FORCES DRIVING THE DEVELOPMENT OF HERBICIDE-RESISTANT WEEDS

David E. Stoltenberg [1/]

Introduction

Herbicide-resistant weed species have become an increasing problem in many cropping systems, due in large part to the widespread reliance on herbicides as a primary method of weed management. Herbicide resistance has been defined as the inherited ability of a plant to survive and reproduce following exposure to a herbicide dose normally lethal to the wild type (Weed Science Society of America 1998). Weed resistance to herbicides has been confirmed in 156 species (94 dicots and 62 monocots) worldwide, most commonly to acetolactate synthase (ALS) inhibitors, triazines, or acetyl-coenzyme A carboxylase (ACCase) inhibitors (Heap 2003). Resistance to herbicides has been selected for in several weed species found in Wisconsin, including resistance to ALS inhibitors in eastern black nightshade (*Solanum ptycanthum*) (Volenberg et al. 2000), giant foxtail (*Setaria faberi*) (Volenberg et al. 2001), and green foxtail (*Setaria viridis*) (Volenberg et al. 2002), resistance to ACCase inhibitors in giant foxtail (Stoltenberg and Wiederholt 1995) and large crabgrass (*Digitaria sanguinalis*) (Wiederholt and Stoltenberg 1995), and resistance to triazine herbicides in several broadleaf weed species (Stoltenberg 1995).

The development of weed resistance has typically been associated with reliance on a single herbicide chemistry over time, i.e. a high level of herbicide selection intensity (Volenberg et al. 2000, 2001, 2002; Stoltenberg and Wiederholt 1995; Wiederholt and Stoltenberg 1995). That is, repeated exposure of a weed community to a specific herbicide chemistry (or related chemistries) has selected for weeds resistant to that chemistry. Once such herbicide use has selected for resistant individuals, continued herbicide use (i.e., continued selection intensity) favors resistant plants over susceptible plants. Over time, the frequency of resistant plants in a weed population increases, representing a potentially serious long-term weed management problem.

Although herbicide selection intensity is a critical factor in the development of weed resistance, predicting what species will develop resistance, when it will happen, where it will happen, and the rate of spread of resistance once it has occurred, has been very difficult. This has been due in large part to many factors (including herbicide selection intensity) that play a role in the selection for herbicide-resistant weeds. Some of these factors include aspects of the weed itself (i.e. weed biology) and the relationship between the weed and its environment (i.e. weed ecology). Other factors include management practices that affect overall selection intensity for individual resistant weed plants. Perhaps most important among these are weed management practices, and herbicide use in particular, but other important management factors include crop rotation and tillage practices, which can effectively disrupt the life cycle of weeds (in effect reducing selection intensity), and nutrient, insect, and pathogen management practices, which can increase the overall competitive ability of crops with herbicide-resistant weeds. A better understanding of these factors and their interactions will allow us to better assess the potential for selection and spread of herbicide-resistant weeds. The effects of genetic variation in weed populations, frequency of resistance traits, herbicide selection intensity, inheritance of resistance traits, and gene flow on the onset and spread of resistance are discussed below.

[1/] Professor, Dept. of Agronomy, Univ. of Wisconsin-Madison, 1575 Linden Dr., Madison, WI 53706.

Critical Factors Affecting Resistance Development

Genetic variation and selection

Weed resistance to herbicides is the result of selection for traits that allow plants to survive specific management practices which would otherwise cause mortality. There are two precursors or conditions necessary for such traits to occur and spread in plant populations: 1) heritable variation for a trait and 2) selection for that trait (Maxwell and Mortimer 1994). Without such precursors, there is little or no biological basis for the onset and spread of resistance. However, the common view is that genetic variation is almost always present in plant populations, although the extent of variation may differ considerably among specific traits. Given the existence of genetic variation, sufficient duration and intensity of selection will likely result in the development of resistance.

Frequency of resistance traits

The probability of resistance occurring in a weed population prior to selection with herbicides is a critical factor that affects resistance development. Traits that confer resistance to herbicides are thought to be due to natural genetic mutations; that is, there is little evidence to suggest that herbicides cause genetic mutations that confer resistance (Jasieniuk et al. 1996). Consequently, resistant weeds can occur in a population that has not been exposed to herbicides, i.e. a non-selected population. The probability of resistance occurring in a weed population prior to selection with herbicides depends on three factors: 1) the mutation frequency for a resistance trait, 2) any selective disadvantage associated with the resistance trait, and 3) the size of the weed population (Maxwell and Mortimer 1994). When attempts have been made to predict the rate of resistance development, the frequency of resistant plants in the non-selected population has typically been assumed to be at the frequency of mutation, unless there is some evidence that there is selective disadvantage associated with the resistance trait, which effectively reduces the mutation frequency (and the frequency of resistant plant or phenotypes in a population). As the mutation frequency increases, the number of plants that need to be exposed to a herbicide decreases greatly in order to select for one resistant plant.

However, we typically don't know the mutation frequency for resistance traits, which is one important reason why accurate prediction of resistance development has been difficult. Estimates of expected mutation rates for resistance traits have ranged from 10^{-5} (i.e., 1 in 100,000 plants) to 10^{-12} (1 in 1,000,000,000,000 plants) (Maxwell and Mortimer 1994). One basis for these estimates is the field histories of confirmed herbicide-resistant weeds and the expected vs. observed time for resistance to become a management problem, which is typically when the frequency of resistant weeds is 30% or more in a population. It is very likely that resistance traits were present (but not detected) in these weed populations before intense selection with herbicides occurred. However, field research to confirm expected estimates in non-selected weed populations has been limited. In Australia, the frequency of herbicide-resistant rigid ryegrass (*Lolium rigidum*) plants in non-selected populations was much greater (10^{-2} to 10^{-3}) than expected, but such a high level may have been due to movement of resistant traits (by either pollen or seed dispersal) into these otherwise susceptible populations (Matthews and Powles 1992).

Selection Intensity

As mentioned above, there are many cropping practices that likely affect the onset and spread of herbicide-resistant weeds, however, selection intensity associated with herbicide use is among the most important of these. Herbicide selection intensity is a critical factor affecting the rate of change in a weed population that consists of a high frequency of herbicide-susceptible weeds to a population with a high frequency of herbicide-resistant plants. Intense selection with herbicides coupled with genetic diversity, provides the elements for rapid development of herbicide-resistant weed populations (Maxwell and Mortimer 1994). The intensity of such selection is largely determined by three factors: 1) the effectiveness of the herbicide, 2) the frequency of herbicide use, and 3) the duration of herbicide effect (Maxwell and Mortimer 1994). It has been difficult to quantify herbicide selection intensity, because these factors themselves are affected by many other factors. For example, herbicide effectiveness can be affected by the inherent susceptibility of a weed species to a herbicide, application rate, application timing (or weed stage of growth), and environmental conditions. Overall, greater herbicide effectiveness, i.e. greater weed mortality, has typically been associated with greater selection intensity for resistant weeds.

Inheritance of resistance traits and gene flow

The manner in which resistance traits are inherited is another important factor affecting the rate of resistance development. Resistance traits can be inherited as nuclear, dominant or semi-dominant alleles (Volenberg and Stoltenberg 2002a, 2002b; Volenberg et al. 2001), recessive alleles (Jasieniuk et al. 1994), or they may be inherited as cytoplasmic or maternal alleles (e.g., those found in the chloroplast genome), such as is the case with many weed species resistant to triazine herbicides (Darmency 1994; Jaieniuk et al. 1996). A nuclear, dominant allele that confers resistance is expected to typically spread faster than a recessive allele. A cytoplasmic inherited trait is expected to spread only marginally faster than a nuclear, dominant trait. The difference in rate of spread is most important in the early stages of selection where traits controlled by nuclear, dominant alleles and those associated with cytoplasmic genes likely reach appreciable frequencies much faster than recessive alleles (Maxwell and Mortimer 1994). Also, the spread of resistance associated with a single major gene (i.e. monogenic inheritance) is expected to be more rapid than that of resistance associated with several genes (i.e., polygenic inheritance) (Jasieniuk et al. 1996; Maxwell and Mortimer 1994). In cases where the number of inherited alleles is low, resistance has increased in weed populations to detectable levels within 3 to 10 generations under continuous herbicide selection intensity

The flow of resistance genes from a herbicide-resistant population to a herbicide susceptible population occurs by two primary mechanisms: pollen dispersal and seed dispersal. The extent to which a species can cross-pollinate, as opposed to being self-compatible with the ability to self-pollinate, is a critical factor that affects the genotypic structure of a weed population, particularly the frequency of resistance traits. The spread of resistance will occur more rapidly in cross-pollinated populations, assuming resistance is associated with a single dominant allele and that cross pollination is as efficient as self-pollination for viable seed production (Maxwell and Mortimer 1994). Also, as the rates of gene flow are estimated to typically be greater than mutation rates (Jasieniuk et al. 1996), gene flow can increase the initial frequency of resistant alleles in a population (as discussed above). Such a situation effectively increases the mutation rate for resistance. Relative to seed dispersal, herbicide-resistant weed species that are prolific seed producers and that have effective seed dispersal mechanisms have the potential to expand rapidly under intense selection with herbicides.

Both pollen and seed dispersal appear to have contributed to the recent, rapid spread of glyphosate-resistant horseweed in the eastern U.S. (VanGessel 2001). The large number of seeds typically produced by horseweed, and their dispersal by wind, are thought to be the principal means of the spread of resistance, but outcrossing between horseweed plants has also likely contributed to the movement of resistance traits (VanGessel 2001). Subsequent research has found that horseweed resistance to glyphosate is due to a nuclear, dominant allele and that the resistance trait can be transmitted by pollen in crosses between resistant and susceptible plants (Heck et al. 2002).

Summary

Weed biology, ecology, and management can interact and influence the onset and spread of resistance to herbicides. Heritable variation for a trait and selection for that trait are necessary precursors for the development of resistance. Intense selection with herbicides coupled with genetic diversity, provides the elements for rapid development of herbicide-resistant weed populations. Greater herbicide effectiveness is typically associated with greater selection intensity for resistant weeds. However, the development of resistance is also affected by several other factors including the mutation frequency for resistant alleles, any selective disadvantage associated with these alleles, and the size of the weed population. If herbicide-resistant plants are selected and reproduce, the spread of resistance will be affected greatly by the manner in which resistant traits are inherited, and the extent that movement of resistant traits can occur by pollen and seed dispersal.

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