Phytoprotection

Herbicide-resistant crops : A weed scientist's perspective

W.E. Dyer

Volume 75, Number 4, 1994

Herbicide Resistance Workshop – Edmonton, Alberta - 9 and 10 december 1993
Atelier sur la résistance aux herbicides – Edmonton (Alberta) – 9 et 10 décembre 1993

URI: https://id.erudit.org/iderudit/706073ar
DOI: https://doi.org/10.7202/706073ar

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Publisher(s)

Société de protection des plantes du Québec (SPPQ)l

ISSN

0031-9511 (print)
1710-1603 (digital)

Explore this journal

Cite this article

Dyer, W. (1994). Herbicide-resistant crops : A weed scientist's perspective. *Phytoprotection*, *75*(4), 71–77. https://doi.org/10.7202/706073ar

Article abstract

Herbicide-resistant crops offer a potentially valuable alternative strategy for weed management. If used appropriately, they may promote the use of agrichemicals more environmentally benign than the herbicides they replace, and provide producers with additional tools for controlling weeds. However, the controversy surrounding the development and use of these cultivars may limit and eventually prevent their widespread adoption. Concerns include: overuse of herbicides, escape of herbicide resistance genes from resistant cultivars into weedy relatives, genetic modifications for resistance conferring weediness to the cultivar (*i.e.* volunteer plants in subsequent crops), potential pleiotropic effects of genetic modifications for resistance, and selection of new herbicide-resistant weeds in the new herbicide regime. Of these concerns, the potential for selecting new resistant weeds may have the highest likelihood of affecting the long-term success of herbicide-resistant crops.

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Herbicide-resistant crops: A weed scientist's perspective

William E. Dyer[1]

Received 1993-11-29; accepted 1994-04-06

Herbicide-resistant crops offer a potentially valuable alternative strategy for weed management. If used appropriately, they may promote the use of agrichemicals more environmentally benign than the herbicides they replace, and provide producers with additional tools for controlling weeds. However, the controversy surrounding the development and use of these cultivars may limit and eventually prevent their widespread adoption. Concerns include: overuse of herbicides, escape of herbicide resistance genes from resistant cultivars into weedy relatives, genetic modifications for resistance conferring weediness to the cultivar (*i.e.* volunteer plants in subsequent crops), potential pleiotropic effects of genetic modifications for resistance, and selection of new herbicide-resistant weeds in the new herbicide regime. Of these concerns, the potential for selecting new resistant weeds may have the highest likelihood of affecting the long-term success of herbicide-resistant crops.

Dyer, W.E. 1994. Les cultures résistantes aux herbicides: le point de vue d'un malherbologiste. PHYTOPROTECTION 75 (Suppl.): 71-77.

Les cultures résistantes aux herbicides représentent une stratégie alternative potentiellement intéressante pour la gestion des mauvaises herbes. Si utilisées de façon adéquate, elles peuvent promouvoir l'utilisation d'herbicides moins dommageables pour l'environnement que ceux qu'ils remplacent, et ainsi procurer aux producteurs des moyens supplémentaires de lutte contre les mauvaises herbes. Cependant, la controverse entourant le développement et l'utilisation de ces cultivars peut limiter et éventuellement empêcher leur adoption sur une grande échelle. Les préoccupations comprennent: la surutilisation d'herbicides, la transmission de gènes de résistance entre les cultivars résistants et les mauvaises herbes qui leur sont apparentées, le risque que les modifications génétiques pour la résistance confèrent des caractères nuisibles au cultivar (*i.e.* plantes spontanées dans des cultures subséquentes), les effets pléiotropiques potentiels des modifications génétiques pour la résistance, et finalement, la sélection de nouvelles mauvaises herbes résistantes aux herbicides dans ce nouveau régime d'herbicides. Parmi ces préoccupations, c'est la propabilité de sélectionner de nouvelles mauvaises herbes résistantes qui peut avoir le plus de chances d'affecter le succès à long terme des cultures résistantes aux herbicides.

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1. Plant, Soil and Environmental Sciences Department, Montana State University, Bozeman, Montana, U.S.A. 59717-0312

Nomenclature of chemical names cited in the text:

Chlorsulfuron: *2-chloro-N-[[(4-methoxy-6-methyl-1,3,5-triazin-2-yl)amino]carbonyl]benzene-sulfonamide;* glufosinate: *2-amino-4-(hydroxymethylphosphinyl)butanoic acid;* glyphosate: *N-[phosphonomethyl]glycine;* paraquat: *1,1'-dimethyl-4,4'-bipyridinium ion.*

INTRODUCTION

Herbicide-resistant crops (HRCs) represent one of the first and most highly publicized applications of plant biotechnology. Of the many traits that can be altered or conferred through biotechnology, herbicide resistance was chosen for three primary reasons. First, the biochemistry and genetics of several mechanisms of herbicide resistance were already understood, mostly from studies of bacterial mutants. It was then a relatively straightforward matter to isolate and characterize the genes responsible for resistance. Concurrently, efficient transformation and regeneration methods were developed for several major crops, allowing successful gene transfer experiments and recovery of transgenic plants. Second, much of this work was and still is carried out by agrichemical companies, whose considerable research budgets permitted rapid advances to be made. Third, this trait was chosen because these companies foresaw the potential for sufficient economic returns from proprietary HRC cultivars and associated herbicide sales to justify their investments.

As of 30 June 1993, the United States Department of Agriculture/Animal and Plant Health Inspection Service (USDA/APHIS) had issued 454 permits for field trials of transgenic plants in 35 states (Anonymous 1993) (Fig. 1). Since these field tests are often carried out at multiple sites, they represent a total of 846 separate trials. Worldwide, at least 14 countries are involved in field testing of transgenic plants. These plants contain genes conferring a wide variety of agriculturally important traits, including modification of food quality, expression of valuable proteins, disease and insect resistance, and herbicide resistance. HRC permits represent about 57% of the total, demonstrating the strong emphasis being placed on this particular trait. The development and history of HRCs have been reviewed (Dyer *et al.* 1993b; Mazur and Falco 1989; Mullineaux 1992; Stalker 1991).

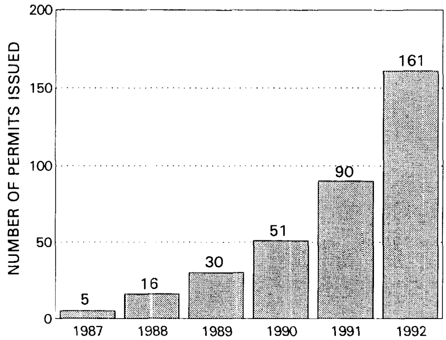

Figure 1. Number of permits issued per year for field trials of transgenic plants in the United States and Puerto Rico.

In this paper, the term HRC is reserved for cultivars created by hybridization, mutagenesis, somaclonal variation, protoplast fusion, introduction of a characterized segment of DNA (transgene) or other novel technologies to be resistant to a previously toxic herbicide. All crops are naturally resistant to certain herbicides because they possess insensitive target enzymes or metabolic capabilities, but are not included in this discussion because there do not appear to be new biochemical or ecological questions about this kind of resistance. Most of the concerns outlined below apply to those HRCs created through introduction of novel genes, either through biotechnology or conventional breeding.

CONCERNS ABOUT HRC USE

The creation of HRCs is generating considerable public and scientific controversy. Critics of these developments, and of biotechnology in general, contend that use of HRCs will encourage increased herbicide use and exacerbate producers' dependence on chemical solutions for weed management problems (Goldburg *et al.* 1990). Those in favor of HRC use counter that most herbicides for which HRCs are being developed are more environmentally benign than the chemicals they replace, and if used judiciously, HRCs can be a valuable addition to the producers' arsenal for combatting weeds. These issues are addressed in an accompanying workshop paper (Shaner 1994) and the argument will most likely continue as more HRCs enter the marketplace. In addition, there are several other concerns of scientific interest that deserve immediate scrutiny and can be tested using available technology. These concerns will be addressed individually, including a scenario that may have the highest likelihood of affecting agricultural production from a weed science perspective.

Escape of resistance genes

A highly publicized and much discussed concern about HRC use is the potential for escape of herbicide resistance genes into weedy relatives through hybridization. This question has recently been investigated for several crops (Cherfas 1991; Dale *et al.* 1992; Darmency *et al.* 1992; Kapteijns 1993; Kerlan *et al.* 1992; Lefol *et al.* 1991; Till-Bottraud *et al.* 1992) and has been reviewed (Raybould and Gray 1993). The fundamental concern is that a gene for herbicide resistance could be transferred by pollination to a weedy relative and confer an ecological advantage and thus an undesirable environmental change. Most researchers agree that presence of a transgene *per se* does not change a crop's breeding system or alter its potential for cross-hybridization with weedy relatives (Raybould and Gray 1993). Since there is no *a priori* reason to believe that transgenic pollen would be dispersed differently than non-transgenic pollen, research previously carried out with unmodified crops can be used to predict the likelihood of cross-hybridization from new HRCs. This likelihood depends almost entirely on the crop species in question, its breeding system and the incidence of wild relatives with which hybridization can occur. Isolation distances for maintenance of varietal purity have been established for many seed crops (Kernick 1961; Levin and Kerster 1974) although these distances may be substantially underestimated when considering transgene movement (Manasse 1992). Since gene flow can be affected by location, weather and other site-specific conditions (Ellstrand *et al.* 1989) field studies addressing transgene escape must be carried out for each new HRC species under several different environments. Even though the risk of transgene escape appears to be extremely low in most situations studied so far (Dyer *et al.* 1993b), the consequences are serious enough to dictate that extreme caution be exercised. Horizontal (nonsexual) gene transfer between microorganisms and host plants (Bryngelsson *et al.* 1988; Ream 1989) as well as between plant-colonizing fungi (Pirozynski 1988) has been documented, representing a possible alternative mechanism for transgene escape and movement (Maxwell and Mortimer 1994).

Information about crops' breeding systems, cross-compatibility with wild relatives and probability distributions for crosses at specific distances can be used to categorize the level of risk associated with transgene escape for individual species. Predominantly self-pollinating crops such as wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.) and flax (*Linum usitatissimum* L.) would appear to offer minimal risk of transgene escape using only this criterion. However, both wheat and barley can form hybrids with weedy relatives (wheat/jointed goatgrass [*Triticum* or *Aegilops cylindrica* Host] and barley/wild barley [*Hordeum spontaneum* L.]) at unknown frequencies in the field (Raybould and Gray 1993). Even though interspecific hybrid offspring are usually sterile, further field studies of this phenomenon are needed before development of HRCs in these and similar species is contemplated. Open-pollinated crops with known conspecific or congeneric weedy relatives such as sugarbeet (*Beta vulgaris* L.), radish (*Raphanus sativus* L.), ryegrass (*Lolium multiflorum* L.), oat (*Avena sativa* L.), carrot (*Daucus carota*

L.), poplar (*Populus* spp.) and some *Brassica* spp. (McNeill 1976) may present a relatively high risk as HRCs and their development should be approached with due caution.

HRCs becoming weedy

Volunteer crop weeds (plants emerging from remnant seed in the subsequent season) are a common problem in most crop rotation systems. Choice of a weed management strategy must include measures that will control these plants. However, producers' choices may be limited if the volunteer plants are HRCs. For example, control of volunteer graminicide-resistant maize (*Zea mays* L.) in a subsequent soybean (*Glycine max* L.) crop would require use of an alternative measure (another herbicide or a cultural practice) to control the HRC, possibly at an additional production cost. The possible development of HRCs with "stacked genes" for multiple herbicide resistance would further complicate management of volunteers. Another consideration is the existence of a persistent HRC seed bank, particularly for crops with hard seed such as alfalfa (*Medicago sativa* L.) which could further limit options in succeeding years. Thus, incorporation of HRCs into a crop production system can offer valuable weed management options as discussed below, but HRC persistence may conversely limit options in some crop rotations.

The possibility exists that introduction of a novel gene for herbicide resistance could sufficiently change the plant's growth characteristics or fitness (survival and reproductive success) so that it becomes a weedy pest in noncultivated or feral habitats. The traits traditionally used to define weediness result from the action of many genes, so it is highly unlikely that introduction of one new gene could cause a crop to become a weed. Cultivated crops generally cannot survive and reproduce without human intervention so the potential for a HRC to invade feral environments seems extremely low. In experiments comparing the invasiveness and ecological performance of transgenic and conventional oilseed rape (*Brassica napus* L. var. *napus*), the herbicide-resistant rape displayed equal or less invasiveness than its non-transformed counterparts in 12 different non-agricultural environments and in the presence or absence of various stresses (Crawley *et al.* 1993).

Scenarios can be conceived in which introduced herbicide resistance could provide a plant with a competitive advantage under certain conditions. Novel enzymes for herbicide metabolism could be sufficiently promiscuous to recognize and inactivate an insect or pathogen toxin and thus render the HRC resistant to this stress. Although such added resistance could be considered a production advantage in the target HRC, its presence could also increase a persistent HRC's potential for weediness.

Pleiotropic effects of transgenes

A continuing concern about the performance of HRCs and other transgenic crops is whether or not a yield penalty is associated with the introduced trait. Companies developing a new HRC would most likely not continue with its development or release if it was impaired in any obvious aspect of yield or quality. However, more subtle changes could occur in the genomes of HRCs as a result of mutagenesis or transgene introduction. Because the location of transgene insertion into the host plant's genome is essentially random, unknown resident genes may be altered or inactivated by the process with unpredictable effects. A gene involved in winter hardiness could be knocked out by transgene insertion thus causing the HRC to be more cold sensitive than its nontransgenic predecessor. Such changes would most likely be detected during the HRC backcrossing and testing program during development (Dyer *et al.* 1993b), but perhaps only if the testing is carried out under multiple varied environments.

Several HRCs have been made resistant by the introduction of a mutant gene encoding an insensitive form of the herbicide's target enzyme, such as 5-enolpyruvylshikimate-3-phosphate (EPSP) synthase for glyphosate resistance (Mazur and Falco 1989). Presence of mutant but homologous transgenes could theoretically lead to novel recombinational events during meiosis, thus creating altered gametes. Enzymes encoded by mutant genes could exhibit altered regulatory or kinetic properties or interact with native forms to create heteromultimers with altered properties, perhaps leading to subtle changes in the plant's biochemistry or physiology. Germination characteristics and free levels of certain amino acids were altered in some field-selected chlorsulfuron-resistant *Kochia scoparia* (L.) Schrad. accessions as compared to susceptible types, possibly as a result of the mutation(s) conferring resistance (Dyer *et al.* 1993a). The synthesis of novel allergens or altered secondary products from endogenous pathways in HRCs and other transgenic crops has been postulated, but this possibility seems unlikely for two reasons. First, a herbicide-insensitive target enzyme encoded by an introduced gene would of necessity carry out the same biosynthetic reaction as the native form of the enzyme. Second, enzymes for herbicide metabolism encoded by introduced genes are involved in degradation of specific compounds, and the by-products of such reactions must be identified and tested during the HRC registration process.

For some herbicides that are not rapidly metabolized by plants, presence of an insensitive target enzyme in the HRC may lead to an accumulation of the parent herbicide in harvested portions of the crop, particularly after pre-harvest treatments. Other HRCs created by introducing microbial genes encoding herbicide metabolic enzymes may produce novel metabolites not encountered during the initial herbicide registration process. Transgenic carrot plants expressing a fungal gene for resistance to glufosinate contained different herbicide metabolites than those produced by non-transformed plants (Dröge *et al.* 1992). Such a possibility would be investigated during the HRC registration process, since all herbicide and metabolite residues are identified, quantified, and their toxicology determined before HRC release (Dyer *et al.* 1993b).

Selecting resistant weeds

Intensive use of herbicides over the last 40 years has led to the selection of resistant plants and subsequent populations within formerly susceptible species. This phenomenon is rapidly becoming an important agricultural problem in many countries and the subject has been recently reviewed (Caseley *et al.* 1991; Holt *et al.* 1993; Moss and Rubin 1993; Powles and Holtum 1994). Primary factors controlling the incidence and evolution of resistance include the initial frequency of the resistance trait in a population, extent of selection pressure, and the comparative fitness of resistant and susceptible types. Of these factors, the only one that can be controlled by agricultural producers is the extent of selection pressure, by manipulating the type and efficacy of weed management methods they employ. Current recommendations for resistance prevention and management focus on crop and herbicide rotations and herbicide mixtures to interrupt selection pressures imposed by continuous use of chemicals having the same mechanism of action (Gressel and Segel 1990; LeBaron and McFarland 1990).

HRCs can fulfill a valuable role in such a resistance prevention strategy by allowing producers the flexibility to use alternative herbicides not traditionally used in the crop. The commercial development of triazine-resistant canola (Beversdorf and Kott 1987) has provided a useful means of controlling certain troublesome weeds. Ideally, the novel herbicide used on a HRC would have a mechanism of action substantially different from herbicides previously used on that species. HRCs thus incorporated into ongoing crop and herbicide rotations will undoubtedly provide a significant weed management advantage to producers. However, the likelihood of this scenario becoming a reality depends entirely on how HRCs are perceived and marketed. If HRCs prove to be very successful in some situations, particularly in continuous cropping areas with few available rotations, producers' natural tendency will be to continue using the same HRC cultivar for several consecutive years. Producers growing HRCs may be tempted to make multiple herbicide applications during one season to control successive weed flushes. Both of these situations will surely help set the stage for selecting resistant weeds by increasing the effective selection pressure. This possibility is particularly disturbing for HRCs resistant to environmentally benign herbicides such as glyphosate and glufosinate for which the evolution of weed resistance has not been reported (Dyer 1994). Multiple applications over several consecutive years would compensate for these herbicides' nonresidual characteristics and undoubtedly increase the chances of selecting resistant weeds, as has been shown for other non-residual herbicides like paraquat (Holt *et al.* 1993).

The long-term goal of agriculturalists should be to work towards developing environmentally compatible systems for crop production. In the interim, we must continue to optimize and attempt to minimize agrichemical use for weed control. The questions now before us are: Who will monitor HRC use in order to protect this potentially valuable weed management tool and prevent its loss of usefulness due to selection for weed resistance? Will marketing strategists for agrichemical companies be willing to forego some short-term profit maximization and promote stewardship of their products by encouraging prudent and responsible use of HRCs? Perhaps a long-term perspective will prevail in this situation so that HRCs can be successfully used in concert with practical non-chemical strategies now in development.

ACKNOWLEDGEMENTS

The helpful comments of two anonymous reviewers are gratefully acknowledged. Research in the author's laboratory is supported by the National Science Foundation (OSR-9350546), USDA/NRICGP (92-37303-7614), and the Montana Agricultural Experiment Station.

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