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REVIEW

An analysis of polygenic herbicide resistance evolution and its management based on a population genetics approach

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Abstract

Globally, the intensive herbicide usage has resulted in the evolution of many herbicide-resistant weeds. Rigorous herbicide usage and lack of diversity in herbicide management would rapidly accumulate resistance mutations in the weed populations. Therefore, applying herbicides at a reduced rate that provides satisfactory weed control was believed to be a strategy to reduce the frequency of herbicide resistance mutations in weed populations with the additional benefits of low input cost and less herbicide load to environment. All these considerations would have contributed to the absence of regulations in many countries to mandate the strict adherence of recommended herbicide rates. Paradoxically, lack of diversity in herbicide usage coupled with faulty herbicide management practices has resulted in the emergence of herbicide-resistant weeds in different agro-ecosystems. Evolution of herbicide resistance was very rapid in Australia, where the recommended rates of herbicides was the lowest in the world and farmers use lower than recommended rates of herbicides for economic reasons. In the light of the alarmingly increasing herbicide resistance cases, in the mid-1990s, scientists hypothesized the possibility of the accumulation of minor resistance mutations, in addition to major herbicide resistance mutations as a possible reason for the rapid evolution of herbicide resistance, although there were no studies to support this theory at that time. However, recent studies have confirmed that the recurrent application of a herbicide and herbicide selection at low dosages can be a major reason for the rapid evolution of herbicide resistance. This paper reviews the potential of major weed species to evolve rapidly under low herbicide through the accumulation of polygenic resistance traits. In addition, the feasibility of a population genetics approach in herbicide resistance management in tune with the high dose refuge strategy for insecticide resistance management is proposed for the first time and discussed.

Zusammenfassung

Weltweit hat der intensive Einsatz von Herbiziden zur Evolution zahlreicher herbizid-resistenter Unkräuter geführt. Der rigorose Herbizideinsatz und wenig variables Herbizidmanagement sollten Resistenzmutationen in den Unkrautpopulationen schnell akkumulieren lassen. Deshalb nahm man an, dass das Ausbringen der Herbizide mit einer verringerten Dosierung, die aber befriedigende Unkrautkontrolle ermöglicht, eine Strategie zur Reduktion der Häufigkeit von Resistenzen bei den Unkräutern sein könnte mit dem zusätzlichen Vorteil von geringeren Kosten und verminderter Umweltbelastung. Alle diese Überlegungen

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würden zum Fehlen von Regeln beigetragen haben, die in vielen Ländern die strikte Befolgung der empfohlenen Herbizidraten anordnen. Paradoxerweise hat der Mangel an Flexibilität beim Herbizideinsatz zusammen mit fehlerhafter Herbizidmanagementpraxis zum Auftreten von herbizidresistenten Unkräutern in verschiedenen Agroökosystemen geführt. Die Evolution der Herbizidresistenz erfolgte sehr schnell in Australien, wo die empfohlenen Herbizidraten die weltweit geringsten sind und die Landwirte geringere als die empfohlenen Dosierungen aus wirtschaftlichen Gründen anwenden. Angesichts der alarmierend zunehmenden Fälle von Herbizidresistenz Mitte der 90er Jahre hielten Wissenschaftler es für möglich, dass eine Akkumulation kleinerer Resistenzmutationen zusätzlich zu großen Herbizidresistenzmutationen der Grund für die rapide Ausbildung von Herbizidresistenzen sein könnte, obwohl es damals keine Studien gab, die diese Ansicht belegen konnten. Indessen haben rezente Studien bestätigt, dass wiederholte Gabe eines Herbizids und Herbizidselektion bei geringer Dosierung wichtige Gründe für die schnelle Ausbildung einer Herbizidresistenz sein können. Diese Arbeit untersucht das Potential bedeutender Unkrautarten unter geringem Herbizideinfluss durch eine Anreicherung von polygenetischen Resistenzmerkmalen schnell zu evoluieren. Außerdem wird die Praktikabilität eines populationsgenetischen Ansatzes für das Management von Herbizidresistenzen in Abstimmung mit der Hochdosierungs-Refugialstrategie für das Management von Insektizidresistenzen erstmals vorgeschlagen und diskutiert.

Keywords: Dose refuge strategy; Low dosage; Polygenic evolution; Selection pressure

Introduction

Although herbicides are very effective and successful as a weed management tool, the rigorous use of these chemicals has resulted in the rapid evolution of more than 327 resistant weed biotypes around the world (Heap 2014). In many instances, the evolved resistance against herbicides was through the selection of a single gene with a major effect (target site herbicide resistance) and typically this involves a mutation at the herbicide target site (Jasieniuk, BruleBabel, & Morrison 1996; Delye 2005; Powles & Yu 2010). In an evolutionary perspective, artificial selection (pesticide selection) will lead to sudden heritable changes in a population, as opposed to natural selection which proceeds in a slow step-by-step process. Therefore, lowering the pesticide selection pressure would reduce the pace of pesticide resistance evolution (Lande 1983; Orr & Coyne 1992), if major target site mutations are the only reasons for pesticide resistance development. This is because such a strategy would slow down rate at which major resistance genes accumulate in a population. The resistance evolution is expected to be slowed down by this approach (Jasieniuk & Maxwell 1994) and, probably for that reason, scientists and planners did not advocate regulations to mandate the usage of recommended rates of herbicide as in the case of antibiotic usage. For many reasons, application of herbicides at reduced rates does occur in global agriculture (Zhang, Weaver, & Hamill 2000). Paradoxically, the last few decades have witnessed an escalation of resistance cases in Australia, where the recommended herbicide rates are the lowest in the world and farmers cut herbicide rates for input minimization and for profitable cropping (Neve 2007; Manalil 2014).

In the mid-1990s, scientists hypothesized the possibility of the selection and accumulation of minor herbicide resistance traits as a possible reason for the rapid evolution of herbicide resistance in weed populations (Gressel, Gardner, & Mangel 1996). This hypothesis was in line with the micro-mutational evolutionary theory or polygenic evolutionary theory. In an artificially selected population, evolutionary changes would be rapid due to the selection of major mutations that confer sudden heritable changes. As an example, target site mutations leading to herbicide resistance are selected by the intensive use of herbicides and that resulted in the rapid evolution of herbicide resistant weed populations (Preston, Wakelin, Dolman, Bostamam, & Boutsalis 2009; Powles & Yu 2010). However, as per the micro-mutational theory, less intense selection even in the artificially selected populations has the potential to channel the evolution by a step-by-step process as in the Darwinian mode by the accumulation of minor traits (Lande 1983; Orr & Coyne 1992). However, there were no studies in the field of herbicide resistance evolution to support such a hypothesis. In due course, research unraveled many herbicide resistance mechanisms (other than major target site mutations) such as enhanced metabolism of herbicides, reduced translocation and uptake of herbicides, and compartmentalization of herbicides or their metabolites (Yuan, Tranel, & Stewart 2007). Many of these mechanisms vary in their levels of herbicide resistance indicating the possibility of polygenic mode of resistance evolution (Yuan et al. 2007). Most recently, the few but important studies (Neve & Powles 2005; Manalil, Busi, Renton, & Powles 2011; Manalil, Renton, Diggle, Busi, & Powles 2012b) carried out on a troublesome weed, the annual ryegrass *Lolium rigidum* Gaud., provide a reasonable explanation for the evolution of herbicide resistance in line with the polygenic evolutionary theory.

This paper reviews the available literature that supports the polygenic evolutionary theory and explores the possibilities to minimize the herbicide resistance evolution. Most importantly, the feasibility of a population genetics approach in weed management in similar line with the successful high dose refuge strategy (Meihls et al. 2008; Tabashnik 2008) for

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