A. (1987)
25.	*Conyza bonariensis*	Hairy fleabane	Asteraceae	Dicot	Spain (1987), Israel (1993)
26.	*C. canadensis*	Horseweed	Asteraceae	Dicot	France (1981), Switzerland (1982), United Kingdom (1982), Poland (1983), Czech Republic (1987), Spain (1987), Belgium (1989), Israel (1993)
27.	*Crypsis schoenoides*	Swamp pricklegrass	Poaceae	Monocot	Israel (1995)
28.	*Datura stramonium*	Jimsonweed	Solanaceae	Dicot	U.S.A. (1992), Chile (1995)
29.	*Digitaria sanguinalis*	Large crabgrass	Poaceae	Monocot	France (1983), Poland (1995)
30.	*Echinochloa crus-galli*	Barnyardgrass	Poaceae	Monocot	U.S.A. (1978), Canada (1981), France (1982), Spain (1992), Poland (1995)
31.	*Epilobium adenocaulon*	American willowherb	Onagraceae	Dicot	Belgium (1980), United Kingdom (1981), Poland (1995)
32.	*E. tetragonum*	Square-stalked willowherb	Onagraceae	Dicot	France (1981), Germany (1988)
33.	*Fallopia convolvulus*	Climbing buckwheat	Polygonaceae	Dicot	Austria (1980), Germany (1988)
34.	*Galinsoga ciliata*	Hairy galinsoga	Asteraceae	Dicot	Germany (1980), Switzerland (1991)
35.	*Kochia scoparia*	Kochia	Chenopodiaceae	Dicot	U.S.A. (1976)
36.	*Lolium rigidum*	Rigid ryegrass	Poaceae	Monocot	Israel (1979), Australia (1988), Spain (1992)
37.	*Lophochloa smyrnacea*	Catstail	Poaceae	Monocot	Israel (1979)
38.	*Matricaria matricarioides*	Pineapple-weed	Asteraceae	Dicot	United Kingdom (1989)
39.	*Panicum capillare*	Witchgrass	Poaceae	Monocot	Canada (1981)

TABLE 1.3 (CONTINUED)
The Occurrence of Triazine-Resistant Weeds Worldwide

	Species	Common Name	Family	Weed Group	Country and Year
40.	*P. dichotomiflorum*	Fall panicum	Poaceae	Monocot	Spain (1981)
41.	*Phalaris paradoxa*	Hood canarygrass	Poaceae	Monocot	Israel (1979)
42.	*Plantago lagopus*	Plantain	Plantaginaceae	Dicot	Israel (1992)
43.	*Poa annua*	Annual bluegrass	Poaceae	Monocot	France (1978), Germany (1980), Belgium (1981), The Netherlands (1981), United Kingdom (1981), Japan (1982), Czech Republic (1988), U.S.A. (1994), Norway (1996)
44.	*Polygonum aviculare*	Prostrate knotweed	Polygonaceae	Dicot	The Netherlands (1987)
45.	*P. hydropiper*	Marshpepper smartweed	Polygonaceae	Dicot	France (1989)
46.	*P. lapathifolium*	Pale smartweed	Polygonaceae	Dicot	France (1979), Czech Republic (1982), Germany (1988), Spain (1991)
47.	*P. pennsylvanicum*	Pennsylvania smartweed	Polygonaceae	Dicot	U.S.A. (1990)
48.	*P. persicaria*	Ladysthumb	Polygonaceae	Dicot	New Zealand (1980), France (1980), Czech Republic (1989)
49.	*P. monspeliensis*	Rabbitfoot polypogon	Poaceae	Monocot	Israel (1979)
50.	*Raphanus raphanistrum*	Wild radish	Brassicaceae	Dicot	Australia (1999)
51.	*Senecio vulgaris*	Common groundsel	Asteraceae	Dicot	U.S.A. (1970), United Kingdom (1977), Germany (1980), Belgium (1982), Switzerland (1982), The Netherlands (1982), France (1982), Czech Republic (1988), Chile (1995), Norway (1996)
52.	*Setaria faberi*	Giant foxtail	Poaceae	Monocot	U.S.A. (1984), Spain (1987)

53.	*S. glauca*	Yellow foxtail	Poaceae	Monocot	Canada (1981), France (1981), U.S.A. (1984), Spain (1987)
54.	*S. verticillata*	Bristly foxtail	Poaceae	Monocot	Spain (1992)
55.	*S. viridis*	Green foxtail	Poaceae	Monocot	France (1982), Spain (1987)
56.	*S. viridis* var. *major*	Giant green foxtail	Poaceae	Monocot	France (1982)
57.	*Sinapis arvensis*	Wild mustard	Brassicaceae	Dicot	Canada (1994)
58.	*Solanum nigrum*	Black nightshade	Solanaceae	Dicot	France (1979), Italy (1980), Germany (1980), Belgium (1981), The Netherlands (1981), Switzerland (1983), United Kingdom (1983), Spain (1987), Poland (1995)
59.	*Sonchus asper*	Spiny sowthistle	Asteraceae	Dicot	France (1980)
60.	*Stellaria media*	Common chickweed	Caryophyllaceae	Dicot	Germany (1978)
61.	*Urochloa panicoides*	Liverseedgrass	Poaceae	Monocot	Australia (1996)

Source: Compiled from data in Reference 37.

Amaranthus spp. and four ALS-herbicide-resistant *Setaria* spp. have evolved in the midwestern United States. The rapid adoption of glyphosate-resistant soybean in the United States has curbed the rate of spread of many biotypes that evolved resistance to other herbicides in soybean (see Chapter 4). South American soybean growers face increasing problems of ACCase-herbicide-resistant populations of *Brachiaria plantaginea*, *Eriochloa punctata*, and *Sorghum sudanese*.

1.2.3.1.5 Canola

Eleven cases of herbicide-resistant weed biotypes have been reported in canola. The most serious of these are ACCase-herbicide-resistant *Avena fatua* and *Setaria viridis* and the ALS-herbicide (ethametsulfuron-methyl)-resistant *Sinapis arvensis*. While the ALS-herbicide-resistant *S. arvensis* is not currently widespread (approximately 200 ha) it is particularly troublesome, as ethametsulfuron-methyl is the only solution for removal of *Sinapis* from conventional canola crops. Fortunately, glyphosate- and glufosinate-resistant canola varieties have alleviated this problem for some growers.

1.2.3.2 Resistance in Other Ecosystems

1.2.3.2.1 Cotton

Given the intensive use of herbicides in cotton production it is surprising that only five weeds have been recorded as having evolved resistance to herbicides in cotton (Table 1.2). This low number, despite the propensity of monoculture cotton, is probably due to the multiplicity of different herbicides typically used throughout the cotton-growing season and the continued use of mechanical weed control, often including hand-removal of survivors. In the cotton-growing regions of the southern United States, *Sorghum halepense* has evolved ACCase-herbicide resistance; *Amaranthus palmeri*, *Eleusine indica*, and *S. halepense* have evolved dinitroaniline resistance; and *Xanthium strumarium* has resistance to MSMA/DSMA.

1.2.3.2.2 Perennial crops

Thirty-seven herbicide-resistant weed biotypes have evolved in orchards and vineyards worldwide (Table 1.2). The majority are triazine-resistant weeds of orchards (19 species) and 11 species with resistance to bipyridilium herbicides. On the whole, these have been easily controlled with alternative herbicides or cultural controls, but typically at a substantially increased cost of weed control to the grower. The economic impact of herbicide-resistant weeds in these crops has been far less than in annual cropping systems because of the alternatives available and the lower impact of weeds in general on perennial crops. Two recent and important cases of resistance in orchards are those of glyphosate-resistant *Lolium rigidum* in an apple orchard in Australia[39] and in an almond orchard in the United States and glyphosate-resistant *Eleusine indica* in a fruit orchard in Malaysia.[41] These cases are of interest not because of their economic importance in orchards but because they show that glyphosate-resistant weeds will evolve given sufficient selection pressure, a point that was debated in the early and mid-1990s by industry and academia.

1.2.3.2.3 Noncrop

There have been 35 herbicide-resistant weed biotypes recorded for roadside, railway, and industrial sites. Nineteen of these species have evolved resistance to triazine herbicides and eight to ALS herbicides. Considering that only about 10% of the total herbicide usage is for these purposes, this is well above average. A major reason is that, traditionally, only the least expensive herbicides are used, leading to repeated use of the same herbicide at high rates without other herbicides, or other control measures such as tillage or competition from crops. Resistance evolved to the most persistent herbicides that exert the greatest selection pressure. Persistence of the herbicide can derive from the inherent slow degradation of a herbicide used often at high rates or from the propensity to make multiple applications of a herbicide throughout the year.

It is notable that many of the same resistant biotypes occur on railway lines/roadsides and in adjacent fields, which may indicate that the spread of resistant weeds in either direction has been a factor in exacerbating resistance management strategies. This is certainly the case for ALS-herbicide-resistant *Kochia scoparia* where resistant populations selected through usage of ALS herbicides along railway lines and roadsides have spread and have subsequently been detected in potato fields of Idaho where no ALS herbicides had been used.

There are many alternatives for control of weeds in noncrop situations and undoubtedly many resistant weeds of noncrop situations have gone undetected due to the ease of changing herbicide mixtures when weed populations survive treatment.

1.2.4 Weeds That Are Resistance Generalists

Some weed species have a far greater propensity to evolve resistance than other species. Of the 152 weed species that have evolved resistance to one or more herbicide modes of action (MOA), 106 have evolved resistance to only 1 MOA, 28 species to 2 MOA, 10 species to 3 MOA, 2 species to 4 MOA, 2 species to 5 MOA, 3 species to 6 MOA, and 1 species (*Lolium rigidum*) has evolved resistance to 8 MOA. Grass weed species account for all the cases of weed species that have evolved multiple-resistance to five or more herbicide modes of action. These grasses are *L. rigidum* (8 MOA and 16 countries), *Echinochloa crus-galli* (6 MOA and 15 countries), *Avena fatua* (6 MOA and 16 countries), *Poa annua* (6 MOA and 15 countries), *Alopecurus myusoroides* (5 MOA and 8 countries), and *Eleusine indica* (5 MOA and 5 countries). These grasses have evolved resistance to many of the herbicides used against them. The first three account for hundreds of thousands of hectares of herbicide-resistant weed infestations throughout the world, representing the most intractable cases of herbicide resistance worldwide.

Few dicot weed species have evolved resistance to a wide range of herbicide modes of action. The most widespread herbicide-resistant dicot biotypes are *Chenopodium album* (18 countries), *Amaranthus retroflexus* (15 countries), *Conyza canadensis* (14 countries), *Senecio vulgaris* (12 countries), and *Solanum nigrum* (10 countries). *Amaranthus* spp. in general appear to be the most resistance prone of the dicot weeds. *A. retroflexus* has evolved resistance to 3 MOA; *A. hybridus*, *A. lividus*, and *A. palmeri* to 3 MOA; *A. powellii, A. blitoides,* and *A. rudis* to 2 MOA; and *A. albus* and *A. cruentus* to 1 MOA. The *Amaranthus* spp. have shown the capacity to evolve resistance to ALS, triazine, urea, bypyridilium, and dinitroaniline herbicides. It is also feared that *A. rudis* may have evolved resistance to glyphosate in the midwestern United States.[46]

Initially, triazine-resistant dicot weeds accounted for the greatest area infested by herbicide-resistant weeds. This has changed over the last 10 years and now ALS-herbicide-resistant weeds account for the greatest number of resistant species and probably the largest area affected by resistance. ALS-herbicide-resistant populations of *Kochia scoparia* and *Salsola iberica* are now so widespread throughout the northern United States that few growers consider using an ALS herbicide for control of these species.

The area infested by a given species provides the most agronomically significant description of the extent of resistance. Unfortunately, there are few estimates of areas, and most are only based on educated guesses. The 2 million ha of butachlor/thiobencarb cross-resistant *Echinochloa crus-galli* is a local scientist's estimation.[44] The millions of hectares of resistant *L. rigidum* in Australia are based on limited data. It may be more appropriate to see which weed species have evolved in the greatest numbers of locations, with the greatest numbers of reports. Using these criteria, the 25 most prevalent resistant species are summarized in Table 1.4. By analyzing the data amassed in the resistance Web site it is evident that some weed species are on the list due to biological factors, as they have the ability to evolve resistance to many herbicide groupings or in diverse agroecosystems. Some weed species appear on the list because they exist in many cropping systems, and a single herbicide group is used in all those systems. Many weed species could be there because, based on educated guesswork, they are in the top 76[47] or the top 180[24] listing of the world's worst weeds, and their distribution is widespread. Still, some of the top 76 weeds have not evolved herbicide resistance, including some of the top 10.

1.3 RESISTANCE IN THE DEVELOPED VS. DEVELOPING WORLD

Based on the survey by Heap,[37] the following countries are reporting the greatest number of herbicide-resistant biotypes: United States, 80; Australia, 32; Canada, 32; France, 30; Spain, 24; U.K., 19; Israel, 18; Germany, 15; Belgium, 15; Switzerland, 14; and Japan, 12. These and many other developed countries already have serious infestations of herbicide-resistant weeds, especially in major crops, and in the most productive and fertile areas where herbicides are most essential. The comparison of countries based on their present economies and high technology agriculture, however, presents some important ironies and paradoxical challenges. The developing countries have not depended as much on herbicides due to economic limitations and the availability of cheap labor. They therefore have fewer problems with herbicide-resistant weeds, yet these developing countries suffer the greatest losses from weeds. Where food production is least efficient and subsistence farming is commonly practiced, the needs are acute for better weed control tools, including herbicides. As economies and farming efficiency improve, the farm workers presently used for hand-hoeing find more satisfying and profitable occupations elsewhere. Conversely, the more extensive use of herbicides will bring with it greater problems from resistant weeds and require better management of weeds and herbicides. Over the next decade this will be most evident for rice-growing regions in developing nations (see Chapter 6).

Resistance is widespread throughout the developed world. The control of weeds that have a propensity to evolve resistance (Table 1.4) is most likely to result in the rapid evolution of resistance. While resistance is inevitable wherever herbicides are persistently used, the preemptive practices outlined throughout this book can slow the evolutionary processes leading to resistance. Herbicide use is sporadic in the developing world, and thus resistance is found only in pockets. Where there is resistance (mainly in high-value plantation crops and in dwarf or semidwarf wheat and rice), the areas affected are quite extensive. As developing countries industrialize and herbicide use replaces farm labor, more cases can be expected of the same resistances as have occurred in the grass weeds of wheat and rice in the developed countries. It is typical of developing countries to develop and produce a single herbicide for a single weed problem, and farmers have fewer alternatives and are less likely to rotate herbicide chemistries than in the developed world. This happened in Hungary, where almost all the corn land was infested with triazine-resistant weeds because of monoculture and the local production of cheap atrazine. For reasons such as these we anticipate a rapid increase in the number of herbicide-resistance problems appearing in the developing nations.

1.4 SUMMARY

As will be elaborated in the following chapters, there have been considerable advances in our understanding of the causes, nature, genetics, mechanisms, and solutions for herbicide-resistant weeds since the first triazine-resistant *Senecio vulgaris* was documented 30 years ago. Understanding these factors is a necessary step in devising effective herbicide-resistance management strategies. However, implementing these resistance management strategies has proven to be the most difficult step. Cooperation among academia, industry, and growers is necessary in devising management strategies that are attractive for growers to adopt (see Chapter 7). Most growers still consider herbicide-resistance avoidance a low priority and do not change their weed control programs to avoid resistance because of financial or logistic constraints (see Chapter 7). New biotechnology-derived technologies, such as herbicide-resistant crops, will provide us with opportunities for management of existing herbicide-resistance problems, but in the long run may themselves cause future resistance problems. As outlined throughout this text the solutions to achieve sustainable weed management practices will differ between regions and agroecosystems but will, inevitably, involve more diversity in weed control technologies than is currently evident in many developed nations. It is hoped that this chapter and book can help catalyze more diverse weed control systems in world agriculture.

TABLE 1.4
The Top 25 Worst Herbicide-Resistant Weeds Weighted by Propensities in Countries, MOA, Sites, Hectares, and Cropping Systems

	Common Name	Species	No. Countries	No. MOA	No. Sites	No. Hectares	No. Cropping Regimes
1.	Rigid ryegrass	*Lolium rigidum*	16	8	7,000	836,400	6
2.	Wild oat	*Avena fatua*	16	6	22,100	2,941,200	4
3.	Redroot pigweed	*Amaranthus retroflexus*	15	3	11,500	31,900	10
4.	Lambsquarters	*Chenopodium album*	18	2	19,700	463,600	5
5.	Green foxtail	*Setaria viridis*	6	4	3,800	1,220,900	5
6.	Barnyardgrass	*Echinochloa crus-galli*	15	6	1,200	817,600	4
7.	Goosegrass	*Eleusine indica*	5	5	6,300	20,100	6
8.	Kochia	*Kochia scoparia*	4	3	50,400	189,200	4
9.	Horseweed	*Conyza canadensis*	14	4	1,400	7,300	7
10.	Palmer amaranth	*Amaranthus palmeri*	3	3	12,000	356,200	5
11.	Common groundsel	*Senecio vulgaris*	12	3	1,900	6,800	6
12.	Smooth pigweed	*Amaranthus hybridus*	8	2	10,200	32,900	4
13.	Annual bluegrass	*Poa annua*	15	6	1,100	5,200	4

14.	Blackgrass	*Alopecurus myosuroides*	13	4	1,900	9,300	3
15.	Black nightshade	*Solanum nigrum*	10	2	1,600	4,500	6
16.	Italian ryegrass	*Lolium multiflorum*	7	2	4,200	26,200	3
17.	Common waterhemp	*Amaranthus rudis*	2	2	8,300	25,800	5
18.	Common ragweed	*Ambrosia artemisiifolia*	3	2	2,200	15,900	3
19.	Prostrate pigweed	*Amaranthus blitoides*	3	2	800	2,500	4
20.	Powell amaranth	*Amaranthus powellii*	7	2	100	700	5
21.	Little seed canary grass	*Phalaris minor*	3	2	55,800	609,300	1
22.	Sumatran fleabane	*Conyza sumatrensis*	4	1	900	2,200	5
23.	Wild poinsettia	*Euphorbia heterophylla*	3	2	800	24,600	2
24.	American willowherb	*Epilobium adenocaulon*	5	2	900	300	2
25.	Hood canary grass	*Phalaris paradoxa*	3	2	800	2,500	2

Note: These 25 weeds were chosen by cycling through the whole database[37] five times summing the ranks for each of the 150 weed species. The weeds were then sorted and ranked separately by the number of countries, MOA, etc. for each of the categories. The cumulative rank for each species for each of the five categories was determined and the 25 with the highest ranks are shown. The rest may be seen on the Web site.[37] Despite being performed by numeric criteria, there is an arbitrariness of having large and small countries equalized. There is good genetic reason to consider the *Amaranthus* spp. as a single complex, which would enhance its position.

Source: Compiled from data in Reference 37.

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