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Authors: Vencill, William K., Nichols, Robert L., Webster, Theodore M., Soteres, John K., Mallory-Smith, Carol, et al.

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Herbicide Resistance: Toward an Understanding of Resistance Development and the Impact of Herbicide-Resistant Crops

William K. Vencill, Robert L. Nichols, Theodore M. Webster, John K. Soteres, Carol Mallory-Smith, Nilda R. Burgos, William G. Johnson, and Marilyn R. McClelland*

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Executive Summary

Development of herbicide-resistant crops has resulted in significant changes to agronomic practices, one of which is the adoption of effective, simple, low-risk, crop-production systems with less dependency on tillage and lower energy requirements. Overall, the changes have had a positive environmental effect by reducing soil erosion, the fuel use for tillage, and the number of herbicides with groundwater advisories as well as a slight reduction in the overall environmental impact quotient of herbicide use. However, herbicides exert a high selection pressure on weed populations, and density and diversity of weed communities change over time in response to herbicides and other control practices imposed on them. Repeated and intensive use of herbicides with the same mechanisms of action (MOA; the mechanism in the plant that the herbicide detrimentally affects so that the plant succumbs to the herbicide; e.g., inhibition of an enzyme that is vital to plant growth or the inability of a plant to metabolize the herbicide before it has done damage) can rapidly select for shifts to tolerant, difficult-to-control weeds and the evolution of herbicide-resistant weeds, especially in the absence of the concurrent use of herbicides with different mechanisms of action or the use of mechanical or cultural practices or both.

The purpose of this paper is to introduce the basic tenets of weed management, to define herbicide resistance and tolerance and how they affect crop production and are affected by management practices, and to present the environmental impacts of herbicide-resistant crops. This paper will summarize aspects of herbicide resistance in five different sections: (1) a description of basic weed science management practices and concepts, (2) definitions of resistance and tolerance in weed science, (3) environmental impacts of herbicide-resistant crops, (4) strategies for management of weed species shifts and herbicide-resistant weeds and adoption by the agricultural community, and (5) gene-flow potential from herbicide-resistant crops.

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* First author: Professor, Department of Crop and Soil Sciences, University of Georgia, 3111 Miller Plant Science Building, 120 Carlton Street, Athens, GA 30502; second author: Cotton Incorporated, 6399 Weston Parkway, Cary, NC 27513; third author: Research Agronomist, Crop Protection and Management Research Unit, USDA–Agricultural Research Service, Tifton, GA 31794; fourth author: Global Weed Resistance Management Lead, Department of Scientific Affairs, Monsanto Company, 800 N. Lindburgh Boulevard, St. Louis, MO 63167; fifth author: Professor, Department of Crop and Soil Science, Oregon State University, Corvallis, OR 97331; sixth and eighth authors: Professor and Research Assistant, Department of Crop, Soil, and Environmental Sciences, University of Arkansas, 1366 West Atheimer Drive, Fayetteville, AR 72704; seventh author: Professor, Department of Botany and Plant Pathology, Purdue University, West Lafayette, IN 47907-1155. Corresponding author's E-mail: wvencill@uga.edu

Section 1: Introduction. To avoid or delay the development of resistant weeds, a diverse, integrated program of weed management practices is required to minimize reliance on herbicides with the same MOA. Weed management diversity must include herbicidal and nonherbicidal weed control strategies. One nonherbicidal strategy is prevention of physical movement of weed seeds or propagules to uninfested areas by cleaning equipment, using clean crop seed, preventing movement of plant reproductive structures, and by the timely scouting of fields and controlling of weeds that escape herbicidal control. Other methods are the use of biological control and cultural control tactics: crop rotation, cover crops (including those with allelopathic activity—the ability to suppress growth of other plants by chemicals released from the allelopathic plant), intercropping, mulches, water management, and manipulation of crop planting dates, seeding rates, cultivar choice, fertilization, and row spacing. These methods can be used to give the crop a competitive advantage over the weeds. For example, crop rotations improve weed control by periodically changing the weed community because various crops differ in planting and harvest dates, growth habit, competitive ability, fertility requirements, and associated production practices, thereby favoring different weed associations and allowing the use of herbicides having different MOAs. Planting dates can disrupt the growth season of a weed, and tillage affects crop and weed interactions. Although there is a place for tillage in resistance management, conservation-tillage production offers many benefits to producers (among them, savings of time, labor, equipment use, and fuel; nitrogen fixation when legumes are used as cover crops; decreased soil erosion by wind and water; and increased soil tilth), and its sustainability should be protected.

Section 2: Resistance and Tolerance. To avoid confusion about the differences in plant tolerance and plant resistance, the Weed Science Society of America (WSSA) defined both terms. *Tolerance* is "the inherent ability of a species to survive and reproduce after herbicide treatment. This implies that there was no selection or genetic manipulation to make the plant tolerant; it is naturally tolerant." Tolerance is the basis for selectivity in herbicide use, whereby certain weeds are

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susceptible to the effects of a herbicide that the crop can easily withstand. *Resistance* is "the inherited ability of a plant to survive and reproduce following exposure to a dose of herbicide normally lethal to the wild type. In a plant, resistance may be naturally occurring or induced by such techniques as genetic engineering or selection of variants produced by tissue culture or mutagenesis."

Herbicide resistance in weeds is a global problem. As of the beginning of 2012, 372 unique, herbicide-resistant biotypes have been confirmed worldwide. The United States has 139 of these biotypes, Australia has 60, Canada has 52, France and Spain have 33 each, Brazil has 25, Germany has 26, Israel has 27, the United Kingdom has 24, and there are from 1 to 19 in most other countries with intensive agriculture. Each of these biotypes is resistant to at least one herbicide MOA, and many MOAs have selected for a number of resistant weeds. For example, 116 weed biotypes are resistant to the acetolactate synthase (ALS)-inhibiting herbicides (e.g., chlorimuron, pyrithiobac, imazaquin), and there are 21 glyphosate-resistant biotypes—13 of them in the United States.

The advent of herbicide-resistant weeds, however, did not begin with herbicide-resistant crops; resistant weeds have been evolving in conventional crop cultivars worldwide from selection pressure placed on them from repeated use of herbicides. A plant does not evolve resistance because herbicides cause a genetic change in the plant that makes it resistant. Rather, a few plants with natural resistance to the herbicide survive an application of the herbicide, and as those plants reproduce and each generation is exposed to the herbicide, the number of resistant plants in the population increases until they dominate the population of susceptible plants.

Section 3: Environmental Impacts of Herbicide-Resistant Crops. Conservation tillage used in crop production has increased in part because of the adoption of broad-spectrum herbicides and herbicide-resistant crops. Adoption of conservation tillage in the United States since 1982 is credited with reducing average soil erosion by 30%, raising the amount of soil carbon, and lowering CO_2 emissions. From 1996 through 2005, years of rapid adoption of genetically modified crops, the global use of pesticides, including herbicides, was reduced by 224 million kg ai (a 6.9% reduction), and the overall environmental impact associated with pesticide use on these crops was reduced by 15.3%. The number of herbicides that required U.S. Environmental Protection Agency (USEPA) groundwater advisory labeling was reduced by 60% or 7.7 million kg. Reports on the effects of herbicide-resistant crops on biodiversity vary, with some indicating that plant diversity is affected early in the season, but not later, and some reporting weed shifts, but no changes in weed density or diversity.

Section 4: Management Strategies for Weed Species Shifts and Herbicide-Resistant Weeds and Adoption by the Agricultural Community. Herbicide-resistant weed management practices most often recommended by weed scientists include (1) using different herbicide MOAs in annual rotation, tank mixtures, and sequential applications; (2) adopting crop rotations that allow use of alternative MOAs or that change the balance of weeds in a field or both; (3) expanding the use of cultural control measures, such as increased seeding rates and altered planting dates; (4) using only labeled herbicide rates at labeled application timings; (5) preventing seed movement and using clean crop seed; (6) scouting fields; and (7) controlling weed escapes. An understanding of grower perception of weed management and herbicide resistance informs weed scientists as to where and how best to focus education and training programs. Strategies to improve education about herbicide resistance include (1) expanding efforts by university and industry scientists to understand growers' perceptions of weed management, recommended resistance-management practices, and herbicide-resistant weeds; (2) implementing communication that is more effective and grower education programs; and (3) publishing management strategies designed to address mitigation and management of herbicide-resistant weeds.

Section 5: Gene Flow from Herbicide-Resistant Crops. Of potential concern with herbicide-resistant crops, especially transgenic crops, is the possibility of the transfer of genetic material from one plant population to another. Concerns include herbicide-resistant crop plants becoming weeds in other crops, transfer of the resistance gene to conspecific crops or wild or weedy relatives, and the adventitious presence of unintended genetic material in grain, feed, or food products. Gene flow via pollen and seeds from both transgenic and conventionally bred, herbicide-resistant crops has been documented. In general, gene flow via pollen occurs at relatively short distances because pollen is viable for only hours or days. Movement of seeds, however, can occur at any point from planting to the final destination of the crop.

New herbicide-resistant crop varieties will continue to be released, some with resistance to more than one herbicide. As with new technology in general, the benefits of herbicide-resistant crops must be weighed against their risks, and management practices must be used that reduce even minor risks as much as possible. The use of herbicide-resistant crops is a valuable tool in agriculture, and efforts to make their use sustainable must continue.

Introduction

A Summary of Weed Science Practices and Concepts. All means used for pest management impose genetic selection on the treated populations. When selection occurs within a sufficiently large population, individuals that are unaffected or less affected than the general population may survive and produce progeny in succeeding generations. Weed communities have evolved over time in response to control practices imposed on them. For the past half century, a principal method of weed management in commercial crops in the United States and in most developed countries has been the use of herbicides. Herbicide-resistant weeds have been an issue since the early 1970s (Timmons 1970), although it was described as a potential problem as early as 1957 (Hilton 1957; Switzer 1957). Resistant weeds have been evolving worldwide from selection pressure caused by the repeated use of herbicides with the same mechanism of action (MOA) in conventional crop cultivars. However, "resistance evolution" does not mean that a herbicide directly changes a plant genetically (i.e., by causing mutations). Instead, the herbicide selects for plants with some level of natural genetic resistance to that MOA.

Herbicide-resistant crops, however, have been developed to withstand treatment with a herbicide that the conventional cultivar could not tolerate. Not all herbicide-resistant crops

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are a product of gene insertion (transgenic). However, introduction of transgenic, herbicide-resistant crop cultivars substantially changed virtually all aspects of weed management and changed the herbicide-selection pressure on weed populations because of significant shifts in herbicide usage. Transgenic crops resistant to glyphosate are now grown on approximately 70 million ha worldwide (Price et al. 2011) and dominate the production of corn (*Zea mays* L.), soybean [*Glycine max* (L.) Merr.], cotton (*Gossypium hirsutum* L.), and canola (*Brassica napus* L.). Transgenic crop technology has allowed the use of the broad-spectrum herbicides glyphosate and glufosinate. Use of these herbicides intensifies selection of weed populations against those MOAs because repeated use of a single, broad-spectrum MOA replaces use of multiple MOAs and tillage. The use of herbicide-resistant crops created a reduction in the diversity of weed-management techniques previously employed over broad areas.

The single, most important lesson learned in managing weed resistance to herbicides is that the maintenance of a diversity of weed-management tactics is critical for sustaining the use of herbicide options. Overreliance on a single herbicide or a group of herbicides within the same MOA group without concurrent use of other weed-management options has encouraged the evolution of weed populations resistant to these intensively used herbicides. The introduction to this paper will provide an understanding of basic weed-management strategies—prevention, cultural and mechanical techniques, biological methods, and herbicidal management—and how they affect weed populations in conventional and herbicide-resistant crops. These are tactics used to develop and maintain the diversity of crop management practices to mitigate the evolution of resistant weeds.

The rest of the paper will review current knowledge of, and concerns about, herbicide-resistant crops and weeds in agroecosystems, in the following sections: (1) definitions and basic information about herbicide resistance and tolerance; (2) weed population shifts; (3) environmental effects of herbicide-resistant crops, especially transgenic crops; (4) adoption of strategies for managing resistant weeds; and (5) the potential for gene flow from herbicide-resistant crops to other plants. This review will provide a background for understanding the adoption of best management practices (BMPs) and the recommendations offered in the accompanying paper.

Description of a Weed. To call a plant a weed is to relate that plant to the human environment. *Weeds* are plants that grow where their presence can interfere with human intention: in crops, gardens, pastures, ranges, lawns, and landscapes; along thoroughfares; in areas of commerce and recreation; and in natural areas, where invasive species may alter the native flora. Human intentions define weeds, and human activities physically support weed establishment and propagation. Disturbance of the environment creates opportunities for plants whose biological capacities predispose them to rapidly colonize open space. Many of the weeds that infest annual cropping systems are those plant species best suited to colonizing frequently disturbed habitats. The weed species composition and ditribution of any given area are influenced by environmental and biological factors that determine the habitat type (Radosevich et al. 1997). Environmental factors, such as soil type, pH, soil moisture, light quantity and quality, precipitation patterns, and temperature, and biological factors, such as crop type, crop–weed interactions, insects, plant pathogens, and other biota in the area, affect weed species composition. As species change, weed composition and distribution are further affected by human efforts to control weeds in a crop.

Common Categories and Specific Methods of Nonherbicidal Weed Control. An integrated weed management (IWM) or integrated pest management program for weeds is developed by combining strategies from several broad categories of weed control tactics: preventive, cultural, mechanical, biological, and chemical control (herbicides).

Prevention. Prevention is one of the most basic of weed control methods (Buhler 2002). This tactic, which uses methods to prevent the introduction of a weed into an area or to prevent its spread, is a vital part of an IWM program. Laws regulating seed purity and prohibiting the spread of noxious weeds contribute to prevention. Other methods include planting crops that are not contaminated by weed seed; cleaning field machinery, so that weed seeds and propagules will not be transported to other fields; and preventing the spread of weed propagules by transport of livestock, manures, or compost, or through irrigation or drainage waters (Walker 1995). Timely scouting of fields, another preventive method, allows early detection of uncontrolled, potentially resistant weeds or of shifts to difficult-to-control weeds when the weeds are small and there are still effective control options.

Cultural Control. Cultural weed management refers to agronomic practices that use competitiveness of the crop to maximize its growth while diminishing the growth and subsequent competitiveness of associated weeds. Interest in cultural weed control was renewed in the 1980s and 1990s because of mandatory, government-imposed reductions in pesticide use in European countries and growing public support for similar reductions in North America (Hansen and Zeljkovich 1982; King and Buchanan 1993; Liebman and Dyck 1993b). Cultural strategies include such tactics as rotating crops, improving crop competition through crop variety selection and planting date, and optimizing seeding rates (Beckie and Gill 2006; O'Donovan et al. 2007).

Crop Rotation. Before the introduction of modern herbicides in the 1940s, crop rotation was a primary method of weed control. Crop rotations are one method of preventing weed shifts (change in the composition or relative frequencies of weeds in a plant population or community because of environment or agronomic practices that favor one species over another). For example, a rotation from rice (*Oryza sativa* L.) to crops such as cotton, tomato (*Lycopersicon esculentum* L.), safflower (*Carthamus tinctorius* L.), grain sorghum [*Sorghum bicolor* (L.) Moench. ssp. *bicolor*], or wheat (*Triticum aestivum* L.) reduced aquatic weed populations in flooded rice production (Hill and Bayer 1990). A green foxtail [*Setaria viridis* (L.) Beauv.] population was 960 plants m^{-2} in monoculture wheat vs. 3.5 m^{-2} in wheat with a summer fallow rotation (Liebman and Dyck 1993a). In a corn monoculture, a single weed species comprised 94% of weeds present, whereas in a corn–wheat rotation, no single species contributed more than 43% of the total weeds present (Liebman and Dyck 1993a).

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Crop rotations improve weed control by periodically changing the weed community because various crops differ in planting and harvest dates, growth habit, competitive ability, fertility requirements, and associated production practices, thereby favoring different weed associations (Buhler 2002; Forcella et al. 1993; O'Donovan et al. 2007). Weeds can adapt to a specific crop (Labrada 2006), and a rotation between different crop types can help break the cycle of adapted weeds (Buhler 2002). Ecologically, the rotation crop may inhabit niches that weeds occupied in the previous crop, or it may be a highly competitive crop that prevents weeds from thriving and producing seeds (Melander and Rasmussen 2001). Herbicide use in different crops may also result in control of different species. For example, a grass crop (corn, grain sorghum, wheat, or rice) can be rotated with a broadleaf crop, such as soybean; herbicides used in the broadleaf crop can effectively control grass weeds that were not controlled well in the grass crop. Before more-effective herbicides were introduced for grass control in rice, one of the recommendations for control of red rice (*Oryza sativa* L.) in commercial rice was to rotate to soybean, where herbicides to control grasses could be used more effectively.

For resistance management, crop rotation allows the introduction of herbicides having different MOAs to avoid successive use of a single MOA (Anderson et al. 1999; Buhler 2002; HRAC 2009a). Additionally, the life cycle of the weed can be disrupted or avoided by rotating crops (HRAC 2009a). Crops with different times of planting and different production practices allow a variety of cultural techniques to be used to optimize crop competitiveness at the expense of weed growth and reproduction.

Cover Crops, Intercropping, and Mulches. Cover crops are a way of minimizing weed populations while maintaining seasonal vegetative cover to prevent soil erosion (Moore et al. 1994). A cover crop is usually a "noncash" crop that can be grown before, or in the case of a living mulch or smother crop, with, a cash crop so that vegetative cover remains on the field for as long as possible during the year (Melander et al. 2005). Several advantages accrue from cover crops. They help producers meet conservation-tillage requirements for year-round vegetation cover; aid in soil erosion prevention; improve soil structure and, often, organic matter content; protect plants in sandy areas from sand-blow injury; fix nitrogen if the cover crop is a legume; and possibly suppress weed emergence and growth (Akemo et al. 2000; Krutz et al. 2009; Melander et al. 2005; Norsworthy et al. 2011; Snapp et al. 2005; Teasdale 1998). Some research has shown that cover crops can provide enough early season weed control that a PRE application of herbicide can be eliminated (Ateh and Doll 1996; Fisk et al. 2001; Isik et al. 2009; Malik et al. 2008; Reddy 2001). Suppression of weeds by cover crops depends partly on biomass production of the crop. In a comparison of nine cover crops in Kentucky, biomass from cereal rye (*Secale cereale* L.) and wheat was greater than that from fescue (*Festuca*) species and legumes, provided a more-compatible planting situation for seedling establishment of soybean, and provided greater suppression of weed growth. Some cover crops also have allelopathic potential (discussed in a later section). Cover crop systems that included tillage to stimulate weed seed germination, followed by a cover crop to suppress weed growth, resulted in a significant decrease in the weed seedbank (Mirsky et al. 2010). Although tillage may not be desirable for many row-crop producers, the Mirsky et al. (2010) results demonstrate the success of integrated methods in reducing the weed seedbank.

Intercropping (growing two cash crops simultaneously) has also been used to reduce weed growth (Liebman and Davis 2000; Liebman and Dyck 1993a; Melander et al. 2005). Intercropping combinations allow for the exploitation of more available resources compared with one crop and may suppress weed growth by use of those resources (Ballare and Casal 2000; Liebman and Dyck 1993b). Intercropping grain sorghum with cowpea [*Vigna unguiculata* (L.) Walpers] resulted in lower weed densities and less weed dry matter than did grain sorghum alone because the cowpea intercepted light and used N, P, and K that were then unavailable for weed growth (Abraham and Singh 1984). Weed seed populations have also decreased because of intercropping (Wilson and Phipps 1985), which is also a tool for maintaining ecological diversity (Barberi 2002). Intercropping is often accepted by producers because of income from two cash crops (Barberi 2002; Melander et al. 2005).

Nonliving mulches are another means of reducing weed infestations. Mulches can consist of organic materials, such as tree bark, straw, or litter composts (Niggli et al. 1990), or of inorganic materials, such as plastic mulches. Black plastic mulches are widely used in high-value crops, such as ornamentals and vegetables (Bangarwa et al. 2009). They prevent light from reaching the soil surface, thereby inhibiting weed growth, and can conserve soil moisture and reduce herbicide dissipation (Bangarwa et al. 2009, 2011). Black polyethylene mulch is often used in tomato, bell pepper (*Capsicum annuum* L.), and some herbs. It effectively controlled weeds in sweet basil (*Ocimum basilicum* L.) and rosemary (*Rosmarinus officinalis* L.) but not in parsley [*Petroselinum crispum* (Mill.) Nyman ex A.W. Hill](Richards and Whytock 1993).

Although these methods of cultural control add expense to total production costs (Snapp et al. 2005), the cost for establishing cover crops and buying mulches may ultimately be a better alternative than the cost of controlling weeds that have evolved resistance.

Planting Date. Crop planting date can affect the severity of a weed infestation. Rapid and consistent emergence of the crop is critical to its success and competitive advantage over associated weeds. Crops sown very early may emerge slowly and have uneven establishment, which makes them more susceptible to weed competition (Lutman 1991; Radosevich et al. 1997). However, crop planting date can be manipulated to provide the crop a competitive advantage over weeds (Walsh and Powles 2007; Williams 2006). Delayed seeding is used in IWM strategies in Australia to help manage herbicide-resistant ryegrass (*Lolium* spp.)(Walsh and Powles 2007). Delaying crop seeding by 2 wk allows emergence of annual weeds that can be controlled with a nonselective herbicide before planting (Walsh and Powles 2007). O'Donovan et al. (2007) suggest that late crop seeding, with control of weeds by tillage or herbicides before planting, could be an advantage in areas with early emerging weeds, such as wild oat (*Avena fatua* L.), as long as the growing season is not too short to risk a delay in planting. Williams (2006) reported that weed management tactics in June-planted sweet corn were less intense than were those in May-planted corn because of the greater weed pressure in May.

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Crop Cultivar Choice. Crop cultivars that mature at different rates or have different competitive abilities may be used to suppress weed populations and weed growth (Froud-Williams 1988; Richards 1989). Use of competitive crop cultivars has been examined in crops as varied as vegetables and grains in organic crop production (Barberi 2002), soybean (Nordby et al. 2007), canola (Beckie et al. 2008; Blackshaw et al. 2008; Harker et al. 2003), wheat (Wicks et al. 2004), peanut (*Arachis hypogaea* L.)(Place et al. 2010), rice (de Vida et al. 2006; Gealy et al. 2003), and potatoes (*Solanum tuberosum* L.)(Colquhoun et al. 2009). Factors affecting competitive ability include height, density, leaf area, tillering, canopy type, allelopathic potential, and cultivar differences in competition for light, water, and soil nutrients (Grundy et al. 1992; Lotz et al. 1991; Moss 1985; Pyšek and Lepš 1991; Richards and Whytock 1993; Standifer and Beste 1985). For example, early released varieties of canola were poor competitors, but hybrid cultivars were more competitive with weeds than were the earlier cultivars and had higher yields (Blackshaw et al. 2008). Barnyardgrass [*Echinochloa crus-galli* (L.) Beauv.] was consistently suppressed to a greater extent by highly competitive, high-yielding Asian rice cultivars than it was by U.S. cultivars 'Starbonnet', 'Kaybonnet', 'Lemont', and 'Cypress', suggesting that growing weed-suppressive rice cultivars could be a component of an effective and economical weed management strategy for rice (Gealy et al. 2003). Even though cultivars may not differentially suppress weeds, their yield potentials may differ in the presence of weeds (Colquhoun et al. 2009).

Seeding Rate. Increased crop population density can improve the competitive ability of a crop against weeds because of rapid canopy development. Increased seeding rates are used as a weed management strategy in Australia's dryland wheat to manage herbicide-resistant rigid ryegrass (*Lolium rigidum* Gaudin.)(Gill and Holmes 1997; Walsh and Powles 2007). Lemerle et al. (2004) reported reduced ryegrass biomass with wheat seeding rates that increased wheat density from 100 to 200 plants m^{-2}. Increased seeding rates of winter wheat also reduced the number of flowering heads of blackgrass (*Alopecurus myosuroides* Huds.) and the total biomass of sterile oat (*Avena sterilis* L.)(Anderson 1986; Froud-Williams 1988). Increased crop density and narrow row widths were used to reduce the competitive ability of wild oat in spring barley (*Hordeum vulgare* L.)(Anderson 1986). Greater seeding rates of safflower hastened the formation of dense canopies and improved crop competitiveness with associated weed species (Blackshaw and O'Donovan 1993). Increasing wheat seeding rate from approximately 60 to 90 kg ha^{-1} helped combat resistant weeds and increase yields (Llewellyn et al. 2004). Because of the benefits, increased seeding rate is now a standard practice in Australia's dryland crop production (Walsh and Powles 2007).

Row Spacing. In most crops, a narrower row spacing can increase the competitiveness of a crop by allowing the crop to form a canopy more quickly and intercept more light relative to the associated weeds (Arce et al. 2009; Norsworthy and Oliveira 2004; Norsworthy et al. 2007). Reduced row crop width has been shown to favor crop development at the expense of weeds in soybean (Anaele and Bishnoi 1992; Freed et al. 1987; Harder et al. 2007), cotton (Vories et al. 2001), peanut, and corn (Froud-Williams 1988). Gunsolus (1990) reported that soybean was better suited than corn to benefit from the competitive advantages offered by narrow row spacing and late planting because it normally reaches canopy closure more slowly than corn does. Cotton planted in 53-cm rows produced greater yields than did cotton planted in rows of 79 or 106 cm and required only 6 wk of weed-free maintenance for maximum yield, whereas cotton planted in 79- and 106-cm rows required 10 and 14 wk, respectively, of weed-free conditions to obtain optimum yield (Rogers et al. 1976).

Soil Fertility. Competition in the rhizosphere for nutrients and moisture is particularly important for crop vigor and competitiveness with associated weed species. The relative efficiencies of nutrient acquisition by crops and weeds may be responsible for differences in aboveground competition for light (Aldrich 1984; Siddiqi et al. 1985). Soil fertility can affect weed management by increasing crop vigor, which improves competitiveness of the crop with associated weeds. However, species composition and competitive ability of weeds can also be affected. Weeds usually take up fertilizer more rapidly than do crops (Alkämper 1976). Corn plants growing with pigweed (*Amaranthus* spp.) contained only 58% as much nitrogen (N) as weed-free corn plants (Vengris et al. 1955). Crop varieties vary in their relative competitiveness for N. In competition with yellow foxtail [*Setaria pumila* (Poir.) Roemer & J.A. Schultes], early maturing corn hybrids were more competitive for N than were late-maturing hybrids (Standifer and Beste 1985).

Nutrient management can be used to directly manipulate weed populations (Pyšek and Lepš 1991). Fertilizer treatments may be used in fallow years to promote weed seed germination; a grower then controls the seedlings, thereby reducing the amount of seed in the soil seedbank. Placement and timing of fertilizer can be manipulated to reduce weed interference in crops (Blackshaw et al. 2003, 2004a,b; Kirkland and Beckie 1998; Melander et al. 2003; Rasmussen et al. 1996). Blackshaw et al. (2004b, 2008) and Kirkland and Beckie (1998) reported that N fertilizer applied as a subsurface band, rather than broadcast, reduced competition from several weed species, including wild oat, green foxtail, wild mustard (*Sinapis arvensis* L.), and common lambsquarters (*Chenopodium album* L.). Fertilizer applied in spring, rather than in fall, often reduced weed biomass and increased yield of barley, wheat, and garden pea (*Pisum sativum* L.) (Blackshaw et al. 2004b, 2005). Not all weeds, however, respond equally to N. Competitiveness of redroot pigweed (*Amaranthus retroflexus* L.), an N-responsive species, increased as N rate increased. However, wild oat competitiveness was unaffected by N fertilizer rate (Blackshaw and Brandt 2008). This result suggests that fertilizer management strategies should be based on weed management as well as crop yield.

Irrigation. Water early in the season is important as a weed management tool to promote healthy crop growth and improve the ability of the crop to compete with associated weeds (Zimdahl 1971). Water management practices are especially important for weed control in rice production (Caton et al. 2002). Flooding rice fields is primarily for weed control because rice can grow under flooded conditions where water-saturated soil limits oxygen availability, but many weeds cannot grow under these low-oxygen conditions. Effective

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water management is critical in IWM programs for rice (Bhagat et al. 1996; Gealy et al. 2003), and control of many weeds depends on flood timing and depth (Rao et al. 2007; Williams et al. 1990), as well as on weed size and herbicide use. For example, for red rice control, flooded conditions needed to be established within 14 d after early POST application of imazethapyr but within 7 d after late POST application (Avila et al. 2005b).

The type and amount of irrigation water can also influence weed seed germination. Weed emergence in tomato was 46 to 96% lower with subsurface drip irrigation than it was with furrow irrigation, and weed emergence in furrows with the drip irrigation system was almost eliminated (Shrestha et al. 2007). In garden lettuce (*Lactuca sativa* L.), preplant irrigation and shallow tillage 14 d later reduced in-crop weed density by up to 77% and allowed effective use of lower herbicide rates (Shem-Tov et al. 2006).

Allelopathy. The term *allelopathy* has been used since 1937, when Molisch (1937) first described the phenomenon of plants affecting one another through the release of toxic chemical agents. A well-documented case of allelopathy is the production of juglone by black walnut (*Juglans nigra* L.) to eliminate surrounding vegetation (Weston and Duke 2003). Allelopathy has been recognized as having untapped potential as a weed management tool (Crutchfield et al. 1985; de Almeida 1985; Purvis et al. 1985; Putnam 1994; Smeda and Putnam 1988). Allelopathic potential exists in both weeds and crops. Rice (Dilday et al. 1991), wheat, barley, sorghum (Belz 2007; Putnam and DeFrank 1985), rye (Burgos and Talbert 2000; Barnes and Putnam 1986; Dhima 2006), wild radish (*Raphanus raphanistrum* L.)(Norsworthy 2003), and several Brassicaceae species (Haramoto and Gallandt 2005: Norsworthy et al. 2011) have been shown to have allelopathic potential. Species in the Brassicaceae family have received attention because of the known suppressive ability of isothiocyanates, which are derived from glucosinolates, produced by these species after the plants are crushed or decomposed. Norsworthy and Meehan (2005) tested isothiocyanates for control of Palmer amaranth (*Amaranthus palmeri* S. Wats.), pitted morningglory (*Ipomoea lacunosa* L.), and yellow nutsedge (*Cyperus esculentus* L.) and found several that suppressed emergence of weeds, reducing even yellow nutsedge emergence 95%. In other studies, barley, oat, wheat, and cereal rye residues reduced total weed biomass and the weight of several indicator species (Putnam and DeFrank 1985). Allelopathic activity could be attained through use of allelopathic cover crops, allelochemicals as natural herbicides, or allelopathic crops (Weston and Inderjit 2007). Although much is known about allelopathy, future research is needed on the mechanisms of allelochemical selectivity, the modes of release, and the environmental and fertility effects on activity, persistence, and potential for synthesizing bioactive products as herbicides. Allelopathic crops open the potential for development of higher levels of weed suppression through conventional breeding or biotechnology (Singh et al. 2003).

Mechanical Methods with an Emphasis on Tillage. Before crop emergence, the type of tillage employed by a grower, whether no tillage, ridge tillage (cleaning 3 to 6 cm of soil off the top of the planting bed, or ridge, that was formed in the autumn), harrowing (shallow disturbance of the soil with one of several types of harrows), moldboard plowing (deep cutting and inverting the soil layer), or some other form, has a profound effect on crop and weed interactions. More specifically, tillage affects the crop's competitive ability and the type of weed species present, and it defines the agroecosystem in which the crop and weeds exist (Malhi et al. 1988). Disadvantages of tillage as a weed control method are potential crop injury with in-season tillage, increased disease incidence, and lack of residual control (Wiese and Chandler 1988). Additionally, selective cultivation is dependent on the weather and if not performed in a timely manner, ineffective. Tillage also is a major reason for loss of soil moisture and increased water and wind erosion. For many years, however, tillage was the primary method of weed control. Moss (1979, 1980, 1985) compared cultivation systems (plowing, tine cultivation, and direct drilling) for control of blackgrass in spring barley. Blackgrass infestations in tine-cultivated wheat were similar to those in direct-drilled wheat. In contrast, plowing buried blackgrass seeds from the previous crop, reducing blackgrass populations by burying the seed to a depth from which it could not emerge. In a similar experiment, shallow cultivation reduced weed seed populations in cereals by 34%, and plowing to a depth of 20 cm eliminated blackgrass infestations (Froud-Williams 1981).

The effect of conservation-tillage systems on weed population dynamics has been evaluated in numerous studies. Wicks et al. (1994) reported the results of a 40-yr study in North Platte, NE, in which tillage shifted from plowing to disking to ridge tillage. In the plow system, kochia [*Kochia scoparia* (L.) Schrad.], redroot pigweed, and green foxtail were predominant. Annual grasses dominated when disking supplanted plowing as the tillage system, whereas ridge tillage favored the emergence of winter annual broadleaf weeds. Similarly, in conservation-tillage fields, there was an increase in the density of perennial weeds, annual grasses, windblown weeds, and native plant species that were not normally found in cultivated fields (Donaghy 1980). Biennial and perennial weeds increased in conservation-tillage sorghum. In Brazil and Argentina, annual weed populations declined in zero-tillage systems (Ferrando et al. 1982), but Zentner et al. (1988) found that annual grass weeds were favored by conservation-tillage systems.

In 1983, Froud-Williams et al. hypothesized that windblown weed species may be favored by conservation-tillage systems, and this has since been shown in several studies. Derksen et al. (1993) found wind-dispersed weeds to be more numerous in no-till treatments. Fay (1990) reported that weeds in the Poaceae (grass) family with wind-borne seeds that were not well adapted to burial were favored in conservation-tillage systems. It was theorized that larger and heavier seeds have greater biological reserves to emerge from greater depths in the soil compared with smaller seeds.

Hartmann and Nezadal (1990) observed that weed cover in the field was reduced from 80% when tillage was performed in daylight to 2% after 7 yr when all tillage operations were performed between 1 h after sunset and 1 h before sunrise. The success of this system is attributed to the weed seeds requiring light for germination by means of a response to the photoreceptor, phytochrome (Buhler 1997; Mancinelli 1994; Smith 1995). The germination of many crop plants, however, is light independent. The authors hypothesized that this type of system could reduce herbicide inputs dramatically.

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Stale seedbed is a conservation-tillage technique that combines cultural, mechanical, and chemical weed control methods. It involves disking or harrowing a field well before seeding, applying a nonselective herbicide to weeds that germinate, and planting the crop with minimal soil disturbance to reduce weed seed germination (Elmore and Moorman 1988). The technique incorporates the use of timely planting, irrigation, and effective weed control with preplant herbicides. Unless continual weed control without soil disturbance is used, a stale seedbed is a means of creating a weed-suppressing mulch by leaving vegetative residue on the surface and reducing light penetration to the soil surface. Large crabgrass [*Digitaria sanguinalis* (L.) Scop.] was eliminated from the upper 2 cm of soil, and populations of flatsedge (*Cyperus* ssp.) and bluegrass (*Poa* ssp.) species were significantly reduced using stale seedbed techniques (Standifer and Beste 1985).

The ''judicious use of tillage'' is a tactic that can delay or manage resistance (Beckie and Gill 2006). However, in some countries, especially the United States, Argentina, and Brazil, the adoption of glyphosate-resistant crops made it possible for producers to adopt conservation-tillage production, including no-tillage (Duke and Powles 2009; Givens et al. 2009). Conservation tillage has many environmental and economic advantages, but the reliance on glyphosate as a sole method of weed control reduced the use of mechanical weed control, which reduced weed-control diversity, and, in turn, placed great selection pressure on weeds in glyphosate-resistant crops (Duke and Powles 2009). The many benefits from conservation tillage, however, make it even more important to adopt integrated management practices so that conservation tillage will be a sustainable production practice.

Biological Weed Control. Biological control of weeds is broadly defined as the use of a biological agent, a complex of agents, or biological processes to bring about weed suppression (WSSA 2007). Biological control has been used successfully as a practical and economically affordable weed control method in many situations. However, it should be emphasized that biological control has seldom been used in annual agricultural situations so will likely not have a role to play in controlling herbicide-resistant weeds in herbicide-resistant crops. Classical biological control, which is biological control of nonnative, invasive weeds with natural enemies originating from the native range of the weed, has proven a viable strategy for managing weeds in areas subjected to low-intensity management, such as rangelands, forests, preserved natural areas, and some waterways. The use of an inundative method, also called the *bioherbicide strategy*, where an organism is applied to achieve rapid reduction in weed populations, has also proven successful in some instances. In the future, pathogens may also be used to introduce or alter specific genes to control growth, flowering, seed set, and competitiveness of weeds.

Appleby (2005) provided an excellent history of biological weed control in his history of weed control in the United States and Canada. The cases of the cactus moth (*Cactoblastis cactorum* Berg) on pricklypear cactus (*Opuntia* spp.) and the success of the Klamath weed beetle (*Chrysolina quadrigemina* Suffrian) in reducing a population of common St. Johnswort (*Hypericum perforatum* L.) are classic cases of biological weed control. The cinnabar moth [*Tyria jacobaeae* L.) was marginally successful against tansy ragwort (*Senecio jacobaea* L.) in western North America, but the addition of the ragwort flea beetle (*Longitarsus jacobaeae* Waterhouse) to help the cinnabar moth has been dramatically successful. Other success stories include alligatorweed flea beetle (*Agasicles hygrophila*) on alligatorweed [*Alternanthera philoxeroides* (Mart.) Griseb], mottled waterhyacinth weevil (*Neochetina eichhorniae*) on water hyacinth [*Eichhornia crassipes* (Mart.) Solms], and the salvinia weevil (*Cyrtobagous salviniae* Calder and Sands) on giant salvinia (*Salvinia molesta* Mitchell). Many other insects have been introduced with varying degrees of success.

The first commercially available mycoherbicide, *Phytophthora palmivora* Butl. (trade name, Devine), was introduced in 1981 for control of stranglervine [*Morrenia odorata* (Hook. & Arn.) Lindl.] in citrus (*Citrus* spp.). In 1982, the causal agent of mango anthracnose (*Colletotrichum gloeosporioides* Penz., f . sp. *aeschynomene* [trade name, Collego]) was introduced for control of northern jointvetch [*Aeschynomene virginica* (L.) B.S.P.] in rice and soybean. Considerable work continues in the search for mycoherbicides, and a number of promising leads have developed, but biological effectiveness is only one requirement for commercial success. BioMal [*Colletotrichum gloeosporioides* (Penz.) Penz. and Sacc. f. sp. *malvae*), for control of common mallow (*Malva neglecta* Wallr.), was the first bioherbicide introduced in Canada, but production was discontinued because production costs were too high for commercial acceptance. In addition, generalist fish, such as grass carp (*Ctenopharyngodon idella* Val.), have been used to graze down biomass of aquatic plants without specific target weeds. A few other vertebrate species, such as geese (Anseriformes; Anserinae), goats, and sheep have been used to remove weeds from localized areas (DeBruin and Bork 2006). More than 1,000 releases of more than 350 biological control agents have been used against more than 100 target weed species around the world since the late 1800s (Julien and Griffiths 1998).

Chemical Weed Control—Use of Herbicides. Herbicides are chemicals that kill plants or inhibit plant growth. They can be classified in numerous ways: by crop (e.g., a soybean herbicide), by their application timing (e.g., PRE or POST to the crop or weeds), by their chemical family (e.g., sulfonylureas, dinitroanilines), by their path of mobility in the plant (e.g., translocation by phloem, xylem, or both), and by the MOA (e.g., photosystem II inhibitors, ALS inhibitors). In the context of herbicide resistance in crops and weeds, MOA is the most relevant classifier because it best describes the means by which the herbicide imposes selection pressure on weeds, and its manipulation can be used for herbicide-resistant weed management.

More than 200 active ingredients are registered as herbicides around the world, and this estimate does not include compounds that are used exclusively as crop growth regulators or crop desiccants. There are, however, only 29 major mechanisms of herbicide action, including a group of herbicides for which the MOA is unknown (WSSA 2012).

Herbicide Classification Based on Timing of Application: Soil-Applied Herbicides. Soil-applied herbicides generally affect seed emergence or the growth of weed seedlings and must persist in the soil to be effective. When applied before the crop is planted, these herbicides are referred to as preplant or presowing herbicides. Some preplant herbicides must be

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incorporated into the soil to be effective and are referred to as *preplant incorporated* (PPI) herbicides. Preplant herbicides are applied from a few days to several months before crop sowing, depending on their soil persistence and tolerance of the crop to be planted. Herbicides applied at planting or within a few days before crop emergence are referred to as *preemergence* (PRE) herbicides. In row crops, preplant and PRE herbicides can be applied in a band over the crop row to reduce herbicide costs, especially if cultivation will be used to control weeds between the rows. A soil-applied herbicide, in some cases can also be applied after the crop is established (POST) to lengthen residual weed control in the crop. In glyphosate- or glufosinate-resistant crops, for example, metolachlor can be sprayed POST, usually in a tank mixture with glyphosate or glufosinate. Metolachlor has almost no activity on emerged plants but provides residual control between applications of the broad-spectrum herbicides glyphosate or glufosinate, which have no residual activity.

Soil-applied herbicides are important as assurance that weeds will not emerge with the crop and be too large to control with the first POST application. Before the release of glyphosate-resistant cotton, soil-applied herbicides were especially important in cotton because there was no broad-spectrum POST herbicide that could be applied over-the-top of the crop. Because of resistant weeds, the use of residual soil-applied herbicides in corn and soybean has increased over the past 5 to 10 yr (Owen et al. 2011). Modeling of resistance in Palmer amaranth indicated that resistance could be delayed with the use of soil-applied herbicides (Neve et al. 2010, 2011). A soil-applied herbicide can also introduce another MOA into an integrated resistance-management program.

Foliar-Applied Herbicides. Foliar-applied herbicides are applied to weed foliage, with or without contact of the spray with the crop, and are effective generally against young weed seedlings. POST herbicides are generally considered to be those applied after crop emergence. The spray can be applied broadcast over the crop and weeds, directed to the weeds at the base of the crop if there is limited crop selectivity, or applied under shields if there is no crop selectivity. Foliar sprays also are used for controlling emerged weeds present at planting in conservation-tillage systems, referred to as *burn-down* herbicides. Foliar-applied herbicides are referred to as *contact* herbicides when only the treated part of the plant is affected and are called *systemic* or *translocated* when the herbicide enters the plant and moves within it to the site of herbicide action. Translocation can be either through the phloem, which carries the herbicides to aboveground and belowground growing points, or through the xylem, where they move with the transpiration stream and accumulate at leaf margins.

Herbicide Classification Based on MOA. Good resistance-management programs recommend diversification of herbicide MOAs as a key resistance-management strategy. In 1997, herbicides were classified by MOA (Retzinger and Mallory-Smith 1997) with the idea that if herbicides with a similar MOA were placed in groups, it would be easier to recommend and use appropriate herbicides for resistance management. Each MOA group is assigned a number. Within each MOA group are the families of herbicides with that MOA. Families are groups of herbicides with similar chemical properties and activity; e.g., pendimethalin, trifluralin, and ethalfluralin are members of the dinitroaniline family). A complete list of MOA groups with site of action and the number of resistant weed biotypes and species is included in Table 1. A complete list of weed species that have been documented to have herbicide-resistant biotypes, with the corresponding list of herbicide MOAs to which resistance has been documented and the number of states in which they occur, is included in Table 2. Below is a summary of herbicide MOAs (WSSA 2012).

Table 1. Site of action and Weed Science Society of America mode of action group for herbicide-resistant weeds in the United States based on the number of resistant weed biotypes (summed across states) and number of the weed species (Heap 2012).

Site of action	Group	No. of biotypes	Weed species
ACCase	1	34	13
ALS	2	121	37
Auxins	4	12	8
Carotenoid biosynthesis	28	1	1
Chloroacetamides	15	1	1
Dinitroaniline	3	12	5
EPSPS	9	39	9
Not classified	27	3	1
Organic arsenicals	17	7	1
Protox	14	3	1
PS I	22	5	4
PS II (nitriles)	6	1	1
PS II (triazines)	5	91	25
PS II (ureas)	7	11	7
Thiocarbamates	8	6	5
Total		347	119

Abbreviations: ACCase, acetyl-coenzyme A carboxylase; ALS, acetolactate synthase; EPSPS, enolpyruvyl shikimate-3-phosphate synthase; PS, photosystem.

Group 1: Inhibitors of Acetyl-Coenzyme A Carboxylase. The acetyl-coenzyme A carboxylase (ACCase)-inhibiting herbicides include the cyclohexanedione, phenoxyproprionate, and phenylpyrazolin herbicides. These herbicides block the first committed step in de novo fatty acid synthesis (Burton et al. 1989; Focke and Lichtenthaler 1987). The growth of susceptible plants is halted, and plants gradually die because of the absence of phospholipids for building new cell membranes.

Group 2: Inhibitors of ALS. ALS inhibitors are also called *acetohydroxy acid synthase* inhibitors. These herbicides are inhibitors of a common enzyme leading to the synthesis of the branch-chain amino acids leucine, valine, and isoleucine (Devine et al. 1993). ALS inhibitors are used in all of the major agronomic crops (i.e., corn, cotton, pastures, peanut, small grains, soybean, turf, and wheat) and typically have residual activity. Symptoms of these herbicides include growth cessation, internodal shortening, purple foliage, and shortened lateral roots (''bottle-brush'' roots). Five herbicide families comprise the ALS-inhibiting herbicides: the sulfonylureas, imidazolinones, triazolopyrimidine sulfonanilides, pyrimidinylthiobenzoic acids, and sulfonylaminocarbonyltriazolinones.

Groups 5, 6, and 7: Photosynthesis Inhibitors. The phenylcarbamates, pyridazinones, triazines, triazinones, and uracils (group 5); benzothiadiazinones, nitriles, and phenylpyridazines (group 6); and amides and ureas (group 7) include herbicides that inhibit photosynthesis by binding to the Q_B-binding niche of the D1 protein of the photosystem II complex in chloroplast

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Table 2. Weed species documented to have herbicide-resistant biotypes in the United States, the herbicide site of action for which resistance has been documented, and the number of states where the species have been documented (Heap 2010).

Scientific name	Weed	Site of action	Group	States
Abutilon theophrasti Medik.	Velvetleaf	PS II (triazines)	5	4
Amaranthus hybridus L.	Smooth pigweed	ALS	2	4
		PS II (triazines)	5	11
Amaranthus blitum L.	Livid amaranth	ALS	2	1
Amaranthus palmeri S. Wats.	Palmer amaranth	ALS	2	6
		PS II (triazines)	5	2
		EPSPS	9	5
		DNA	3	1
Amaranthus powellii S. Wats.	Powell amaranth	ALS	2	1
		PS II (triazines)	5	2
		PS II (ureas)	7	1
Amaranthus retroflexus L.	Redroot pigweed	ALS	2	4
		PS II (triazines)	5	12
		PS II (ureas)	7	1
Amaranthus rudis Sauer	Common waterhemp	ALS	2	11
		PS II (triazines)	5	5
		Protox	14	3
		EPSPS	9	4
Amaranthus tuberculatus (Moq.) Sauer	Tall waterhemp	ALS	2	1
Ambrosia artemisiifolia L.	Common ragweed	ALS	2	6
		PS II (triazines)	5	2
		EPSPS	9	4
Ambrosia trifida L.	Giant ragweed	ALS	2	4
		EPSPS	9	6
Ammannia auriculata Willd.	Eared redstem	ALS	2	1
Ammannia coccinea Rottb.	Redstem	ALS	2	1
Anthemis cotula L.	Mayweed chamomile	ALS	2	1
Atriplex patula L.	Halberdleaf orach	PS II (triazines)	5	1
Avena fatua L.	Wild oat	ACCase	1	8
		ALS	2	2
		DNA	3	1
		Thiocarbamates	8	2
		Not classified	27	3
Bromus tectorum L.	Downy brome	ALS	2	1
Camelina microcarpa Andrz. ex DC.	Smallseed falseflax	ALS	2	1
Capsella bursa-pastoris (L.) Medik.	Shepherd's-purse	PS II (triazines)	5	1
Centaurea solstitialis L.	Yellow starthistle	Auxins	4	1
Chenopodium album L.	Common lambsquarters	ALS	2	2
		PS II (triazines)	5	19
Commelina diffusa Burm. f.	Spreading dayflower	Auxins	4	2
Conyza bonariensis (L.) Cronq.	Hairy fleabane	EPSPS	9	1
Conyza canadensis (L.) Cronq.	Horseweed	ALS	2	3
		PS II (triazines)	5	1
		PS II (ureas)	7	1
		PS I	22	2
		EPSPS	9	15
Cyperus difformis L.	Smallflower umbrella sedge	ALS	2	1
Daucus carota L.	Wild carrot	PS II (triazines)	5	1
		Auxins	4	2
Digitaria ischaemum (Schreb.) Schreb. ex Muhl.	Smooth crabgrass	ACCase	1	1
		Auxins	4	1
Digitaria sanguinalis (L.) Scop.	Large crabgrass	ACCase	1	2
Echinochloa crus-galli (L.) Beauv.	Barnyardgrass	PS II (triazines)	5	1
		PS II (ureas)	7	5
		Thiocarbamates	8	1
		Auxins	4	2
Echinochloa oryzoides (Ard.) Fritsch	Early watergrass	Thiocarbamates	8	1
Echinochloa oryzicola (Vasinger) Vasinger	Late watergrass	ACCase	1	1
		Thiocarbamates	8	1
Eleusine indica (L.) Gaertn.	Goosegrass	PS I	22	1
		DNA	3	7
Helianthus annuus L.	Common sunflower	ALS	2	5
		PS II (triazines)	5	1
Hydrilla verticillata (L. f.) Royle	Hydrilla	Carotenoid biosynthesis	28	1
Iva xanthifolia Nutt.	Marshelder	ALS	2	1
Kochia scoparia (L.) Schrad.	Kochia	ALS	2	19
		PS II (triazines)	5	10
		Auxins	4	3
Lactuca serriola L.	Prickly lettuce	ALS	2	3
		Auxins	4	1
Landoltia punctata (G. Mey.) D.H. Les & D.J. Crawford	Dotted duckmeat	PS I	22	1

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Table 2. Continued.

Scientific name	Weed	Site of action	Group	States
Lolium perenne L.	Perennial ryegrass	ALS	2	3
Lolium perenne L. ssp. *multiflorum* (Lam.) Husnot	Italian ryegrass	ACCase	1	10
		ALS	2	2
		EPSPS	9	2
		Chloroacetamides	15	1
Lolium persicum Boiss. & Hohen. ex Boiss.	Persian darnel	ACCase	1	1
Lolium rigidum Gaudin	Rigid ryegrass	EPSPS	9	1
Phalaris minor Retz.	Littleseed canarygrass	ACCase	1	1
Poa annua L.	Annual bluegrass	PS II (triazines)	5	5
		PS II (ureas)	7	1
		DNA	3	1
		Thiocarbamates	8	1
Polygonum pensylvanicum L.	Pennsylvania smartweed	PS II (triazines)	5	3
Portulaca oleracea L.	Common purslane	PS II (ureas)	7	1
Rottboellia cochinchinensis (Lour.) W.D. Clayton	Itchgrass	ACCase	1	1
Sagittaria montevidensis Cham. & Schlecht.	California arrowhead	ALS	2	1
Salsola tragus L.	Russian-thistle	ALS	2	5
Schoenoplectus mucronatus (L.) Palla	Ricefield bulrush	ALS	2	1
Senecio vulgaris L.	Common groundsel	PS II (triazines)	5	4
		PS II (nitriles)	6	1
Setaria faberi Herrm.	Giant foxtail	ACCase	1	2
		ALS	2	4
		PS II (triazines)	5	2
Setaria pumila (Poir.) Roemer & J.A. Schultes	Yellow foxtail	PS II (triazines)	5	1
Setaria viridis (L.) Beauv.	Green foxtail	ALS	2	2
		DNA	3	1
Setaria viridis var. *robustaalba* Schreb.	Robust white foxtail	ACCase	1	1
		ALS	2	1
Setaria viridis var. *robustapurpurea* Schreb.	Purple robust foxtail	ACCase	1	1
Sida spinosa L.	Prickly sida	ALS	2	1
Sinapis arvensis L.	Wild mustard	ALS	2	1
Solanum americanum P. Mill.	American black nightshade	PS I	22	1
Solanum ptychanthum Dunal	Eastern black nightshade	ALS	2	3
		PS II (triazines)	5	1
Sonchus asper (L.) Hill	Spiny sowthistle	ALS	2	1
Sorghum bicolor (L.) Moench ssp. *arundinaceum* (Desv.) de Wet & Harlan	Shattercane	ALS	2	7
Sorghum halepense (L.) Pers.	Johnsongrass	ACCase	1	5
		ALS	2	1
		EPSPS	9	1
		DNA	3	1
Xanthium strumarium L.	Common cocklebur	ALS	2	9
		Organoarsenicals	17	7

Abbreviations: PS, photosystem; ALS, acetolactate synthase; EPSPS, enolpyruvyl shikimate-3-phosphate synthase; Protox, protoporphyrinogen oxidase; ACCase, acetyl-coenzyme A carboxylase.

thylakoid membranes. A distinction among groups within the photosynthetic inhibitors refers to the different pockets where they bind in the Q_B-binding site. Herbicide binding in this site negatively affects processes and products necessary for the transport of chemical energy. Death in susceptible plants generally occurs via cell membrane disintegration because of the creation of triplet state chlorophyll, singlet oxygen, and lipid peroxidation.

Group 22: Photosystem I inhibitors (Electron Diverters). The bipyridyliums (e.g., paraquat, diquat) are examples of herbicides that accept electrons from photosystem I and reduce them to form a herbicide radical. The radical then reduces molecular oxygen to form superoxide radicals. The superoxide radicals lead to the formation of hydrogen peroxide and hydroxy radicals that destroy lipid membrane fatty acids and chlorophyll, thereby causing membrane destruction, cellular leakage, and a very rapid plant death in sunlight.

Group 14: Inhibitors of Protoporphyrinogen Oxidase. These chlorophyll synthesis inhibitors (PPO-inhibitors) comprise several herbicide families: the diphenylethers (e.g., fomesafen), *N*-phenylphthalimides (e.g., flumioxazin), oxadiazoles (e.g., oxadiargyl), oxazolidinediones, phenylpyrazoles (e.g., flufenpyr-ethyl), pyrimidindiones (e.g., butafenacil), thiadiazoles, and triazolinones (e.g., azafenidin, sulfentrazone). Herbicides in this category inhibit protoporphyrinogen oxidase (PPG oxidase or Protox), an enzyme involved in chlorophyll and heme synthesis. Inhibition leads to an accumulation of PPIX, the first light-absorbing chlorophyll precursor. Light absorption by PPIX apparently produces triplet state PPIX that interacts with ground state oxygen to form singlet oxygen. Triplet PPIX and singlet oxygen lead to the formation of lipid radicals that initiate a chain reaction of lipid peroxidation and cause cellular leakage and plant death (Duke et al. 1991).

Groups 11, 12, 13, and 27: Carotenoid Biosynthesis Inhibitors. Herbicides in group 12 include the amides, anilidex, furanones, pheno'xybutan-amides, pyridazinones, and pyridines that block carotenoid synthesis by inhibition of phytoene desaturase (Bartels and Watson 1978; Sandmann and Böger 1989). Carotenoids play an important role in dissipating the oxidative energy of singlet oxygen and other radicals. Callistemon, isoxazole, pyrazole, and triketone herbicides (group 27) inhibit

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a key step in plastoquinone biosynthesis; its inhibition gives rise to bleaching symptoms on new growth. Symptoms on plants result from an indirect inhibition of carotenoid synthesis because of the involvement of plastoquinone as a cofactor of phytoene desaturase. Clomazone (group 13) is metabolized to the 5-keto form of clomazone that is herbicidally active. The 5-keto form inhibits 1-deoxy-D-xylulose 5-phosphate synthase, a key component of plastid isoprenoid synthesis for production of carotenoids (Ferhatoglu and Barrett 2006). Amitrol and aclonifen make up group 11. Amitrol inhibits accumulation of chlorophyll and carotenoids in light, and aclonifen acts similarly to carotenoid inhibiting/bleaching herbicides, although the specific mechanisms of action of these herbicides have not been determined.

Group 9: Enolpyruvyl Shikimate-3-Phosphate Synthase. Group 9, the glycines, includes only glyphosate. Glyphosate inhibits enolpyruvyl shikimate-3-phosphate synthase (EPSPS)(Amrhein et al. 1980), which leads to depletion of the aromatic amino acids tryptophan, tyrosine, and phenylalanine, all needed for protein synthesis or for biosynthetic pathways leading to growth.

Group 10: Glutamine Synthetase Inhibitors. Herbicides in group 10 are glufosinate and bialaphos, the phosphinic acids. They inhibit the activity of glutamine synthetase (Lea 1984), the enzyme that converts glutamate and ammonia to glutamine. Accumulation of ammonia in the plant (Tachibana et al. 1986) destroys cells and directly inhibits photosystem I and photosystem II reactions (Sauer 1987). Ammonia also reduces the pH gradient across the membrane that can uncouple photophosphorylation.

Group 18: Dihydropteroate Synthase Inhibitor. A unique carbamate herbicide, asulam, appears to inhibit cell division and expansion in plant meristems, perhaps by interfering with microtubule assembly or function (Fedtke 1982; Sterrett and Fretz 1975). Asulam also inhibits 7,8-dihydropteroate synthase, an enzyme involved in folic acid synthesis and crucial for purine nucleotide biosynthesis (Kidd et al. 1982; Veerasekaran et al. 1981).

Groups 3, 15, and 23: Inhibitors of Mitosis. Benzamide, dinitroaniline, phosphoramidate, and pyridine compounds are group 3 herbicides that bind to tubulin, a major microtubule protein. The herbicide–tubulin complex inhibits polymerization of microtubules at the assembly end of the protein-based microtubule leading to a loss of microtubule structure and function, and cell wall formation is negatively affected. Dinitroaniline herbicides are volatile, readily dissipating into the atmosphere and. therefore. often require soil incorporation (either disked into the soil or through irrigation) for maximum efficacy. The carbamate herbicides, carbetamide, chlorpropham, and propham are group 23 compounds and inhibit cell division and microtubule organization and polymerization. Acetamide, chloroacetamide, oxyacetamide, and tetrazolinone compounds are group 15 herbicides that are thought to inhibit very long chain fatty acid synthesis (Böger et al. 2000; Husted et al. 1966). These compounds affect susceptible weeds before emergence but do not inhibit seed germination.

Groups 20, 21, 28, and 29: Cellulose Inhibitors. The benzamides (group 21), nitriles (group 20), and triazolocarboxamides (group 28) are herbicides that inhibit cellulose and cell wall synthesis in susceptible weeds (Heim et al. 1990). Indaziflam is an alkylazine compound (group 29) that disrupts cellulose biosynthesis (Myers et al. 2009).

Groups 8 and 16: Fatty Acid and Lipid Biosynthesis Inhibitors. The benzofuranes (group 16) and the phosphorodithioates and thiocarbamates (group 8) are herbicides known to inhibit several plant processes, including biosynthesis of fatty acids and lipids, proteins, isoprenoids, flavonoids, and gibberellins. It is currently thought that these effects may be linked by the conjugation of acetyl-coenzyme A and other sulfhydryl-containing molecules by thiocarbamate sulfoxides (Casida et al. 1974; Fuerst 1987). Herbicides with this MOA may be referred to as the lipid and secondary biosynthesis inhibitors. To maximize efficacy in controlling weeds, thiocarbamates are typically incorporated into the soil. Seedlings of susceptible weed species fail to emerge, and phytotoxic symptoms are characterized by tightly whorled leaves that do not unroll in a normal fashion.

Group 4: Synthetic Auxins. The benzoic acids, phenoxycarboxylic acids, pyridine carboxylic acids, and quinoline carboxylic acids collectively form the group of synthetic auxin herbicides. Herbicides in this group have activity similar to that of endogenous auxin, although the true mechanism is not well understood. Symptoms include abnormal growth and eventual plant death. The oldest selective herbicide, 2,4-D, is categorized in this group.

Group 19: Auxin Transport Inhibitors. The phthalamates (e.g., naptalam) and semicarbazones (e.g., diflufenzopyr) are group 19 herbicides. These herbicides inhibit polar transport of naturally occurring auxin, indoleacetic acid, and synthetic auxin-mimicking herbicides in sensitive plants. Auxin-transport inhibition causes an abnormal accumulation of auxin in the meristematic regions, thereby disrupting the auxin balance needed for plant growth (Grossmann 2010).

Groups 17, 25, and 26: Potential Nucleic Acid Inhibitors or Unclassified Herbicides. Herbicides in these groups have an unknown MOA.

Knowledge of basic weed science principles and practices are needed for understanding herbicide resistance and for planning and implementing sound IWM programs. The last new herbicide MOA discovery was inhibition of the enzyme hydroxyphenylpyruvate dioxygenase, which was discovered more than 20 yr ago (Lee et al. 1997) and from which the herbicide mesotrione was developed. Before this, a new MOA was introduced approximately every 3 yr (Duke 2012). The search for new herbicide chemistry has slowed to the extent that producers can no longer count on ''the next new herbicide'' to control resistant weeds. Instead, herbicide programs must be integrated with preventive, cultural, biological, and mechanical weed control practices to develop diversified resistance management programs.

Resistance and Tolerance in Weed Science

Herbicide Tolerance and Resistance Defined. Standard definitions of the terms ''resistance'' and ''tolerance,'' based

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on weed and crop response in the context of biology, herbicides, and weed management, were defined by the WSSA in 1998:

''*Herbicide tolerance* (HT) is the inherent ability of a species to survive and reproduce after herbicide treatment. This implies that there was no selection or genetic manipulation to make the plant tolerant; it is naturally tolerant.''

''*Herbicide resistance* (HR) is the inherited ability of a plant to survive and reproduce following exposure to a dose of herbicide normally lethal to the wild type. In a plant, resistance may be naturally occurring or induced by such techniques as genetic engineering or selection of variants produced by tissue culture or mutagenesis.''

Herbicide Tolerance and Herbicide Selectivity. At least until the advent of herbicide-resistant crops, herbicide selectivity, which is the differential response among plants to a herbicide, had been based on natural tolerances of plants (Devine et al. 1993; Kreuz et al. 1996) or selective herbicide application, such as spraying weeds but avoiding the crop. When weed control was effective and the crop was tolerant to the herbicide, a herbicide was considered to have good selectivity. A weed can have tolerance because of a mechanism that prevents the herbicide from binding to the site where it normally disrupts biological activity, or the plant may be able to degrade the herbicide to a nonphytotoxic molecule (de Carvalho et al. 2009) or prevent the herbicide from entering or moving in the plant. Although these mechanisms could also be responsible for resistance, the difference lies in the definition that, with tolerance, the wild type (often the weed) was never controlled by the herbicide. Even a herbicide such as glyphosate, which is considered to be nonselective, is not equally effective on all weed species (Norsworthy et al. 2001; Owen 2008); that is, some species have a level of natural tolerance, although if the normal use rate of the herbicide is increased, the plant may then succumb to the herbicide. Variable response among weed species to herbicides is addressed on herbicide labels. Most labels recommend different application rates for different weed species at different sizes and indicate weeds whose growth may be suppressed but that most likely will not be killed.

Herbicide Resistance. Herbicide resistance is the heritable capacity for plants to grow and reproduce following treatment with a herbicide that would have been fatal to all but one or a very few progenitors in an antecedent population. Herbicide-resistant weeds occur in both herbicide-resistant crops and conventional crops in response to selection pressure from a herbicide. A herbicide selects for plants with natural genetic resistance to that MOA. Those plants survive and reproduce, and if selection by the herbicide continues for several generations, the population of the resistant weed biotype increases until there is a noticeable population of weeds that the herbicide will no longer control.

On the other hand, both transgenic and nontransgenic herbicide-resistant crop cultivars are resistant to specific herbicides because they have been bred to survive a field application of the herbicide. Therefore, susceptible crop genotypes can be killed by a herbicide whereas the resistant cultivar is not. When the identity of a conventional cultivar is mistaken for a resistant cultivar in the field, the conventional cultivar is killed or severely injured by the herbicide that the resistant cultivar resists without adverse effects.

Target-Site Resistance. A plant may express ''target-site'' or ''nontarget-site'' resistance (Prather et al. 2000). A target site is a location, usually an enzyme, in a plant where the active ingredient in a herbicide binds and interferes with physiological processes (Nandula 2010). A widely studied mechanism of resistance in weeds has been an altered herbicide–target enzyme in which resistance is conferred by a genetic mutation in the target enzyme so that the herbicide can no longer inhibit enzyme activity (Neve 2007; Powles and Preston 2006). This is the primary (but not only) weed-resistance mechanism reported for ALS-inhibitors, ACCase-inhibitors, mitotic inhibitors, PPO-inhibitors, and some PSII-inhibiting herbicides (Powles and Preston 1995, 2006).

As of the beginning of 2012, there were 116 weed species resistant to various ALS-inhibiting herbicides (Heap 2012). These herbicides control weeds by inhibiting the ALS enzyme, which is critical for biosynthesis of branch-chained amino acids. Because ALS-inhibiting herbicides do not bind within the catalytic site of the target enzyme, there is a wide variation of potential mutations at different sites, or domains, on the ALS gene and a high frequency of occurrence of resistance to ALS-inhibiting herbicides (Tranel and Wright 2002). Substitutions of amino acids can occur at the various sites, resulting in increased resistance to different herbicide families in the ALS-inhibitor group of herbicides (Powles and Yu 2010). For example, commonly occurring mutations that confer resistance are at amino acids residues Ala 122, Pro 197, Ala 205, Asp 376, Trp 574, Gly 654, and Ser 653 (Powles and Yu 2010).

PSII-Inhibiting Herbicides. Photosystem II-inhibiting herbicides, such as the triazines, block photosynthetic electron transfer from chlorophylls associated with the P680 chlorophyll center to the initial electron acceptor, a compound known as plastoquinone. In a normal functioning plant, plastoquinone accepts an electron from the chlorophyll in the initial step of the electron-transfer process. This transfer occurs at the Q_B binding site of a 32-kDa protein known as D1 of photosynthesis. Triazines and other PSII herbicides compete with plastoquinone for the binding site on the Q_B protein. There are several mutations to the Q_B protein that prevent PSII herbicides from binding while allowing plastoquinone to bind, albeit with reduced efficiency. The most prevalent mutation occurs at the Ser 264 and involves an amino acid change from serine to glycine. Other mutations conferring herbicide resistance are Ser 264 to Thr and Asn 266 to Thr (Oettmeier 1999; Powles and Yu 2010).

ACCase-Inhibiting Herbicides. Acetyl-coenzyme A carboxylase is the key enzyme in lipid biosynthesis. In plants, there are two forms of ACCase, a prokaryotic form made up of multiple subunits and eukaryotic ACCase that is a large multidomain protein. Plants contain cytosolic as well as plastidic forms of ACCase. In grasses, the plastids contain the eukaryotic form of ACCase and are sensitive to three chemical classes of herbicides known as the graminicides. Most dicot plant species contain the prokaryotic form of the enzyme that is insensitive to graminicide herbicides.

There are eight mutations to the ACCase enzyme leading to target-site resistance to ACCase-inhibiting herbicides (Powles and Yu 2010). The most common is a Leu to Ile substitution at residue 1781. Different substitutions in the ACCase

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enzyme lead to differing patterns of resistance among the graminicide herbicides.

Mitotic Inhibitors. Herbicides such as the dinitroanilines inhibit mitosis through the disruption of microtubule assembly. Specifically, microtubules comprise α-tubulin and β-tubulin dimers. In mitosis, the microtubules are involved in chromosomal migration to the daughter cell. Mitotic-inhibiting herbicides bind to the α-tubulin, preventing it from binding to the β-tubulin dimer and inhibiting dimer formation. In dinitroaniline-resistant weed species, a substitution of Ile for Thr at the 239 base pair prevents the dinitroaniline herbicide from binding to the α-tubulin (Smeda and Vaughn 1994). Other less-common mutations at amino acid position 268 (Met to Thr) and 136 (Leu to Phe) have been reported (Deleye et al. 2004).

PPO-Inhibiting Herbicides. Protoporphyrinogen IX oxidase is a key enzyme in the synthesis of chlorophyll and heme in plants. PPO catalyzes the oxidation of protoporphyrinogen (protogen) to protoporphyrin IX (Proto IX). In plants, there are two nuclear-encoded isoforms (PPO1 and PPO2). The PPO1 product is targeted to the chloroplast while the PPO2 product is targeted to the mitochondria. Several groups of herbicides, including diphenyl ethers, inhibit PPO. PPO resistance has been limited to one species, tall waterhemp [*Amaranthus tuberculatus* (Moq.) Sauer], with a novel target-site–resistance mechanism. In the PPO gene, there is a codon deletion at position 210 leading to the loss of a Gly residue conferring herbicide resistance (Patzoldt et al. 2006).

Enolpyruvyl shikimate-3-phosphate synthase. The target-site mechanism of glyphosate is inhibition of the enzyme EPSPS, which is a key enzyme in the shikimic acid pathway leading to the aromatic amino acids of phenylalanine, tyrosine, and tryptophan. Glyphosate is a competitive inhibitor of EPSPS, competing with phosphoenolpyruvate (PEP) at the catalytic site. Thus, there are few mutations that confer glyphosate resistance without leading to enzyme failure and a lethal mutation. There is only one reported mutation (a Pro to Ser mutation at amino acid position 106) in weeds that confer resistance to glyphosate via a target-site mutation, whereas most glyphosate-resistant weeds are resistant via nontarget-site resistance mechanisms. A special case of target-site resistance has been associated with glyphosate-resistance in some weed species where an amplification of the target site is noted (Gaines et al. 2010).

Target-Site Resistant Crops. Herbicide-resistant crops can be developed by whole-cell selection, mutagenesis, selection, and breeding from plants with natural resistance or by genetic engineering (Duke 2005; Tan and Bowe 2009). Imidazolinone-resistant crops are based on target-site mutations that reduce the sensitivity of the ALS enzyme to those herbicides. Most of these crops were created by chemical mutagenesis, where cells were mutated by chemical treatment, and then, crops were commercialized as Clearfield crops (BASF, 26 Davis Drive, Research Triangle Park, NC 27709) using conventional breeding methods. Imidazolinone crops include Clearfield corn (maize), canola, wheat, rice, and common sunflower (*Helianthus annuus* L.). Clearfield common sunflower was developed by breeding cultivated sunflowers with a resistant wild sunflower (Tan and Bowe 2009). Another example of breeding a crop from a wild relative is triazine-resistant canola, in which resistance from a triazine-resistant weed, birdsrape mustard (*Brassica rapa* L.), was moved into canola, which is also a *Brassica* species, by breeding (Hall et al. 1996).

Transgenic crops that have target-site resistance have been created by artificially inserting a gene or genes from another organism into the crop to give it a desirable characteristic that it does not naturally possess. Transgenic crops for herbicide resistance have been developed for glyphosate, glufosinate, and bromoxynil. (Bromoxynil-resistant crops were removed from the market because bromoxynil is not a broad-spectrum herbicide and the crops competed poorly in the market [Duke 2005].) Most glyphosate-resistant crops were developed by inserting a bacterial EPSPS known as CP4 from a *Agrobacterium* sp. bacterium, which encodes a glyphosate-insensitive form of EPSPS (Duke 2005; Powles and Preston 2006). The binding of glyphosate is excluded by conformational changes resulting from those amino acid sequence changes in CP4 outside the glyphosate/PEP binding region (Dill 2005).

Nontarget-Site Resistance. A plant with nontarget-site resistance may metabolically detoxify a herbicidal active ingredient, prevent a herbicide from reaching its target site by reducing herbicide absorption or translocation, or sequester the herbicide in a cellular site that is not vulnerable to the active ingredient (Cummins and Edwards 2010; Prather et al. 2000; Tharayil-Santhakumar 2004; Yuan et al. 2007).

Metabolic detoxification is a mechanism of herbicide resistance in barnyardgrass, junglerice [*Echinochloa colona* (L.) Link](Carey et al. 1997; Hoagland et al. 2004), and velvetleaf (*Abutilon theophrasti* Medik.)(Anderson and Gronwald 1991), among other species (Burgos 2004). Propanil, for instance, is hydrolyzed at a much higher level in resistant barnyardgrass than it is in the susceptible biotype (Carey et al. 1997). Reduced translocation, a nontarget site resistance mechanism, is the basis of resistance for some populations of glyphosate-resistant rigid ryegrass in Australia (Lorraine-Colwill et al. 2002; Powles and Preston 2006; Wakelin et al. 2004). *Sequestration*, also sometimes referred to as *compartmentation*, means that the herbicide is inactivated either through binding (often to a sugar moiety) or is removed from metabolically active regions of the cell, often to a vacuole (postulated for certain types of resistance to aryloxyphenoxypropionate [APP] herbicides, glyphosate, and paraquat). For example, Ge et al. (2010) reported that some biotypes of glyphosate-resistant horseweed [*Conyza canadensis* (L.) Cronq.] actively transported glyphosate to the vacuoles of the cell compared with the cytoplasm and prevented it from getting to the target site.

Cross-Resistance and Multiple Resistance. A plant or plant population may also be resistant to more than one herbicide, herbicide chemical family, or MOA group. Cross-resistance occurs when plants possess one mechanism that provides the ability to withstand herbicides from different chemical families (HRAC 2009b). For cross-resistance to occur, the families must act at the same site of action (i.e., have the same MOA). For example, a single-point mutation in the ALS

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enzyme may provide resistance to both the sulfonylurea and imidazolinone herbicide families, both ALS-inhibitors (HRAC 2009b). Some rigid ryegrass populations in Australia are resistant to a number of herbicide families, whereas a few are resistant only to the herbicides in one family (Powles and Preston 1995). Plants can have target-site or nontarget-site cross-resistance. In rigid ryegrass, selection from a herbicide in either the APP family or the cyclohexanedione (CHD) family, both ACCase-inhibiting herbicides, has led to cross-resistance to both herbicides, although the level of resistance is usually greater to the APP than it is to the CHD herbicides (Holtum et al. 1991; Powles and Preston 1995). Because the patterns of resistance to the ACCase-inhibiting herbicides can be so different, even in the same species, resistance to different biotypes is suspected to be due to different mutations of the ACCase gene. Nontarget-site cross-resistance explains resistance of some biotypes of blackgrass that have resistance to both diclofop and fenoxaprop (ACCase-inhibitors) because of increased metabolism (Holtum et al. 1991).

Multiple resistance occurs when a plant has more than one resistance mechanism (HRAC 2009b; Powles and Preston 1995). A plant with multiple resistance may have two or more resistance mechanisms that confer resistance to a few or many herbicides either with the same or different MOA. For example, a kochia population is resistant to triazine (PS-II inhibitors) and to ALS-inhibiting herbicides because the plants have two mutations, one for resistance to each class of herbicide (Foes et al. 1999). Multiple resistance of common waterhemp (*Amaranthus rudis* L.) to glyphosate and ALS- and PPO-inhibiting herbicides was confirmed in Missouri (Legleiter and Bradley 2008), and multiple resistance of Palmer amaranth to ALS inhibitors and glyphosate was recently confirmed in Georgia (Sosnoskie et al. 2011).

Quantitative Resistance. Gressel (2009) described how suboptimal herbicide rates applied repeatedly can select for resistance in some plants. When a herbicide is sprayed in a field, some individual weeds do not receive the registered use rate because of uneven spray patterns, partial protection from spray by neighboring plants, or by being slightly larger plants and having more natural tolerance than other plants in the field do. In that scenario, there may be some plants that have a low level of resistance, but not enough to survive a higher herbicide rate. However, when those surviving plants combine sexually, the low level of resistance may be increased in some progeny, and the population begins to shift to a higher level of resistance (Gressel 2009). Quantitative resistance can be described as one in which multiple gradations of a phenotype can be detected and measured on a continuous scale, as opposed to a simple trait for which phenotypes can be placed in discrete classes. It is suspected that different mechanisms of resistance are involved, with several different, perhaps minor, genes affecting several processes that will rapidly add up to a high level of resistance (Neve and Powles 2005). For instance, one gene may limit translocation of the herbicide, another may cause more rapid metabolism, and another may affect the target site slightly (Gressel 2009). Awareness of the possibility of quantitative resistance has led to recommendations to apply labeled herbicide rates to weeds of the size recommended by the registration.

Many factors determine how a plant population will respond to selection from a herbicide. These factors include the frequency of herbicide use, the MOA of the herbicides used, the degree of selection pressure exerted by particular herbicide families and MOA groups, the ease with which a plant can adapt genetically to herbicide selection, and the effects of weed/crop biology and ecology, environmental factors, and production practices on the propensity for development of resistance or tolerance. As the following section, ''Environmental Impacts of Herbicide Resistance in Crops,'' will show, even if a weed population does not evolve resistance to a herbicide, the presence of naturally tolerant species in the population can result in a shift to weeds that can still be a challenge to control.

Environmental Impacts of Herbicide Resistance in Crops

The adoption of herbicide-resistant crops has resulted in significant changes to agronomic practices. Herbicide-resistant crops have allowed for the adoption of effective, simple, low-risk crop production systems with less dependency on tillage (Carpenter and Gianessi 1999; Service 2007) and lower energy requirements. Overall, the changes have had a positive environmental effect by reducing soil erosion, fuel use for tillage, and the number of herbicides with groundwater advisories, leading to a slight reduction in the overall environmental impact quotient of herbicide use (Foresman and Glasgow 2008; Service 2007; Young 2006).

Conservation tillage used in crop production has increased in part because of the adoption of herbicide-resistant crops (American Soybean Association 2001; Brookes and Barfoot 2011a; Cerdeira and Duke 2006; Dill et al. 2008; Service 2007). By 2008, herbicide-resistant cultivars accounted for an estimated 99% of total no-till soybean in the United States (Brookes and Barfoot 2011a). Adoption of conservation tillage by farmers in the United States since 1982 has been credited with reducing soil erosion by 30%. Savings due to reduced soil sedimentation were estimated at $3.5 billion for 2002 (Fawcett and Towery 2002). Reduced reliance on cultivation for weed control also leads to more stored carbon in the soil and lower carbon emissions. A no-till system is estimated to store 300 kg of carbon ha^{-1} yr^{-1}, whereas reduced tillage stores 100 kg of carbon ha^{-1} yr^{-1}, and conventional tillage releases 100 kg carbon ha^{-1} yr^{-1} (Brookes and Barfoot 2009, 2011b).

Fuel savings are associated with fewer trips across the field for seedbed preparation, cultivation, and herbicide application (Duke and Powles 2009). Fuel savings associated with the absence of plowing resulted in CO_2 emission reductions of 88.81 kg ha^{-1} if no-till was used and 35.66 kg ha^{-1} if reduced tillage was used (Brookes and Barfoot 2009). Tractor fuel consumption for traditional tillage (moldboard plow, disk, and seed planting) was 47 L ha^{-1}, compared with 29 L ha^{-1} for reduced tillage (chisel plow, disk, and seed planting) and 14 L ha^{-1} in no-till systems (Fawcett and Towery 2002; Jasa 2002). In soybeans in the United States, fuel for tillage has been reduced by an estimated 834.7 million L or 3.5% based on the 1996 average use rate (Brookes and Barfoot 2009, 2011b). For all genetically modified, biotech crops, the reduction in CO_2 emissions in 2009 was equal to removing 7.85 million cars from the road.

Many studies report a reduction in herbicide usage with genetically modified crops (Brookes and Barfoot 2005; Duke

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and Powles 2009). Herbicide use is reflected in the environmental impact quotient (EIQ)(Kovach et al. 1992). The EIQ comprises numerous variables, including individual pesticide toxicology, soil persistence, half-life, leaching, runoff, potential exposure times for various types of contact (farm workers and consumers), and reproductive effects, to name only a few, and formulates a single value based on the effects of a pesticide on farm workers, consumers, and ecological components (Brookes and Barfoot 2011b; Kovach et al. 1992). Transgenic crops have contributed to a significant reduction in the global EIQ of production agriculture (Brookes and Barfoot 2006). From 1996 through 2005, the global use of pesticides was reduced by 224 million kg ai (a 6.9% reduction), and the overall environmental impact associated with pesticide use on these crops was reduced by 15.3%. From 1996 through 2008, the volume of herbicides used in herbicide-resistant soybean crops decreased by 50 million kg, or a 3% reduction, whereas the overall environmental impact associated with herbicide use decreased by 16.6% (Brookes and Barfoot 2009). Reductions of herbicide use and EIQ have also been reported for genetically modified sugarbeet (*Beta vulgaris* L.) in Europe (Kleter et al. 2008) and in Canadian canola (Smyth et al. 2011).

From the introduction of transgenic, herbicide-resistant soybean in 1996 until 2001, the number of herbicides used that required USEPA groundwater advisory labeling was reduced by 60% or 7.7 million kg (Krueger 2001). However, many of the herbicides that are being used now to control glyphosate-resistant weeds, such as Palmer amaranth, have USEPA groundwater advisories (e.g., metolachlor and fomesafen), and some, such as diuron and fluometuron, are under increasing scrutiny for contamination of surface and groundwater. The spread of glyphosate-resistant weeds will likely increase the use of herbicides with less environmental safety compared with glyphosate.

The effect of genetically modified crops on soil and plant microbial populations has not been shown to be a potential environmental risk. Dunfield and Germida (2004) concluded that transgenes can be transferred into soil organisms through horizontal gene transfer in the laboratory, but the process has not been shown to occur in a natural soil environment. Diversity of microbial populations can be affected by the presence of transgenic crops, but the effects, to this point, have been found to be minor, and when an effect does occur, it is transient (Dunfield and Germida 2004). The Food and Agriculture Organization of the United Nations (FAO 2003) also reported that genetically modified crops do not currently present any undue risk to soil ecosystems.

Plant biodiversity is inherently affected by any cropping system (Dollacker and Rhodes 2007; Marshall 2001). For example, tillage tends to select for certain plants, such as increased annual grasses and decreased broadleaf weeds in no-till systems (Tuesca et al. 2001; Wruke and Arnold 1985). However, herbicides also influence biodiversity (Owen 2008). Puricelli and Tuesca (2005) reported that regardless of crop rotation or tillage system, glyphosate reduced the richness and density of most early season weeds but increased biodiversity of those emerging later in the season in summer crops. After 10 yr of herbicide-resistant crops in Canada, Beckie et al. (2006) reported that, although weed shifts were documented as a result of the change from nonherbicide-resistant to herbicide-resistant canola, weed species diversity did not change.

Strategies for Managing Weed Species Shifts and Development of Herbicide-Resistant Weeds

Weed shifts and herbicide-resistant weeds create significant challenges in crop management. Considerable research has been published on reducing the onset of herbicide-resistant weeds and management of herbicide-resistant weeds and weed shifts. Elements of these strategies include (1) expanded efforts by university and industry scientists to understand growers' perceptions of weed management and herbicide-resistant weeds, (2) implementation of more-effective communication and grower education programs, (3) publishing of management strategies designed to address mitigation and management of herbicide-resistant weed populations, and (4) investigation into growers' perceptions of recommended herbicide-resistant weed management practices.

Resistance-Management Practices. Because of early reports of herbicide resistance (Ryan 1970), research has been directed toward determining which practices are best for managing herbicide-resistant weeds and which can most effectively slow the evolution of additional populations of herbicide-resistant weeds and weed shifts. Scientists have employed direct field testing to evaluate management strategies in varied agronomic environments and used simulation models to predict the potential for evolution of resistance and the effectiveness of management strategies for mitigating herbicide resistance.

Simulation computer modeling of resistance is becoming an increasingly valuable tool for predicting the probability of resistance evolution and the approximate rate at which resistance will evolve (Gressel 2009; Gustafson 2008; Neve 2008; Neve et al. 2010). Early models were based on population models and the use of single-gene inheritance, with some parameters from insecticide- and fungicide-resistance models (Gressel 2009). Many factors influence the evolution of resistance. Georghiou and Taylor (1986) categorized these as genetic, biological/ecological, and operational. Genetic factors include frequency of resistance alleles in a population, mutation rates, mode of inheritance, and fitness costs (Neve 2008). Biological/ecological factors include breeding system, gene flow among populations, seedling survival, seed production, seed dormancy, seed viability, and soil seedbank longevity. Herbicide programs and management practices comprise operational factors (Neve 2008). Some early modeling efforts gave inaccurate predictions of resistance because they lacked adequate information on biology/ecology of species, on reduced fitness of resistant biotypes, and on the effects of management practices, such as effects of herbicide mixtures, on resistance evolution (Gressel and Segal 1990). Different weed species respond differently to selection pressure from herbicides and management practices, and genetics and biology of the species interact to determine species response to selection pressure (Neve 2008). All these factors should be considered in developing a computer model to simulate resistance.

Simulation models are useful for predicting the probability that a weed species will evolve resistance to a herbicide over a wide range of herbicide use patterns and production practices (Neve et al. 2010, 2011). Models can predict over a time not possible to test empirically in the field and without the need for expensive, long-term field experiments (Jones and Medd 2005), and they can account for demographic and genetic factors that might affect the risk of resistance (Neve et al.

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2010). For example, in a 30-yr simulation of the evolution of glyphosate resistance in Palmer amaranth, it was predicted that in glyphosate-resistant cotton, in which only glyphosate is used, 18% of the Palmer amaranth population would be resistant after 4 yr, 41% would be resistant after 5 yr, and 74% after 20 yr (Neve et al. 2011). That prediction was within the range of observations in commercial fields (Norsworthy et al. 2008). The model also predicted how the risk of resistance could be reduced using different management practices. When glyphosate was applied in combination with other preplant, PRE, and POST herbicides, the risk of Palmer amaranth resistance was only 12% (Neve et al. 2011). A rotation of cotton and conventional corn cultivars or those with other resistance traits—thus diversifying herbicide MOAs—reduced the risk of resistance approximately 50% and delayed the evolution of resistance 2 to 3 yr. Those models serve as a guideline for developing resistance-management strategies and also point to research needs for understanding and mitigating herbicide resistance (Neve et al. 2011). Modeling is currently the primary tool used to compare the side-by-side advantages of management practices. However, researchers are implementing long-term field trials to evaluate practices.

Dissemination of Information and Grower Adoption of BMPs. After herbicide resistance in a weed has been confirmed, weed scientists and other agricultural professionals notify the agricultural community via multiple media sources, such as printed and electronic publications, videos, interviews with the agricultural media, and presentations to growers. Herbicide resistance, in general, is a topic of discussion at most training meetings conducted by university and industry weed scientists. Likewise, many universities, herbicide manufacturers, and crop commodity groups publish information on the mitigation and management of herbicide-resistant weeds on their Internet sites. A herbicide's MOA, a list of specific weeds with confirmed herbicide resistance, and detailed stewardship and management guidelines are voluntarily published on some herbicide labels from major U.S. manufacturers, based on cooperative scientific support from local universities (Boerboom and Owen 2006; Thill and Mallory-Smith 1996).

An understanding of growers' perceptions of weed management and herbicide resistance provides weed scientists with valuable information on where and how to best focus education and training programs. Grower perception of herbicide-resistant weeds and related management practices varies by geography and size of farming operation. In a 2007, Ohio study, on grower perceptions and beliefs about weed management, it was revealed that growers placed greater importance on the control of existing weed populations than on the prevention of herbicide-resistant weeds or weed shifts (Wilson et al. 2008). The authors proposed that growers did not employ strategies to reduce herbicide resistance because of their underlying beliefs surrounding the inevitability of resistance and their perceived lack of influence on the evolution of herbicide-resistant weeds and weed shifts. In response, the authors recommended that training efforts emphasize the influence of the individual grower on the physical movement (migration) and evolution of herbicide-resistant weeds and weed shifts. Moss et al. (2007) echoed this idea for controlling herbicide-resistant blackgrass in European cereal markets. In a 2005, Indiana survey, however, Johnson and Gibson (2006) reported that although a low percentage (36%) of growers were highly concerned about resistance to glyphosate, most expressed a willingness to use herbicide-resistance mitigation and management strategies. Results from their survey also revealed that growers with larger farm operations (more than 800 ha) were more concerned about herbicide-resistant weeds than were growers with smaller farms.

Implementation by growers of strategies to reduce or delay the onset of herbicide-resistant weeds is highly variable. In the cases of wild oat and green foxtail in the northern U.S. Great Plains, growers were not likely to proactively manage their cropping systems to reduce or delay the evolution of weed resistance (Beckie 2007). When growers in Delaware encountered glyphosate-resistant horseweed, however, approximately 80% responded to a survey that it was worthwhile to incur additional costs to preserve glyphosate for future use (Scott and VanGessel 2007). In Australia, it was determined that most growers would benefit from strategies designed to reduce the onset of glyphosate resistance in weeds such as ryegrass (Weersink et al. 2005). In that example, the weed management practices recommended to reduce the onset of resistance were the same practices recommended to address resistance once it developed. In other situations, the choices among strategies designed to delay the evolution of herbicide-resistant weeds and the costs associated with them were less expensive than the options and related costs associated with remedial actions after herbicide resistance developed (Bryant 2007). In summary, the costs associated with weed prevention and management and the immediate needs of a grower, such as economic constraints and crop rotations, play a critical role in the decision of whether and when to implement herbicide resistance mitigation strategies.

Growers' preferences regarding where they obtain information on herbicide-resistant weeds also vary. At the end of the 2005 growing season, U.S. growers were asked where they obtained information on glyphosate resistance. Farm press publications were their primary source of information (54 to 65%, depending on the state), and the next most-important source of information was agricultural chemical dealers or retailers (15 to 23%) and universities and Cooperative Extension Services (CES)(10 to 24%)(Johnson et al. 2009). In that study, ''other growers'' placed a distant fourth, and the Internet was mentioned as a source by less than 1% of the respondents. In a similar study conducted 2 yr after the 2005 study, comparable trends were found in terms of the primary and secondary sources of information on glyphosate resistance. Information acquired from other growers, however, was found to be nearly equivalent to that from agricultural chemical dealers or retailers and universities and CES. Information obtained from Internet sources rose to 4% (Marketing Horizons, Inc., unpublished data, 2007). In the 2007 study, in addition to general information about glyphosate resistance, growers were also asked for their preferred sources of information for managing glyphosate-resistant weeds; for management information, agricultural chemical dealers or retailers ranked first (42%), followed by universities and CES (22%), the Internet at 7%, and other growers at 1%.

Several other surveys have been conducted to gain a better understanding of herbicide resistance management practices and their relationship to the crop being grown. In a survey of Indiana corn and soybean growers conducted in the winter of

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2003 and 2004, Johnson and Gibson (2006) reported that more than 80% of the growers surveyed had already adopted, or were willing to adopt, herbicide resistance management practices by scouting for weeds, using soil-applied herbicides, using 2,4-D or dicamba with glyphosate in preplant burndown programs, and using POST tank mixtures. In a 2007 survey, 400 corn, 400 soybean, and 400 cotton growers across the United States were asked which herbicide-resistant weed-management practices they always or often used in their glyphosate-resistant crop. Cotton growers were more likely to use recommended resistance-management practices often or always, compared with corn or soybean growers. More than 70% of cotton growers in the survey practiced seven or more resistance-management practices often or always, compared with 58% of corn producers and 55% of soybean producers (Frisvold et al. 2009). However, adoption rates of managing weed resistance with supplemental tillage and cleaning of farm equipment was relatively lower for cotton producers than it was for corn or soybean producers, and corn growers were most likely to rotate herbicide MOAs, followed by cotton growers and then soybean growers. Using instant response technology during a 2009 University of Illinois Corn & Soybean Classics (an annual grower and retailer meeting), growers were asked about their herbicide use in glyphosate-resistant soybeans (A. G. Hager, personal communication). Across the state, 62 to 86% of growers indicated that they rotate among herbicides with different MOAs either in tank mix or in sequence with glyphosate. Additionally, 84 to 99% of growers indicated that glyphosate-resistant weeds would change the way they managed weeds in glyphosate-resistant crops. Overall, information obtained on grower perception of resistance management practices, and especially herbicide use patterns in glyphosate-resistant crops, indicates that growers see the need to proactively manage herbicide resistance. However, there is a difference in the perception of the need to manage herbicide resistance and the realities of actually doing so.

Lessons Learned from Management Strategies. Even though the evolution of resistance cannot be predicted precisely, an absence of management strategies to reduce selection for herbicide-resistant weeds can lead to several negative consequences, including crop failure, increased production costs, and negative environmental effects from relying on older herbicide chemistries and tillage. Likewise, although no single management practice or set of management practices can address all interactions among crops, weed species, and herbicides, there are some basic guidelines that have successfully delayed the evolution of herbicide resistance in weeds.

Diversity in weed management tactics is the single, most important tactic for reducing and managing the evolution of herbicide-resistant weeds. Overreliance on a single herbicide or single group of herbicides without concurrent use of other weed management strategies has encouraged evolution of weed populations resistant to the heavily used herbicide, but it is not the only factor. Characteristics of the herbicide and herbicide class, weed biology, and cultural practices. such as crop rotation, tillage practices, and time of planting, all play a role in determining the likelihood and frequency of herbicide resistance. Resistance to herbicides is a function of (1) the frequency of herbicide use, (2) how the herbicide has been used, (3) the strong selection pressure that is characteristic of the herbicide, and (4) the resistance mechanism in the weed—that is, whether changes to the target site occur easily, without affecting plant function (e.g., ALS), or whether the target site is highly conserved so that occurrence of target-site resistance is difficult because of the negative effects on the plant (Tranel and Wright 2002).

The advantages of using multiple MOAs to delay and manage the evolution of herbicide resistance have been reported for many crop–weed, species–herbicide complexes (Kaushik et al. 2006; Legleiter and Bradley 2008; Morrison and Bourgeois 1995; Neve 2008; Norsworthy et al. 2008; Weersink et al. 2005). The type of management sequences studied have included herbicide mixtures applied at a single time; POST applications applied sequentially in the same crop; PRE applications of soil-active herbicides, followed by POST herbicide applications within the same crop; and the alternation of herbicides in different years and in different crops within a crop rotation. Limited data from field studies have been published comparing each of these herbicide management sequences with all the others listed above, but modeling can be used to predict evolution of herbicide resistance under different management practices.

Crop rotations, management of a fallow period, and cover crops, where practiced, have also contributed to the mitigation and management of herbicide-resistant weeds. By design, crop rotation facilitates the use of alternative herbicide MOAs because of the shift in different crop–weed species complexes or differences in the tolerance of crops to different herbicides or both. Crop rotation also leads to the use of additional or different cultural practices to manage weeds (Beckie et al. 2004). In summary, several scientists have even referred to crop rotation as applying "diversity" across cropping and fallow seasons to delay and manage the evolution of herbicide-resistant weeds (Beckie et al. 2004; Powles 2008).

In general, fields managed under conservation tillage (minimum and no-till systems) can create environments in which herbicide-resistant weeds are likely to develop. Because of the reduced tillage, practitioners of conservation tillage rely primarily and, in some cases, solely, on herbicides for weed control, thereby imposing consistent and often uniform selection pressures on weeds. The intensity of selection pressure can, however, depend on herbicide family and tillage type. Legere et al. (2000) reported that an increase in the use of ACCase-inhibitors in conservation-tillage systems did not accelerate the development of wild oat populations resistant to ACCase-inhibitors. Neve et al. (2003) found that the onset of glyphosate resistance in rigid ryegrass was delayed in a minimum-tillage system (100% shallow-depth soil disturbance) compared with a no-till system (15% soil disturbance at sowing). The evolution of resistance of wild oat to APP and CHD herbicides was significantly delayed in systems using deep cultivation rather than shallow cultivation (Cavan et al. 2001). A fallow period combined with tillage delayed the rate of increase of the resistant population by several orders of magnitude but did not slow down the initial appearance of resistance in a simulation conducted by Hanson et al. (2002) evaluating herbicide resistance in jointed goatgrass (*Aegilops cylindrica* Host).

The desire of growers to reduce costs and maximize profitability has led to the application of some herbicides at below-labeled use rates. Beckie (2006) provided a comprehensive review on the effects of reduced herbicide rates on herbicide resistance; many factors influenced weed response to

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low-rate herbicide use, including weed biology, the mechanism of resistance to the particular herbicide, and the effectiveness of the herbicide. Furthermore, if herbicide resistance in a weed species is a dominant trait and the level of resistance is several orders of magnitude, compared with the susceptible biotype, then herbicide rate would not be expected to have a significant effect on selecting for resistance. However, if the resistance trait is recessive, then rate could have an effect. An increase in resistant individuals within a weed population for weeds whose resistance mechanism is based on the metabolism of the herbicide is more dependent on the rate than are other types of resistance mechanisms (Sammons et al. 2007). Reduced rates can also lead to shifts in a weed population to naturally tolerant species, species with inherent biological characteristics that make the population difficult to manage (e.g., delayed emergence) or that increase likelihood of the evolution of herbicide-resistant biotypes (Owen and Zelaya 2005). For example, Wilson et al. (2007) reported an increase in common lambsquarters density after 3 yr of glyphosate use at 0.4 kg ha^{-1} twice per year, compared with use at 0.8 kg ha^{-1} twice per year.

The cleaning of field equipment before it is moved from field to field has been found to be an effective, and in some cases, a critical, practice to delay the migration of herbicide-resistant weeds into adjacent areas. Growers that included sanitation among their weed management practices were less likely to have herbicide-resistant wild oat than did those who did not include sanitation (Legere et al. 2000). Diggle et al. (2003) also reported that practices that limit the movement of weeds were needed in conjunction with combinations of herbicides to substantially delay the onset of herbicide-resistant weeds. That point is illustrated further by the, likely unintentional, movement of glyphosate-resistant johnsongrass [*Sorghum halepense* (L.) Pers.] in Argentina from its origin in the northern Salta region into the southern regions via custom-combining operations (D. Tuesca, personal communication). Practices that minimize the spreading of trash from seed-processing operations on agricultural lands can also minimize the risks associated with herbicide-resistant weeds. Significant numbers of viable Palmer amaranth seed were found in composted cotton seed gin trash spread on farm lands (Norsworthy et al. 2009). Although it is clear that cleaning and sanitizing farm equipment can be important in reducing the movement of herbicide-resistant weeds, it must be recognized that effectively cleaning such equipment, especially combines, is time consuming and difficult. John Deere (One John Deere Place, Moline, IL 61265), a major agricultural equipment manufacturer, has published procedures for cleaning combines that can take as long as 8 h to complete and are estimated to remove only 90 to 95% of weed seeds (J. Aubin, personal communication), which is unacceptable for small-seeded weeds such as Palmer amaranth.

In summary, significant progress has been made in understanding the effects of various management practices on the evolution of herbicide-resistant weeds and how best to communicate the practices and their benefits to growers and other agricultural professionals. There continues to be the need, however, to better understand the science and economics of herbicide-resistant weeds to improve the training and education of growers, agricultural retailers and distributors, and consultants.

Gene Flow from Herbicide-Resistant Crops

Gene flow is the transfer of genetic material or alleles from one plant population to another. Gene flow occurs via the movement of pollen, individual plants, seeds or vegetative propagules, or groups of plants or seeds from one place to another (Mallory-Smith and Zapiola 2008 ; Slatkin 1987). Gene flow via pollen and seeds from both transgenic and conventionally bred herbicide-resistant crops has been well documented (Beckie et al. 2003; Hall et al. 2000; Perez-Jones et al. 2010; Rajguru et al. 2005; Watrud et al. 2004; Zapiola et al. 2008), and this section addresses gene flow from herbicide-resistant crops as it relates to weed management.

Gene flow is not unique to herbicide-resistant and transgenic crops, rather, it occurs independently of the techniques used to produce the crops. Furthermore, gene flow is a natural phenomenon. Wheat and canola are examples of crops that are products of gene flow and natural hybridization (Kimber and Sears 1987; Woo 1935). In the era of herbicide-resistant crops, however, gene flow necessitates a change in our approach to weed management. Weed management concerns relative to gene flow from herbicide-resistant crops include the production of volunteer herbicide-resistant crop plants, which may be more difficult or more expensive to control, or the transfer of the resistance gene to wild or weedy relatives, thus producing a herbicide-resistant plant that requires alternative or additional control measures. When gene flow from a herbicide-resistant crop occurs via pollen, seeds, or vegetative propagules, it can result in adventitious presence of the resistance gene. *Adventitious presence* refers to low levels of unintended genetic material in seeds, grain, or feed and food products (Nair 2005).

Mechanisms of Gene Flow. Most gene-flow studies have focused on pollen movement rather than gene flow via other mechanisms. The movement of crop seeds and vegetative propagules during commerce may be of greater importance, however, in the dispersal of herbicide-resistant genes (Squire 2005). Gene flow via seeds and vegetative propagules occurs when they are moved naturally or by humans during crop production and commercialization. Transport of crop seeds and other contaminants dating back to the 19th century has been linked to the introduction and dissemination of numerous weed species (Muenscher 1936), and this is a natural pathway for the dissemination of genetic material from herbicide-resistant crops. Gene flow via vegetative propagules has been addressed rarely, but it could be an important pathway for gene movement in some crops (Mallory-Smith and Zapiola 2008).

Factors that Influence Gene Flow. Pollen-mediated gene flow is influenced by the biology of the species, the environment, and the agronomic practices, whereas gene flow via seeds and vegetative propagules is independent of mating system (a component of biology). The biology of currently available, herbicide-resistant crops is widely varied. Annual and most biennial crops are commonly grown in one growing season, whereas perennial crops persist in the field for more than one growing season; some perennial crops reproduce by vegetative propagation in addition to seeds. The life cycle of perennial crops means that genetic material persists in the environment for a greater time compared with annual or biennial crops.

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Gene Flow via Pollen Movement. Pollen is an important means of gene flow and is easier to study, given its short viability. Gene flow via pollen movement has the potential to occur in all sexually reproducing crops, even those that are predominately self-pollinated, because all species exhibit some level of outcrossing. Outcrossing values for most plant species are not well known. The extent of outcrossing can also vary with crop cultivar and environmental conditions.

The breeding system of herbicide-resistant crops may be self-pollination, cross-pollination, or mixed. Breeding systems are independent of life cycle (see above). Self-pollinated plants produce both male and female reproductive organs and do not rely on the presence of neighbors for reproduction. By definition, cross-pollinated crops have a greater potential for gene flow via pollen than do self-pollinated crops. Some cross-pollinated plants exhibit self-incompatibility, which prevents self-pollination and promotes outcrossing. Crops with mixed mating systems can produce seeds through either self-pollination or cross-pollination. The likelihood of gene flow via pollen also increases with the neighboring presence of highly compatible related species, synchronous flowering with compatible species, large pollen sources, and strong winds (Bateman 1947; Giddings 2000; Giddings et al. 1997a,b; Levin 1981). The distance at which gene flow occurs via pollen is highly variable, and it is difficult to predict the farthest distance that viable pollen can move. In general, most gene flow via pollen occurs at relatively short distances because pollen is viable for only hours or days. Pollen is subject to desiccation, and its viability is influenced by environmental factors, such as temperature and humidity.

Isolation of a herbicide-resistant crop, either in space or time, is used to lessen the likelihood of gene flow via pollen. A physical buffer, such as increasing the distance between fields, reduces gene flow because most pollen remains close to the source. A temporal buffer, such as the use of staggered planting dates, reduces pollen-mediated gene flow between corn hybrids (Halsey et al. 2005) because flowering times across fields become asynchronous. In alfalfa (*Medicago sativa* L.), cutting the crop for hay at the beginning of flowering can reduce pollen production and the potential for seed set (Van Deynze et al. 2004).

Management of pollen-mediated gene flow into nonagricultural sites is more difficult because the flowering times vary greatly among plant species in native and unmanaged sites, the flowering times of many weeds are not well documented, and some flowering times change with variations in temperatures among seasons. As a consequence, management in these sites generally requires the identification and removal of all potential receptors of pollen.

Despite efforts to mitigate the movement of pollen, natural dispersal of pollen via wind and insects cannot be prevented nor absolutely predicted, and it can occur over considerable distances (Beckie et al. 2003; Reichman et al. 2006; Watrud et al. 2004). Gene flow via pollen could be reduced greatly, however, by placement of the herbicide-resistance gene in chloroplasts, which are maternally inherited, or by using a male-sterile breeding system.

Gene Flow via Vegetative Propagules. Gene flow via vegetative propagules from herbicide-resistant crops has not been studied in depth and is rarely mentioned in the literature. Vegetative propagules, such as stolons, rhizomes, roots, crowns, and bulbs, allow single plants to reproduce in isolation and can become a source of herbicide-resistance genes. Short-distance movement can occur between fields via natural means or on shared equipment as it is moved between fields. Long-distance movement would not be expected except with human intervention or possibly via water ways (similar to the movement of seeds). Long-distance movement of vegetative propagules destined for planting has been reported (Carrier 1923). Vegetative propagules left in the soil can result in an established plant in the following year and makes eradication difficult. Reproduction via vegetative propagules must be considered a risk factor when developing management plans designed to prevent gene flow.

Gene Flow via Seeds. Loss of seeds from herbicide-resistant crops may occur at any point from planting to the final destination or sale. The more steps that occur from planting through postharvest operations, the more opportunities exist for seed-mediated gene flow. The mixing of herbicide-resistant and conventional seeds is known as *commingling* or *admixture* (Mallory-Smith and Zapiola 2008). Losses attributed to human error and plant biology are the biggest culprits of commingling. Commingling may occur at planting if seeds of a herbicide-resistant cultivar are mixed with seeds of a non–herbicide-resistant cultivar. It may occur if seeds from volunteer crop plants (i.e., plants that emerge in-season from seeds via the previous crop) are harvested with the current crop or mixed during postharvest operations, such as seed cleaning, seed conditioning, transport, or storage. The likelihood of gene flow via seed movement can be reduced by the control of volunteer plants, correct cultivar identification, and proper handling at all steps of crop production and postharvest processing and the cleaning of shared equipment. However, some seed loss at each step from planting through final use is inevitable (Mallory-Smith and Zapiola 2008).

Natural dispersal of seeds via wind, water, and animals contributes to gene flow and cannot be prevented. In general, natural seed dispersal occurs at relatively short distances, on the order of meters, away from production fields (Levin 1981), but by being more environmentally persistent than pollen, seeds can be moved farther over time (Squire 2005). Characteristics that can increase seed-mediated gene flow are small seed size, extended seed viability and dormancy, and seed shattering that occurs before or during harvest. Seed longevity varies greatly among species and can affect whether a species produces a persistent (more than 1 yr) seedbank. Dormancy allows herbicide-resistant genes to persist over several years in the soil seedbank. Some herbicide-resistant crops, such as corn, cotton, and soybean, may not produce a persistent seedbank, whereas others such as canola and alfalfa often produce persistent seedbanks. Seeds of some crops, such as canola, are prone to shattering before harvest, and plants can contribute many seeds to the soil seedbank. Herbicide-resistant crops that emerge from the persistent seedbank will be a problem if a herbicide-resistant crop with the same trait is planted in the rotation or if there is no good control option available. Herbicide-resistant rice does not have a persistent seedbank, but once the herbicide-resistant trait escapes to weedy rice, resistance will persist in the weedy rice seedbank. In Arkansas, for example, ALS-resistant weedy rice plants were detected in all sampled fields with Clearfield rice cropping history (Singh, et al. 2012).

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Herbicide-Resistant Crops in the United States. Genetically engineered, herbicide-resistant crops approved for sale in the United States include alfalfa, canola, corn, cotton, soybean, and sugarbeet. The Clearfield system of herbicide-resistant crops, which includes imidazolinone-resistant canola, rice, common sunflower, and wheat, was produced without the insertion of transgenes. Gene flow from herbicide-resistant crops, as it influences weed management, will be presented in greater detail by crop species.

Alfalfa. Alfalfa is a perennial, mainly outcrossing, insect-pollinated crop with no known compatible wild relatives in the United States (St. Amand et al. 2000; Van Deynze et al. 2004). However, feral alfalfa populations are common in areas where alfalfa is grown. The removal of feral populations could reduce the likelihood of gene flow, but that is not easily accomplished because of its perennial life cycle.

In the United States, alfalfa seed is produced primarily in the western states, on approximately 40,500 ha (Van Deynze et al. 2004). Insect-mediated pollination is necessary for alfalfa seed production (Fitzpatrick et al. 2003). In a study that evaluated gene flow from alfalfa fields, gene dispersal via pollen beyond the current isolation distances was reported (St. Amand et al. 2000). Outcrossing rates in seed production fields were 38%, whereas rates in hay fields were lower, but still greater than 25%.

Alfalfa seed is small, approximately 500 seed g^{-1}, which may increase the risk of commingling among alfalfa seed lots. Hard seeds, which are common in alfalfa, may lie dormant for years before germinating (Gunn 1972). Seed dormancy allows alfalfa to persist in the seedbank and produce volunteers in subsequent crops.

Alfalfa can be propagated by stem cuttings and alfalfa crowns can persist and re-grow (Busbice et al. 1972). Alfalfa crowns moved by machinery within and between fields could result in gene flow. Although no studies have reported vegetative gene flow in alfalfa, this mechanism of gene movement needs to be investigated.

Canola. Canola is an annual, self-fertile, and outcrossing species that is both insect- and wind-pollinated and has the potential to establish outside of cultivation. Canola can be either rapeseed (*Brassica napus* L.) or birdsrape mustard (*Brassica rapa* L.)(formerly *Brassica campestris* L.). In North America, most of the canola grown, and all of the herbicide-resistant canola, is *B. napus*.

Gene flow via pollen in canola is significant. Outcrossing rates as high as 47% have been reported (Williams et al. 1986). Canola pollen dispersal ranges from a few meters to 1.5 km (Timmons et al. 1995). Pollen movement depends on wind direction and speed, surrounding vegetation, and topography (Gliddon et al. 1994; Thompson et al. 1999). Bees are known to pollinate canola. Most bees forage close to their hive, but there are reports of bee movement up to 4 km (Mesquida and Renard 1982; Thompson et al. 1999). Because loose pollen grains can be picked up in a hive, a 4-km flying distance could result in pollen being moved 8 km. In Canada, gene movement between two genetically engineered canola lines was found at 800 m, which was the boundary of the study (Beckie et al. 2003). In a Canadian field, volunteer canola plants were identified that contained transgenes for both glyphosate- and glufosinate-resistant canola (Hall et al. 2000).

Although canola does not generally survive in undisturbed habitats, it can establish in areas adjacent to agricultural sites, roadsides, and field edges (Warwick et al. 1999). The occurrence of glyphosate- and glufosinate-resistant canola plants along railways and roadways in Canada was measured in 2005 (Yoshimura et al. 2006). In Saskatchewan, 34% of 300 canola plants tested were glyphosate-resistant; in British Columbia, 43% of 81 plants tested were resistant. One hybrid between *B. rapa* and *B. napus* was identified as glyphosate-resistant.

Volunteer canola plants can be a significant weed problem in subsequent crops (Kaminski 2001; Thomas et al. 1998). In 35 sampled fields, harvest seed loss ranged from 3 to 10%, with an average of about 6% or an equivalent of 107 kg ha^{-1} (Gulden et al. 2003a). In general, canola seedbanks decline quickly, but some seed may persist for several years (Gulden et al 2003b). Canola seeds are reported to survive longer when buried (Pekrun and Lutman 1998).

Many studies have addressed gene flow via pollen from transgenic or conventional canola to weedy or wild relatives (Bing et al. 1996; Chèvre et al. 1998, 2000; Darmency et al. 1998; Jørgenson and Andersen 1994; Jørgenson et al. 1994, 1996; Lefol et al. 1995, 1996; Rieger et al. 2001; Warwick et al. 2003). The movement of a herbicide-resistance gene would lead to herbicide-resistant individuals and the likelihood that resistant populations could occur both within and outside of cultivated fields.

Corn (Maize). Corn is an annual, highly outcrossing species that produces abundant pollen and is primarily wind-pollinated (Brittan 2006; Halsey et al. 2005). Corn has no compatible relatives in the United States, and there is no risk of gene flow that could result in a herbicide-resistant weed by hybridization. Because corn does not persist outside of cultivation, the main dispersal mechanisms for a herbicide-resistance gene are via pollen among neighboring corn fields and seed commingling.

Corn seed does not shatter, and corn rarely sheds its seed. However, corn seed are often scattered by harvest equipment, mature corn plants can lodge and drop ears, intact ears and individual kernels can be removed from fields by small mammals that forage for food, and corn seed can be scattered along commercial transportation routes. Corn grains or ears left in the field after harvest often create volunteer corn plants the following year (Tolstrup et al. 2003). Management of herbicide-resistant volunteer corn plants in continuous corn or soybean resistant to the same herbicide requires the use of additional or alternative herbicides and could become a significant economic problem in areas where corn is planted in rotation with soybean and cotton (Deem et al. 2006; Clewis et al. 2008).

Cotton. Cotton can be either self-pollinated or cross-pollinated by insects. Two species of cotton, upland (*G. hirsutum*) and Pima (*Gossypium barbadense* L.), are grown in the United States, with the largest proportion being upland cotton.

A range of outcrossing rates and a potential for insect pollination provide opportunity for some gene flow via pollen among cotton fields (Meredith and Bridge 1973). Reported outcrossing rates vary widely and depend on the number of pollinators present in a field and, possibly, on the cotton cultivar (Green and Jones 1953; Simpson and Duncan 1956). The introduction of the transgenic, insect-resistant *Bacillus*

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thuringiensis (Bt) cotton may lead to an increase in outcrossing rates because of the greater survival of pollinators as a result of fewer insecticide applications.

Volunteer cotton plants occasionally establish in subsequent crops, but they generally do not survive the winter, except in unusually mild winters in the southernmost U.S. states (Wozniak 2002; York et al. 2004). Because so much of the cotton grown in the United States is herbicide-resistant, the greatest potential for commingling of herbicide-resistant cotton seeds with non–herbicide-resistant cotton seeds may occur during ginning if both types are processed at the same facility.

Grain Sorghum. The *Sorghum* genus includes (*Sorghum versicolor* Anderss.), a wild African grass (sometimes called bruinsaadgras); *Sorghum bicolor* (L.) Moench., which includes all sorghums, shattercane, and Sudangrass; sorghum-almum (*Sorghum almum* Parodi), a weak perennial weed; and johnsongrass [*Sorghum halepens*e (L.) Pers.], a robust perennial and formidable weed throughout its range across the humid areas and irrigation ditches of the southern United States and Ohio River Valley.

The sorghums are wind-pollinated. All the cultivated sorghums are interfertile and spontaneously cross in the field. Arriola and Ellstrand (1996) reported that johnsongrass and grain sorghum cross-pollination rates can be as high as 100% at distances of 0.5 to 100 m. Grain sorghum cultivars with resistance to the ALS- and ACCase-inhibitor herbicides have been developed and licensed by Kansas State University. These herbicide-resistant cultivars are expected to be commercialized. Biotypes of johnsongrass that are resistant to ALS- and ACCase inhibitors, the dinitroanilines, and glyphosate have been reported in the midsouth region of the United States. The emergence and spread of herbicide-resistant populations of johnsongrass is a matter of economic concern in all row crops and along roadsides and other noncrop areas in the South, especially in the midsouth and southern plains. In this respect, the release of herbicide-resistant cultivars of sorghum that may contribute to evolution of new populations of herbicide-resistant johnsongrass is a concern.

Rice. Rice is an annual, predominantly self-pollinated crop with minimal cross-pollination potential; yet, gene flow of herbicide-resistance traits is a global issue because of the widespread occurrence of weedy rice in rice-producing regions and wild relatives in Asia, Africa, and Central America (Delouche et al. 2007). The herbicide-resistant rice technology was developed primarily to control weedy rice in rice production.

Gene flow by seed is a concern because of seed movement from field to field via irrigation systems, farm machinery, and grain trucks. Elimination of the risk of commingling between non–herbicide-resistant and herbicide-resistant rice cultivars is practically impossible because of the bulk handling of rice grains from the farm to the shipping docks. The rice complex comprises seven wild and weedy species, five of which—rice (*Oryza sativa* L.), brownbeard rice/Indian wild rice (*Oryza rufipogon* Griffiths/*Oryza nivara* S.D. Sharma & Shastry), African rice (*Oryza glaberrima* Steud.), wild rice (*Oryza barthii* A. Chev.), and longstamen rice (*Oryza longistaminata* A. Chev. & Roehr.)—are weeds in rice fields worldwide (Vaughan et al. 2003). The *Oryza* species complex can interbreed (Vaughan et al. 2005); thus, their coexistence with cultivated rice results in gene flow via pollen and has produced morphologically and biologically diverse weedy rice populations (Shivrain et al. 2010a; Shivrain et al. 2010b), which reduces the overall efficacy of management tactics. To manage this most difficult weed problem in rice (that is, weedy rice), herbicide-resistant rice was developed. The nontransgenic, herbicide-resistant rice (Clearfield), which is resistant to the imidazolinone herbicides among the ALS inhibitor MOA group, is now widely adopted in the southern United States, with growers in Central and South America following closely behind. This technology is highly effective in controlling weedy rice with control generally above 95% (Avila et al. 2005a; Levy et al. 2006; Ottis et al. 2004; Steele et al. 2002). The bottleneck of this technology in rice are twofold: (1) the escape of herbicide-resistant trait to the weedy or wild relative, which produces herbicide-resistant weedy rice, and (2) selection for herbicide-resistant biotypes of not only weedy rice but also other major weed species in rice that are otherwise controlled by the ALS-inhibitor herbicides (e.g., flatsedge [*Cyperus* L.] spp., cockspur/barnyardgrass [*Echinochloa* P. Beauv.] spp., fringerush [*Fimbristylis* Vahl] spp.). Gene flow from herbicide-resistant rice (Clearfield and Liberty Link [Bayer CropScience, Monheim am Rein, Germany]) to weedy rice is well documented in Asia, Europe, and the Americas, showing pollen flow rates from 0.003% to 0.25% (Chen et al. 2004; Gealy 2005; Lentini and Espinosa 2005; Messeguer et al. 2004; Noldin et al. 2002; Sankula et al. 1998; Shivrain et al. 2006, 2007, 2008; Song et al. 2003; Zhang et al. 2003). These seemingly low numbers, however, have resulted in the presence of herbicide-resistant weedy rice in Arkansas rice fields with at least 2 yr of history with Clearfield rice (Singh et al. 2012). Herbicide-resistant weedy rice resulting from gene flow seems more prevalent in the tropical regions of Central America and South America (B. E. Valverde, personal communication), where there is no winter kill, and rice is generally planted twice a year.

Now that the acreage of hybrid rice in the southern United States has increased significantly, it is important to note that, whereas the highest outcrossing rate with Clearfield nonhybrid rice is 0.25%, with Clearfield hybrid rice, it is up to 1.26% (Shivrain et al. 2009b). Prolonging the utility of this technology rests on the following basic weed management principles: (1) adoption of BMPs that ensure maximum efficacy of the herbicide, (2) minimizing the synchronization of flowering between herbicide-resistant rice and weedy rice (by adjusting planting dates and knowing the phenology of weedy rice relative to the rice cultivars), (3) preventing escaped weedy rice in a Clearfield rice field from producing seed, and (4) preventing volunteer rice or weedy rice from producing seed in the next crop cycle by controlling it in a rotational crop, such as soybean. It is important to consider that once the resistance trait is introgressed into the weedy rice population, it can be transferred to other weedy rice populations or to non–herbicide-resistant rice cultivars (Shivrain et al. 2009a). Thus, weedy rice needs to be controlled not only in the rice paddies but also along field edges and irrigation ditch banks.

How far should rice fields or weedy rice populations be from each other to prevent pollen-mediated gene flow? In general, effective pollen flow is detectable within 1 m and declines significantly beyond that (Messeguer et al. 2001; Shivrain et al. 2007; also, see review by Gealy 2005). Effective

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pollen flow between cultivated rice and Indian wild rice (*O. rufipogon*) was detected up to 40 m (Song et al. 2003). As the population size of the pollen donor increases, effective pollination distance also increases. In field-scale, Clearfield rice-pollen flow experiments, outcrossing was detected up to 297 m (Burgos et al. 2010).

Soybean. Soybean is an annual, highly self-fertile, self-pollinating species (Caviness 1966). Pollen-mediated gene flow from herbicide-resistant soybean is considered a low risk (Gealy et al. 2007). Soybean is generally not found outside of cultivation (OECD 2000), and it has no compatible relatives in the United States. Nevertheless, cross-pollination occurred at low levels between non–herbicide-resistant cultivars at short distances (Caviness 1966), which demonstrates the potential for gene flow between adjacent fields.

Most of the soybeans in the United States are grown for oil extraction and animal feed. Therefore, gene flow could occur during seed transport. Because of the widespread adoption of glyphosate-resistant cultivars, commingling has not generally been a concern. This could change with the introduction of the glufosinate-resistant cultivars. Volunteer soybean plants are common in subsequent crops and are generally well-controlled with herbicides and tillage, except in cotton, where conservation-tillage practices are common and glyphosate may be the only POST herbicide used. Weed management is a greater challenge when herbicide-resistant soybeans are grown in rotation with other crops resistant to the same herbicide; i.e., glyphosate-resistant corn grown in rotation with glyphosate-resistant soybean. Volunteer glyphosate-resistant soybean plants also have been reported in glyphosate-resistant cotton (York et al. 2005), although commingling of soybean and cotton seeds during harvest has not been reported, most likely because of the differences in growth and production practices of the two crop species.

The movement of herbicide resistance genes via either pollen or seeds is of greatest concern for soybean growers that produce non–herbicide-resistant soybeans and where volunteer glyphosate-resistant soybean plants require different management strategies, especially in minimum- or no-tillage environments that depend heavily on the use of glyphosate.

Sugarbeet. Sugarbeet is an outcrossing, wind-pollinated species. Although sugarbeet is a biennial, it is grown as a winter annual crop for seed or as a summer annual for root production. When sugarbeets are grown for their roots, they are harvested before the plants bolt. Occasionally, there will be some plants that set seed before harvest. On the occasion that fields cannot be harvested before winter, they are left in the field. Plants that remain in fields may flower the next cropping season if not killed by winter conditions; however, gene flow via pollen or seed in root production fields generally is not an issue.

All major sugarbeet seed companies have addressed the issue of pollen flow from glyphosate-resistant transgenic sugarbeet to compatible crops by voluntarily increasing the isolation distances from compatible species (G. Burt and J. R. Standard, personal communication). Still, it is possible for a seed-producing field to be planted closer than the recommended isolation distances. At least one seed company has placed the herbicide-resistant trait on the female seed plants, nearly eliminating herbicide-resistant pollen movement in these types of fields. To prevent seed commingling, seed producers are not allowed to grow conventional and herbicide-resistant sugarbeet seed on their farm in the same year and herbicide-resistant seed is cleaned and stored separately (G. Burt and J. R. Standard, personal communication). Seed shattering can occur during harvest, and volunteer sugarbeet plants require control in subsequent crops. Sugarbeet can produce a persistent seedbank if seeds are buried during tillage.

Seed production fields are established by using either seeds or transplants. Viable herbicide-resistant sugarbeet roots that were left after planting a seed field were found in compost sold for use in flower and vegetable gardens (C. A. Mallory-Smith, personal observation). The roots were not disposed of in a manner consistent with the company's prescribed protocol. The use of transplants provides another potential mechanism for gene flow.

Sugarbeet does not produce feral populations in the United States, but it has two compatible relatives, beet [*Beta vulgaris* L. ssp. *macrocarpa* (Guss.) Thell.] and wild beet [*Beta vulgaris* ssp. *maritima* (L.) Arcang.], in California (USDA plant database). Hybridization and introgression of sugarbeet alleles have been reported in an accession of the *B. vulgaris* L. ssp. *macrocarpa*, which is a widespread weed in and near sugarbeet fields in the Imperial Valley, CA (Bartsch and Ellstrand 1999). The authors also suggested that sugarbeet can hybridize with *B. vulgaris* spp. *maritima*. The conspecific crops red beet (*Beta vulgaris* ssp. *vulgaris* var. *conditiva* Alef.) and Swiss chard [*Beta vulgaris* L. ssp. *cicla* (L.) W.D.J. Koch) freely hybridize with sugarbeet. Therefore, there is potential for a herbicide resistance gene to persist in the environment outside of production fields.

Wheat. Wheat is a predominately self-pollinated species. Wheat does not produce a persistent seedbank but does produce volunteers in following crops, and volunteer wheat is a major weed in no-till or minimum-tillage systems. A herbicide-resistant wheat could have a negative effect on volunteer management, especially if it were glyphosate resistant because glyphosate is the foundation for weed control in no-tillage or minimum-tillage wheat production systems.

Wheat hybridizes with jointed goatgrass, a weed found throughout wheat-growing regions in the Pacific Northwest and the Great Plains of the United States. The F_1 hybrids produce very few seeds because they are male-sterile with low female fertility (Zemetra 1998). However, each successive backcross to either parent increases fertility. Selective control of jointed goatgrass with a herbicide was not possible until the introduction of Clearfield (imazamox)-resistant cultivars. In 2008, hybrids carrying the herbicide-resistance gene were found in commercial wheat fields in Oregon (Perez-Jones et al. 2010). In subsequent field surveys in 2009 and 2010, resistant hybrids and putative backcross progenies were widespread across the wheat-growing region in Eastern Oregon (C. Mallory-Smith, unpublished data). The hybrids are not being controlled in the wheat fields with the application of imazamox so remain in the field with the potential for backcrossing to wheat or jointed goatgrass. The number of resistant plants has increased along with a decrease in the benefit derived from planting the herbicide-resistant wheat.

Conclusions

Herbicide-resistant crops have given crop producers agronomic, economic, and environmental benefits, including

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savings in time and production costs and increasing the ease of using conservation-tillage practices. However, repeated use of herbicides with the same MOA in either conventional or herbicide-resistant crops has led to widespread herbicide-resistant weeds. Herbicide-resistant crop technology encouraged a reduction in the use of multiple herbicide MOAs because the technology allowed the use of broad-spectrum herbicides, such as glyphosate and glufosinate, or control of specific problematic weeds, such as red rice in rice. The broad-spectrum herbicides were also an answer to control of weeds that had evolved resistance to other herbicide MOAs. The limited availability of herbicide MOAs and limited development of new MOAs to control the most problematic herbicide-resistant weeds constitute a growing threat to the success of agriculture as we know it in many areas of the United States, including that of conservation tillage.

Much weed science research is focused on predicting the probability of resistance evolution and the rate at which it will evolve. These predictions require knowledge of many factors, including many that are specific to the weed—its biology/ecology and genetics—and to the cropping system and environment to which the weed population is exposed. Some of these factors include mutation rates, modes of inheritance, gene flows among populations, seed production and survival, seed dormancy, and effects of production practices and herbicide interactions on resistance evolution. Computer simulation modeling is a valuable tool for predicting evolution of herbicide resistance, but these and other factors must be considered to develop a successful predictive model.

Through research and modeling efforts, some basic resistance-management strategies have been formulated. One of the most important is diversification of management practices, which includes diversification of herbicide MOAs. To mitigate weed resistance, it is important that crop producers understand and use a variety of weed control tactics: preventive control, cultural and mechanical tactics that provide a competitive advantage for the crop, biological tactics when possible, and judicious and diversified use of herbicides. Producers must decide which set of resistance-management practices will best fit their unique production system.

An understanding of grower perception of weed management and herbicide resistance informs weed scientists as to where and how best to focus education and training programs. Strategies to improve education about herbicide resistance include (1) expanding efforts by university and industry scientists to understand growers' perceptions of weed management, recommended resistance-management practices, and herbicide-resistant weeds; (2) implementing communication that is more effective and grower education programs; and (3) publishing management strategies designed to address mitigation and management of herbicide-resistant weeds. Additionally, as conservators of herbicide-resistant crop technology, the agricultural community as a whole must accept responsibility of sustainable use of the technology.

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