Current Status of Herbicide-Resistant Weeds and Their Management Strategies

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Abstract

Since the first reports of herbicide-resistant weeds in the 1960s, resistance has been confirmed in at least 100 species, affecting many diverse herbicide classes and modes of action. Resistant weeds have been identified worldwide, generally in continuous monoculture crop fields, or non-crop areas, where a single herbicide mode of action was used repeatedly. Resistance to triazines, which are Photosystem II inhibitors, was one of the first confirmed cases, and it is now the most prevalent type of herbicide resistance, with 58 resistant species. Fewer, but significant numbers of species have documented resistance to Photosystem I inhibitors, acetyl CoA carboxylase inhibitors, acetolactate synthase inhibitors, tubulin inhibitors, and auxin analogs, among others. Strategies to minimize and manage herbicide resistance focus on reducing selection by a single mode of action alone, and on depleting the weed population. A long-term, planned approach to weed management should integrate a variety of chemical and non-chemical weed control methods. Judicious selection of mixture, rotational, or sequential applications of herbicides with different modes of action should be implemented in conjunction with cultural practices to reduce production and dispersal of weed seeds. Competitive crop stands, weed-free seeds, crop rotation, tillage or cultivation, non-selective herbicides, grazing, delayed planting, clean machinery and equipment, and removal of weed seeds during harvest are examples of techniques that may be employed with selective herbicides to enhance the ability to manage weeds and maintain efficient crop production in the face of resistance.

Key words: herbicide-resistant weeds, resistance management strategies

Introduction

The evolution of herbicide resistance in weeds resulting from repeated herbicide applications was first reported in the 1960s (Bandeen *et al.*, 1982). Since that time, the numbers of weed species, herbicide classes, and geographical areas affected by resistance have grown continually. Use of the same herbicide for several consecutive years characterizes the situations in which the first resistant weeds developed. After thirty years, and the development of thousands of additional resistance sites, it is still true that resistance generally occurs where the same herbicide, or herbicides with the same mode of action, are used to control the same weed for several years. Weed management strategies to avoid or delay the onset of resistance have been devised to reduce the intensity of selection that such mono-herbicide systems apply to weed populations, and to deplete the weed population by reducing seed production.

Current status

The first reports of weed populations evolving herbicide resistance were of triazine-resistant common groundsel (*Srecio vulgaris* L.) (Ryan, 1970) and 2, 4-D-resistant wild carrot (*Daucus carota* L.) (Whitehead and Switzer, 1963). Since then, at least 30 countries worldwide have reported one or more cases of resistance (LeBaron, 1992). Although species with resistance to members of various other herbicide classes

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have been documented (Holt *et al.,* 1993), triazine resistance is the most prevalent with at least 58 resistant species identified (LeBaron, 1992). Significant numbers of species have developed resistance to other herbicide classes (Fig. 1) including acetolactate synthase (ALS) inhibitors, acetyl CoA carboxylase (ACCase) inhibitors, auxin analogs, Photosystem I (PS I) inhibitors, and tubulin inhibitors, as well as non-triazine Photosystem II (PS II) inhibitors.

In many of the cases studied so far, resistance is due to an alteration of the target site that renders it less susceptible to the herbicide (Holt *et al.,* 1993). On this basis, selection for resistance to one member of a herbicide class often confers resistance to some or all other herbicides with the same mode of action. This phenomenon is known as target site cross resistance, and herbicides with different modes of action generally retain activity on such biotypes.

An important trend during the last decade has been the development of non-target site cross-resistance and multiple resistance, best exemplified by blackgrass (*Alopecurus myosuroides* Huds.) in the United Kingdom and rigid ryegrass (*Lolium rigidum* Gaud.) in Australia (Hall *et al.,* 1994). Biotypes of these species have evolved resistance to many herbicides from different chemical classes and having different modes of action, often without having been treated by some of the herbicides. Resistance is based on one (non-target site cross resistance) or several (multiple resistance) resistance mechanisms. These biotypes can be especially problematic because of the limited number of selective herbicides still capable of controlling them.

Resistance evolution

For resistance to evolve, genetic variation for the resistance trait (s) must exist within a population, and selection events must take place (Maxwell and Mortimer, 1994). Genetic variation for resistance probably arises from spontaneous gene mutation (Jasieniuk and Maxwell, 1994). There are no data to indicate that mutations result from herbicide application (Holt *et al.,* 1993). The rate of resistance evolution depends on initial frequency of resistance alleles, mode of inheritance, relative fitness of the resistant and susceptible phenotypes, soil seed bank dynamics, and selection intensity (Gressel and Segel, 1990 ; Maxwell and Mortimer, 1994), with selection intensity having the greatest influence (Jasieniuk and Maxwell, 1994). Selection intensity on a particular weed by a given herbicide is determined by the intrinsic efficacy of the herbicide and the duration of its effect against that weed, coupled with its frequency of use.

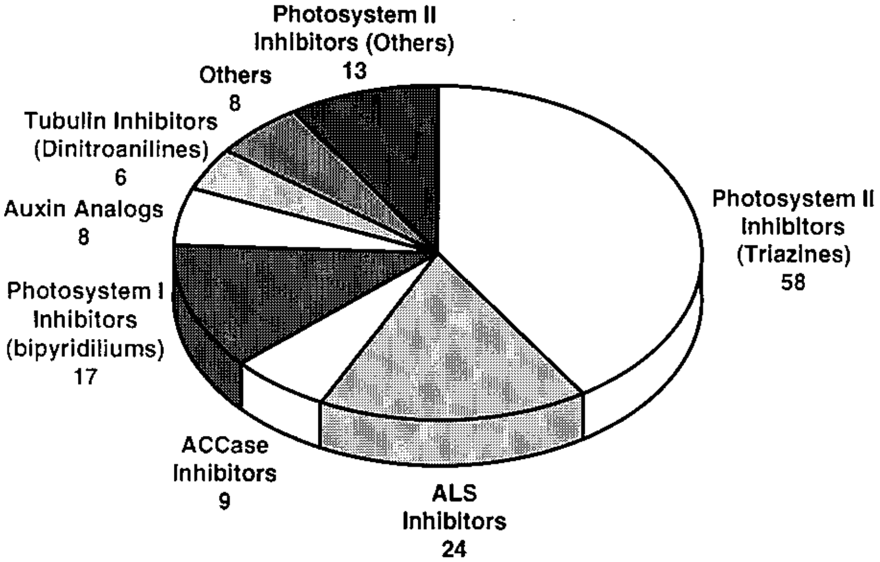

Fig. 1 Worldwide distribution of herbicide resistance in weeds : number of species resistant to each herbicide class. Thirty countries reported occurrence of one or more resistant weed species (see references 3, 10, 14, 15, 25, 26)

Considering the components of selection intensity, as alluded to earlier, the majority of sites where herbicide resistance has developed are characterized by practices that imposed high selection intensity. These practices include:

- Reliance on a single herbicide mode of action in continuous monoculture, rotational cropping, or industrial use (such as roadsides or railroad rights-of-way)
- Use of herbicides with long residual activity (or high application rates that impart long residual) or frequent applications.

Specific examples of situations resulting in high selection intensity, and alternative weed management programs, will be described in a later section.

Compounding the issue of selection intensity is the wide range of inherent sensitivity of different weeds to the same herbicide and the fact that herbicide application rates are typically selected to control numerous species. Consequently, the recommended application rate may be considerably higher than the rate required to control the most sensitive weeds. Species in which resistance has evolved have generally been those that are highly sensitive to the selecting herbicide. Thus at recommended application rates they are exposed to a very high selection intensity.

Once established, the spread of resistance is influenced by gene flow, through either pollen or seed dispersal. Aside from cytoplasmic inheritance of target-site triazine resistance, inheritance is controlled by single, nuclear, dominant or semi-dominant genes in the majority of resistant biotypes where inheritance has been studied (Gasquez, 1995). This implies that pollen dispersal should be a key mechanism in resistance gene flow. However, though pollen movement is involved in spreading resistance for species with a high degree of cross-fertilization and with resistance mechanisms encoded by nuclear genes, seeds likely play a more important role in many instances (Jasieniuk and Maxwell, 1994), especially for long-distance dispersal (Stallings *et al.,* 1995). Many resistant species are prolific seed producers, and some have seed dispersal mechanisms that promote seed spread (Saari *et al.,* 1994; Stallings *et al.,* 1995). Furthermore, harvesting operations and farm implements contaminated with resistant seeds (or vegetative propagules) can increase dissemination of resistance. Therefore, prevention of seed production and dispersal is a key objective of resistance management programs.

Exceptions to the tendency for seed migration to be the major means of gene flow are blackgrass and rigid ryegrass. These species, in which cross and multiple resistances has developed, are obligate cross-pollinators and possess a high degree of genetic variability. It is hypothesized that cross-fertilization among survivors of herbicide applications in large populations results in the exchange of genes for several resistance mechanisms. Consequently, multiple mechanisms accumulate in individuals and populations (Hall *et al.,* 1994; Powles and Matthews, 1992). For these species, pollen movement appears to play a substantial role in resistance spread.

Resistance management strategies

From the previous discussion of factors that affect the rate of resistance evolution and spread, it is clear that strategies to minimize and manage resistance must focus on reducing selection by a single herbicide mode of action alone, and on limiting seed production. Not only are these among the most influential determinants, but they are also among the few factors over which a farmer can exert control. A long-term, planned approach that integrates a variety of chemical and non-chemical methods over multiple years of the rotation is key to successful weed management. Techniques to reduce selection pressure include (Gressel and Segel, 1990; Jasieniuk and Maxwell, 1994; Matthews, 1994):

- Rotating crops in conjunction with rotating herbicide modes of action
- Using mixtures or sequential treatments of herbicides with different modes of action
- Using shorter-residual herbicides
- Limiting the number of treatments per crop with the same mode of action for control of the same species.

When choosing the herbicide(s) with alternative modes of action for mixture, sequential, or rotational treatments with a particular herbicide, the optimal partner with respect to resistance management is one with a similar weed control spectrum and residual activity as the primary herbicide. In addition, the application rate of the partner herbicide should be sufficient to provide effective control of the target species. Regarding the selection of rotational crops, one should consider crops that would allow the use of selective herbicides that are still effective against resistant biotypes that may have been selected by the use of a previous herbicide.

Another means by which herbicides with alternate modes of action may be introduced into the cropping system is through the use of herbicide-resistant crops (Gressel, 1988). For example, as crops resistant to glyphosate and glufosinate become available, growers may break the selection cycle for resistance to selective herbicides by incorporating these non-selective herbicides (with appropriate resistant crop varieties) into their in-crop weed management program.

A wide variety of methods may be used before, during, or after the cropping season, or during a non-crop part of the rotation, to deplete the seedbank and limit new weed seed production (Matthews, 1994 ; Martin et al., 1993 ; Powles and Matthews, 1992). Many of these methods are non-selective and thus control resistant and susceptible biotypes equally. A partial list of measures to prevent spread of resistance by seeds includes :

- Using tillage or cultivation before or after the crop or during a fallow period
- Using non-selective herbicides before or after the crop or during a fallow period
- Delaying planting so that early germinating weeds can be controlled by cultivation or non-selective herbicides
- Making a late season herbicide application to control late maturing weed species
- Producing competitve crop stands
- Using mulches
- Cutting a crop for hay, silage, or green manure before weed seed production
- Rotating to pasture and grazing before weed seed production.

In addition, consideration should be given to rotating to crops grown in different seasons. "Shifting" the cropping season may provide opportunities during the "new" off-season to control problem weeds of the standard crop by alternative herbicides or non-selective methods that are not practical in the cropping season.

Measures should also be taken to minimize weed seed dispersal which may be accomplished by :

- Planting weed-free seeds
- Cleaning farm machinery and implements
- Collecting and removing weed seeds during the harvesting operation (if seeds are not shed at maturity)
- Burning pastures or crop and weed residues to destroy seeds.

The above lists are not intended to be comprehensive. Rather, they should be viewed as providing ideas to form the basis of an integrated weed management plan that is customized for the prevailing local environmental, economic, and cultural conditions, as well as the crop and weed biological characteristics. Such conditions vary dramatically from place to place, as do exploitable characteristics of target weeds. It is therefore imperative that management strategies be devised on a local, and even a field-by-field basis.

Fitness considerations

Empirical models indicate that if the resistant phenotype is associated with reduced fitness (in the absence of the selecting herbicide), resistance evolution will be slower than if the resistant and susceptible phenotypes have similar fitness (Gressel and Segel, 1990 ; Maxwell *et al.,* 1990). The relative fitness of the resistant and susceptible phenotypes can also influence the effectiveness of some resistance management strategies. Specifically, models predict that rotating herbicides will be more effective in slowing the progression toward resistance or in hastening the reversion to susceptibility (when use of the selecting herbicide is discontinued) when the resistant is less fit than the susceptible phenotype (Gressel and Segel, 1990 ; Jasieniuk and Maxwell, 1994 ; Maxwell *et al.,* 1990). These effects are based on the fact that, in the absence of the selecting herbicide, the proportion of the resistant phenotype in the population will decline due to its inferior competitive ability (fitness).

Substantially reduced fitness has been clearly demonstrated in several species with target-site resistance to triazines (Holt and Thill, 1994), and it has probably resulted in a slower progression to resistance than would be predicted based on only selection intensity and initial frequency. Fitness has not been studied as exhaustively for resistance to other modes of action as it has been for triazine resistance. However, from the available results, there does not appear to be a consistent fitness disadvantage in other resistant biotypes (Holt and Thill, 1994 ; Saari *et al*., 1994). In particular, studies of fitness components in biotypes resistant to ALS inhibitors (Saari *et al*., 1994), ACCase inhibitors (Wiederholt and Stoltenberg, 1995), or triallate and difenzoquat (O'Donovan *et al*., 1995) have not revealed consistent fitness penalties compared to susceptible biotypes. Findings in studies of weeds resistant to dinitroanilines (tubulin inhibitors) and PS I inhibitors have been mixed, and they neither support nor refute the hypothesis of a general tendency for reduced fitness in resistant biotypes (Holt and Thill, 1994). Further, inherent intraspecific variation and selection by environmental conditions and cultural practices for specific traits may compensate for fitness effects associated with herbicide resistance in a field environment (Holt and Thill, 1994). Consequently, with the exception of target-site triazine resistance, when rotating to herbicides with a different mode of action, the expected effect will be a delay in resistance evolution proportional to the number of years away from the herbicide of interest. An enhanced delay, greater than the proportion of "off years", will occur only if fitness of the resistant plants is low in the off years (i.e. in the absence of selection by the herbicide of interest) (Gressel and Segel, 1990).

Increased sensitivity of resistant plants to alternative herbicides, or negative cross resistance, can further delay resistance development or speed the return to a largely susceptible population (Gressel and Segel, 1990). This phenomenon may not be widely applicable, however, as most examples of negative cross-resistance so far reported have been among triazine-resistant plants (Gressel and Segel, 1990), just as is true for reduced fitness (Holt and Thill, 1994).

Practical examples of resistance management

Resistance management techniques have been proposed largely based on theory and empirical modelling. Few experiments have been conducted to systematically study the benefits of employing resistance management strategies, or to compare the efficacy of various strategies in delaying the onset of resistance or in managing it once it has evolved. Therefore, it is instructive to review some examples of actual farming situations in which contrasting weed control practices were used and had different results in terms of resistant weed development.

Perhaps the first and most obvious example is that of triazine resistance. Beginning in the 1960s, triazine resistance has developed extensively, and sometimes relatively rapidly (e.g. 6-10 years), in maize (*Zea mays* L.) monoculture, nurseries, orchards, and non-crop areas worldwide, where triazines were used repeatedly and exclusively for weed control (Bandeen *et al*., 1982 ; Gronwald, 1994). In stark contrast is the fact that triazines have been used in other extensive areas of maize for over 30 years without the occurrence of resistance (Bandeen *et al*., 1982 ; Gressel and Segel, 1990). The likely reason for this difference is that in the latter areas, several of the methods that we have listed as resistance management strategies have been typical of crop culture for many years. Maize is regularly rotated with other crops (e.g. soybeans (*Glycine max* (L.) Merr.) in the U. S. Midwest), numerous alternative herbicides with different modes of action are used in maize as well as the rotational crop(s), and tillage or interrow cultivation is practiced. Comparing the resistance outcome of the two situations offers clear support for crop rotation and the use of a variety of herbicide modes of action.

A similar example is that of the development of resistance to ALS inhibitors in broadleaved weeds of cereal crops in North America but not in Europe (Brown and Cotterman, 1994 ; Saari *et al*., 1994). Cereal culture in much of Canada and the northern U. S. is characterized by monoculture, relatively few effective alternatives to ALS inhibitor herbicides for broadleaved weed control, and environmental conditions that favour long residual activity of some ALS inhibitors. Hundreds of sites of resistant kochia (*Kochia scoparia* (L.) Schrad.) have been confirmed among the cereal growing areas of the northern U. S. and Canada (Brown and Cotterman, 1994 ; Saari *et al*., 1994). On the other hand, in northern Europe, cereals are generally grown in rotation with a diversity of crops. Further, a variety of herbicides, herbicide mixtures, and sequential treatments are available for use, not only in cereals, but also in the rotational crops. Consequently, to date there is only one confirmed case of resistance in a broadleaved weed to ALS inhibitors (Brown and Cotterman, 1994 ; Saari *et al.,* 1994) even though ALS inhibitors for cereals have been available in Europe nearly as long as in North America. Significantly, this resistant chickweed (*Stellaria media* (L.) Vill.) developed in a Danish field in which spring barley (*Hordeum vulgare L.*) had been grown continuously and treated with an ALS inhibitor alone for five years (Kudsk *et al.,* 1995). Again, this comparison supports the validity of crop and herbicide rotation and herbicide mixtures for delaying resistance.

A third example also highlights the importance of rotating herbicide modes of action along with crop rotation. ACCase inhibitors are used only for grass control, and dinitroanilines are used for grass and broadleaved weed control. Due to their versatility, members of both of these classes may be used in grain and oilseed crops. In some areas of western Canada, dinitroanilines have been used annually on the same field for control of green foxtail (*Setaria viridis* (L.) BeauV.) for more than 15 years, in spite of rotating crops. The result has been widespread green foxtail resistance to dinitroanilines in these areas (Morrison *et al.,* 1989 ; Smeda and Vaughn, 1994). Similarly, ACCase inhibitors have been used annually as the exclusive control of wild oat (*Avena fatua* L.) in some fields in cereal-oilseed rotations. Predictably, the outcome has been the development of wild oats resistant to ACCase inhibitors (Devine and Shimabukuro, 1994 ; Heap *et al.,* 1993). Although dinitroanilines and ACCase inhibitors are also used for grass control in rotated crops (i.e. maize/soybeans) in the U. S., resistance has not been observed under these circumstances. A possible basis for this absence of resistance is that neither of these two classes of herbicides with different modes of action are used as the sole grass control agent throughout the rotation. Maize-selective ACCase inhibitors are not available, and herbicide mixtures and sequential treatments incorporating grass activity from different modes of action are currently the norm in both maize and soybeans. Thus selection from a single mode faction alone is minimized.

The final example to be discussed emphasizes the importance of carefully selecting partner herbicides for mixture, sequential, or rotational treatments. It is critical that the partner herbicides be active on the species of most concern for resistance development and that they are used at rates that provide effective control. Resistance to the ALS inhibitor bensulfuron methyl developed after 4 years of its continuous use in monoculture rice (*Oryza sativa* L.) in California, U. S. and New South Wales, Australia (Brown and Cotterman, 1994 ; Pappas-Fader *et al.,* 1993 ; Saari *et al.,* 1994). Smallflower umbrella sedge (*Cyperus difformis* L.), an annual sedge, developed resistance in California and New South Wales. California arrowhead (*Sagittaria montevidensis* SPP. calycina), an annual broadleaved weed developed resistance in California. Both of these weeds are very sensitive to bensulfuron methyl and are not controlled by molinate, the predominant partner that was used with bensulfuron methyl. In addition, due to various issues such as water quality and drift potential, few herbicides with other modes of action are available for annual broadleaved and sedge weed control in rice in California or New South Wales. Under these conditions, selection intensity for resistance was high and widespread. In contrast, although rice is also grown in monoculture in Japan, the selection intensity for resistance to the ALS inhibitors is generally low in this country. The reason for the reduced selection intensity is that in Japan, nearly all rice ALS inhibitors are sold in combinations with herbicides having other modes of action and weed control spectra that overlap the ALS inhibitors. Additionally, the mixtures are frequently applied in sequence with other non-ALS inhibitor herbicides. ALS inhibitors have been marketed in Japan since 1987, with the first being bensulfuron methyl. Weed management methods in practice in most of Japan during that time have minimized the potential for resistance development. However, the occurrence of resistance of paddy weeds to ALS inhibitors in California and New South Wales underscores the need for selection of partner herbicides with overlapping weed control spectra and alternative modes of action for mixtures or sequential treatment.

Paradoxes in resistance management

The already complex task of developing effective resistance management strategies is complicated by the existence of several apparent inconsistencies between recommended methods and current agricultural realities. Several examples follow :

- Recommendation : Use tillage or cultivation.

Inconsistency: The trend is toward reduced or no-till practices to conserve soil, water, and energy resources.

- Recommendation: Removal or burning of crop residues or pastures.
  Inconsistency: Trend is to maintain residues for soil conservation; burning is banned in some areas due to air quality concerns.
- Recommendation: Delay planting.
  Inconsistency: Delayed planting often results in less competitive crop stands, which is detrimental to weed control, and reduced yield.
- Recommendation: Rotate crops.
  Inconsistency: Government programs often indirectly encourage monoculture cropping.
- Recommendation: Use herbicide-resistant crops.
  Inconsistency: Repeated use of a single mode of action alone, even with such herbicides as glyphosate or glufosinate, may lead to evolution of resistance or a shift in the population from sensitive to less sensitive species.

The benefits and vulnerabilities of a multitude of factors must be balanced when a comprehensive weed management program is constructed. This is a compelling reason to promote the cooperation of all members of the agricultural community: farmers, academia, government, and industry, in managing resistance to maintain tools for efficient crop production.

Prospects for the future

Currently many chemical and non-chemical weed control tools are available to enable most farmers to adopt integrated weed management programs that will allow efficient crop production and delay the onset of resistance. However, agricultural realities are constantly changing. Regulatory pressures, that for a variety of reasons result in the removal of current herbicides from the marketplace, reduce the number of herbicide options. Furthermore, increasing hurdles for the commercialization of new herbicides slow the rate of introduction of new products and, most importantly, new modes of action. Several new products (e.g. new ACCase inhibitors and ALS inhibitors) have expanded the number of crops in which the same mode of action may be used. Farmers should be aware of the mode of action of herbicides they use and plan for rotating modes of action as well as crops. Herbicide-resistant crops introduce another potentially complicating factor for resistance management. As they become more widely adopted, they should be incorporated into the overall weed management strategy in a way that does not promote continuous reliance on a single mode of action for control of key target weeds. Further, additional methods such as biological control and herbicide synergists may become more available in the future. To continue to meet weed management challenges, farmers will need to be alert to changes in their weed populations, stay well informed and adaptable to new management techniques, and work closely with local extension, academics, and retailers to maintain efficient, productive operations.

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Discussion

Itoh, K. (Japan): Do you have any data about the relationship between the order of plant density or seed density in the seed bank and the order of species showing herbicide resistance, since it was reported in California that there was a relation between the seed density and the appearance of subsequent resistance to herbicides.

Answer: I do not have any specific information about the weeds in California. However the presence of seeds with a short longevity in soil, for example *Kochia scoparia* and high seed density may be correlated with the appearance of resistance to ALS inhibitor. This also applies to annual weeds of Australia, for example ryegrass.

Gawronski, S. (Poland): 1. Are there other examples of resistance to ALS inhibitors and to other classes of herbicides (except in Australia) ? 2. Is it possible to rank weed species that may develop resistance to ALS inhibitors ?

Answer: 1. Yes there are cases where resistance develops successively to various mode of action and classes of inhibitors (biotypes with multiple resistance mechanisms in a single plant or populations). 2. Projections could be made on the species that are likely to develop resistance based on the biological characteristics of the weed species and herbicide properties that contribute to resistance. However, interaction between herbicides and weed biology in relation to the onset of resistance requires further studies.